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Yield response in chickpea cultivars and wheat following crop rotations affecting population densities of *Pratylenchus thornei* and arbuscular mycorrhizal fungi

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Abstract. In Australia, root-lesion nematode (RLN; *Pratylenchus thornei*) significantly reduces chickpea and wheat yields. Yield losses from RLN have been determined through use of nematicide; however, nematicide does not control nematodes in Vertosol subsoils in Australia's northern grains region. The alternative strategy of assessing yield response, by using crop rotation with resistant and susceptible crops to manipulate nematode populations, is poorly documented for chickpea. Our research tested the effectiveness of crop rotation and nematicide against *P. thornei* populations for assessing yield loss in chickpea. First-year field plots included canola, linseed, canaryseed, wheat and a fallow treatment, all with and without the nematicide aldicarb. The following year, aldicarb was reapplied and plots were re-cropped with four chickpea cultivars and one intolerant wheat cultivar. Highest *P. thornei* populations were after wheat, at 0.45–0.6 m soil depth. Aldicarb was effective to just 0.3 m for wheat and 0.45 m for other crops, and increased subsequent crop grain yield by only 6%. Canola, linseed and fallow treatments reduced *P. thornei* populations, but low mycorrhizal spore levels in the soil after canola and fallow treatments were associated with low chickpea yield. Canaryseed kept *P. thornei* populations low throughout the soil profile and maintained mycorrhizal spore densities, resulting in grain yield increases of up to 25% for chickpea cultivars and 55% for wheat when pre-cropped with canaryseed compared with wheat. Tolerance indices for chickpeas based on yield differences after paired wheat and canaryseed plots ranged from 80% for cv. Tyson to 95% for cv. Lasseter and this strategy is recommended for future use in assessing tolerance.

Additional keywords: AMF, arbuscular mycorrhizal fungi, *Brassica napus*, chickpea nematode tolerance, *Linum usitatissimum*.

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Introduction

Chickpea (*Cicer arietinum*) is the second most important cool-season food legume worldwide, and is the largest pulse crop in Australia after lupin in terms of planting area and production. On average, chickpeas are sown on 411 000 ha annually to produce 448 000 t, with an average yield of 1.15 t/ha (ABARE 2012). Ninety per cent of the Australian chickpea crop is produced in the northern grain region (central and southern Queensland and northern New South Wales), where it is grown as a winter crop on soil moisture stored from summer-dominant rainfall. In this region, it is a profitable winter legume and plays a vital role as a rotational crop in cereal-dominated systems, with the majority of cultivars being the long-day phenological types (Berger *et al*. 2004).

Chickpea grown in rotations with wheat (*Triticum aestivum*) can reduce the build-up of pathogens of cereals such as *Fusarium pseudograminearum* (responsible for crown rot), improve soil nitrogen (N) fertility, and facilitate control of grass weeds (Dalal *et al*. 1998; Felton *et al*. 1998). Offsetting these benefits, populations of root-lesion nematode (RLN; *Pratylenchus thornei*), a microscopic vermiform endoparasite that feeds and reproduces in the cortex of plant roots (Fortuner 1977), increase under chickpea, reducing its yield and negatively affecting the yield of subsequent intolerant wheat and other crops (Thompson *et al*. 2000). *Pratylenchus thornei* is distributed worldwide and is the major species damaging chickpea in regions throughout the Mediterranean Basin and Indian subcontinent (Greco *et al*. 1992; Castillo *et al*. 1996; Carrasco-Ballesteros *et al*. 2007). In eastern Australia, yield losses of intolerant chickpea and wheat cultivars of up to ~20% and ~50%, respectively, are attributed to *Pratylenchus* spp. (Thompson *et al*. 1999, 2000).

The most effective strategy to manage RLN is by integrating resistant and tolerant crops and cultivars with appropriate agronomic practices. Resistance is a plant's ability to inhibit or reduce nematode multiplication (Trudgill *et al*. 1998), whereas tolerance is a plant's ability to grow and yield well in nematode-infested soil (Cook and Evans 1987). No fully resistant chickpea cultivar is available, and to provide relevant information for grain

growers and improve cultural management practices, it is essential to test the tolerance of chickpea cultivars under field conditions. A practical method of evaluating tolerance for wheat (Thompson and Clewett 1986; Taylor *et al*. 1999; Thompson *et al*. 2012) and for chickpea (Di Vito *et al*. 1992) is to determine the yield of cultivars grown on a nematode-infested site through use of nematicide to create a population differential. However, use of nematicide has limitations and may cause yield loss to be underestimated when conditions are suboptimal for nematicidal efficacy. Nematicide is less effective in drier soil with little post-application rainfall, when the compound becomes stranded in a dry upper soil layer (Thompson *et al*. 1999), or in soils with high clay content or deeper soil profiles that allow a proportion of the RLN population to escape nematicide control (Spaull and Cadet 1991; Bond *et al*. 2000). In addition, repeated use of some nematicides can render them ineffective because it stimulates rapid microbial breakdown of the compound (Read 1987). Furthermore, nematicides are highly toxic compounds that pose risks to personal safety and the environment.

An alternative to using nematicides is to grow resistant or non-host crops to reduce nematode population densities (Brown 1987; Cook and Evans 1987). However, the effect on subsequent yield of chickpea when pre-cropping with non-host or resistant crops is poorly documented, particularly with pre-crops such as canola and linseed. Information on tolerance levels to *P. thornei* of chickpea cultivars is also limited, as is the availability of a non-nematicidal strategy that allows accurate assessment of yield losses.

Our objectives were to (*i*) evaluate the effectiveness of resistant crop species against *P. thornei* populations compared with aldicarb treatment; (*ii*) assess the effect of these pre-crop treatments on final yields of chickpea and wheat and determine the best strategy for assessing yield loss of chickpea cultivars with and without nematicide treatments. Chickpea is dependent on arbuscular mycorrhizal fungi (AMF), which occur naturally in the soil and facilitate uptake of phosphorus (P) and zinc (Zn) (Thompson 1987). In the course of the experiment, we became aware that AMF populations responding to crop rotation were affecting chickpea growth, and so we quantified them. Our study established that using paired resistant and susceptible crops, such as canaryseed and wheat, respectively, can create a differential in *P. thornei* populations but not in AMF population densities, which allows accurate assessment of tolerance to RLN for chickpea cultivars.

Materials and methods

Trial site and design

A field trial was conducted over two sequential winter cropping seasons (June–November) on a site infested with *P. thornei*, at Formartin (27.46401°S, 151.42616°E; 364 m elevation), 70 km west of Toowoomba on the Darling Downs, Queensland, Australia. The soil at the site is a Haplic, Self-mulching, Black Vertosol (Isbell 1996) of the Waco Series (Beckmann and Thompson 1960), and is characterised by high clay content (70%) and high plant-available water-holding capacity (288 mm to a depth of 1.8 m) (Hochman *et al*. 2001). Chemical analysis of soil samples taken from the 0–0.15 m soil depth interval before planting the first-year crops showed that mean soil pH was 8.7 (1 : 5 water), P concentration was 14.2 mg/kg (Colwell 1963) and Zn was 0.67 mg/kg (DTPA-extractable Zn, (Lindsay and Norvell 1978). In the 0.15–0.3 m interval, mean pH was 8.8, P concentration was 10.3 mg/kg and Zn 0.45 mg/kg.

First-year crops were planted on 28 May 1997 into fallow land (14 months) previously cropped with cotton following a winter fallow previously cropped with sorghum. In the first year, there was a factorial of five treatments with and without the nematicide aldicarb. The five first-year treatments included a weed-free fallow treatment, three crop species that were resistant or moderately resistant to *P. thornei*, namely canaryseed (*Phalaris canariensis*) cv. Moroccan, linseed (*Linum usitatissimum*) cv. Glenelg and canola (*Brassica napus* ssp. *olifera* var. *annua*) cv. Hyola 41, and a susceptible wheat cultivar, Janz (Thompson *et al*. 2000). Each combination of crop–fallow × nematicide treatment was applied to five duplicate plots within three randomised blocks for a total of 150 plots, so that each first-year treatment could be over-sown by four chickpea cultivars and one wheat cultivar in the following year. The nematicide aldicarb was applied as the active ingredient (a.i.) of Temik®150G (150 g aldicarb/kg) at 10 kg a.i./ha by drilling into the soil to 0.1 m depth at 2 weeks before planting. Each plot consisted of seven rows, 0.25 m apart and 11.3 m in length. Planting rates for wheat, linseed, canaryseed and canola were 35, 20, 12 and 3 kg/ha, respectively. Urea, supplying N at 113 kg/ha, was applied to the trial site 1 month before planting.

All first-year crops except canaryseed were machine-harvested at maturity on 29 November to determine grain yield. Canaryseed has summer seed dormancy, so plots were slashed using small-plot machinery following flowering and before seed set to avoid self-sown seedlings in the following winter season. The remaining stubble was retained as part of the normal no-till regional practice. During the summer fallow, and before planting chickpea in the following winter, all experimental plots were sprayed with glyphosate for weed control, and in-crop weeds were removed manually as required.

In the second year (1998), aldicarb (10 kg/ha) was re-applied to previously treated plots at planting on 29 May by drilling into the soil at 0.1 m depth. Plots were re-cropped with four Desi (small brown angular seed) chickpea cultivars (Lasseter, Tyson, Norwin, Barwon) and one intolerant wheat cultivar (Gatcher). Chickpea seed was treated with P-Pickel T® (3.6 g thiram plus 2 g thiabendazole/kg) for early protection from common seed and soil-borne seedling diseases. Chickpea seed was inoculated with rhizobium inoculum Group N before planting and Starter Z (Incitec Pivot, Southbank, Vic.) was applied in seed-rows by drilling into the soil to supply 10.5 kg N, 7 kg P and 0.9 kg Zn/ha at planting. Seed was sown to a depth of 40 mm, at rates of 40 and 100 viable seeds/m^2 for chickpea and wheat, respectively. Six weeks after planting, 120 kg N/ha as urea was broadcast on the wheat plots. Chickpeas were sprayed with Sumi-Alpha® Flex insecticide at 500 mL/ha (a.i. esfenvalerate, 50 g/L) as a precautionary control of *Helicoverpa* spp. moth larvae, and two preventative fungal sprays of Benlate® at 500 g/ha (a.i. 50% benomyl) for control of botrytis grey mould were applied to chickpeas on 7 and 26 October. Grain yield was determined by machine harvesting at maturity and grain moisture content

determined by drying at 80°C for 2 days, to express yields at 12% moisture.

Soil sampling and assessment

Four days before planting chickpea and wheat in the second year, four soil cores 43 mm in diameter were taken with a hydraulically operated soil corer from the middle three rows from each of the previous year's plots to a depth of 1.5 m. Cores were divided into 0.15-m depth intervals to 0.6 m, and into 0.3-m intervals thereafter, and bulked at each interval to give one sample per interval per plot. Samples were kept out of direct heat during collection, and on return to the laboratory, they were stored at 3°C until processing. Each bulked core interval was manually broken into pieces $\leq$10 mm and subsampled to determine nematodes, soil water and soil nitrate concentrations. For assessing nematodes and soil water, subsamples from the bulked core intervals of the depths 0–0.15, 0.15–0.3, 0.3–0.45 m were processed separately for each of the 150 plots. Cores from remaining depths 0.45–0.6, 0.6–0.9, 0.9–1.2, 1.2–1.5 m were composited according to the five pre-crop treatments and previous aldicarb treatment within each replicate, to make 30 bulked samples for each depth interval.

Nematodes, soil water and nitrate

Nematodes were extracted from a 150-g field-moist soil subsample using the Whitehead tray method (Whitehead and Hemming 1965) for 48 h at 22°C, then collected on a 20-µm mesh sieve in 10–15 mL of tapwater. Numbers of *P. thornei* were counted in a 1-mL Hawksley slide under a compound microscope at ×40 and ×100 magnification and expressed as number of nematodes/kg soil (oven-dried equivalent). In each sample, *P. thornei* and *Merlinius brevidens* were identified morphologically (Siddiqi 1972; Fortuner 1977) and non-plant-parasitic nematodes, mainly bacterivores and fungivores, were identified by absence of a strong stylet.

Gravimetric soil water content (SWC%) for each interval was determined by oven drying a 100 g sub-sample at 104°C for 48 h. The available water (AW, mm/depth interval) above wilting point (WP, mm) was determined by subtracting the appropriate gravimetric wilting point and multiplying by the appropriate bulk density (BD, g/cm^3) and the depth interval in the following equations.

$$\mathrm{AW} = (\mathrm{SWC\%} - \mathrm{WP}) \times \mathrm{BD} \times 1.5, \text{ for depth intervals of } 0.15\,\mathrm{m}\,(0-0.6\,\mathrm{m})$$

$$\mathrm{AW} = (\mathrm{SWC\%} - \mathrm{WP}) \times \mathrm{BD} \times 3, \text{ for depth intervals of } 0.3\,\mathrm{m}\,(0.6-1.5\,\mathrm{m})$$

The WP ranged from 32.6% to 33.8% and BD increased with depth from 1.0 to 1.2 g/cm^3.

Subsamples of soil cores were analysed for nitrate concentration in 1 N KCL extracts, and quantity of nitrate-N (in kg/ha) was calculated for each depth interval using the following calculations:

$$\text{Nitrate-N}\,(\mathrm{mg/kg}) \times \mathrm{BD} \times 1.5, \text{ for depth intervals of } 0.15\,\mathrm{m}$$

$$\text{Nitrate-N}\,(\mathrm{mg/kg}) \times \mathrm{BD} \times 3, \text{ for depth intervals of } 0.3\,\mathrm{m}$$

Arbuscular mycorrhizal fungi assessment

Spore numbers of AMF were assessed in soil samples collected before planting chickpea and wheat in the second year (50-g subsample stored for 6 months at 3°C) from 0–0.15 m depth with a modified technique suitable for clay soils based on the method of McKenney and Lindsey (1987). A 50-g field-moist soil sample was added to 800 mL deionised water with 5 g tetra-sodium pyrophosphate in a flask that was mechanically agitated by end-over-end shaking for 1 h. The sample was then transferred to a 38-µm sieve and washed with tapwater until all clay was removed and clear water ran through the sieve. The sample was then transferred to a conical flask with 1 L of water, inverted six times, and then let stand for 10 s before repeated decanting through a series of mesh sieves 500, 250, 150, 106, 63 and 38 µm. Spores retained on each sieve were collected in 10–15 mL water in separate 30-mL containers. Protoplasmic spores from the sieves at 38, 63, 106, 150 and 250 µm were counted in a 1-mL subsample in a Hawksley slide under a compound microscope at ×40 and ×100 magnifications. Suspensions from the 500-µm sieve were poured into a Doncaster dish (Doncaster 1962) and assessed for AMF spores and sporocarps using a stereo microscope. Spores had subtending hyphae, placing them in the genus *Glomus*; species identification was not attempted. Results were expressed as number of AMF spores/g soil (oven-dry equivalent).

Plant biomass

At 137 days after sowing the second-year crops, when chickpeas were at pod ripening (growth stage BBCH 8.0; Lancashire *et al.* 1991) and wheat was at dough-development (growth stage 85; Zadoks *et al*. 1974), two quadrats were selected randomly (each 2 rows by 1 m) and cut at ground level for determination of biomass (calculated after oven drying at 80°C for 2 days).

Statistical analyses

All analyses were performed using GENSTAT 14th Edition (VSN International 2011) with the level of significance set at $P = 0.05$. A linear mixed model was fitted to traits, where one measurement was taken per plot for plant biomass, grain yield and AMF spore count. Crops grown in the first year in the presence or absence of aldicarb and crops grown in the second year were fitted in a factorial combination as fixed effects with replicates fitted as random.

The linear model was extended for each trait measured down the soil profile (*P. thornei*, *M. brevidens*, non-parasitic nematodes, soil water and soil nitrate) to include soil depth as a factor. The covariance between depths was modelled for each trait with the most parsimonious structure chosen based on the likelihood ratio test. The covariance structures for each trait are summarised in Table 1.

Since nematodes were counted in individual plots and depth intervals from 0 to 0.45 m, and then on samples bulked at each depth interval to 0.9 m, separate analyses were performed for three depths in the 0–0.45 m interval, and two depths in the 0.45–0.9 m soil interval (no depths below 0.9 m were included as numbers of nematodes were mostly zero). Preliminary analyses showed heterogeneity of variance within each depth interval for nematodes and soil nitrate, so nematode data was transformed by

ln(x + c), where x is number of nematodes/kg soil and c is a constant chosen to stabilise the heterogeneity of the residuals. Transformed means were back-transformed after analysis and numbers are reported as nematodes/kg oven-dry soil. Soil nitrate was transformed by the square-root transformation before statistical analysis.

A tolerance index was calculated by dividing mean grain yield of cultivars after wheat without aldicarb by mean grain yield after canaryseed without aldicarb, and results used to classify the cultivars into one of nine categories ranging from tolerant (T) to very intolerant (VI), according to the Australian national disease rating and management guide for nematode tolerance (www.nvtonline.com.au/: Resources—Disease rating definitions).

Multiple regression analyses were conducted to relate biomass and grain yield of chickpea and wheat as response variates to measures of *P. thornei* (0–0.9 m), *M. brevidens* (0–0.9 m), AMF spores (0–0.15 m), plant-available water and soil nitrate (N) at soil intervals of 0–0.15, 0.15–0.6 and 0.6–1.2 m. Final models were obtained by examining all possible regressions and selecting models with the highest R^2 and with all terms significant ($P \leq 0.05$).

Results

Rainfall and irrigation

Monthly rainfall received during the 2 years of the experiment is shown in Table 2. During the first year, 77 mm of rainfall was recorded during the first 4 months, with the bulk in February. One week before aldicarb application on 14 May 1997, a further 12 mm of rain was recorded, followed by another 30 mm at 2 days after application. Ten mm of rain was recorded 2 days before planting on 28 May, which ensured good crop establishment. There was 198 mm of in-crop rainfall, and 88 mm of irrigation water was applied to the trial over 15 and 16 July. The weed-free fallow period before planting in the second year (1998) received 121 mm of rainfall, with 53 mm of rain recorded in May before soil sampling, aldicarb application and the planting of second-year chickpea and wheat. During the 1998 growing season, there was good in-crop rainfall of 281 mm.

Table 1. Summary of the covariance structures and transformation used in analyses for traits *Pratylenchus thornei* (Pt), *Merlinius brevidens* (Mb), non-parasitic nematodes (Np), soil water and soil nitrate

The constant 'c' in ln(x + c) was chosen to stabilise the variance; ln refers to the natural logarithm

Trait	Covariance structure between depths	Transformation
Pt (0–0.45 m) unbulked soil	Uniform	ln(Pt + 1000)
Pt (0.45–0.9 m) bulked soil	Uniform (heterogeneity)	ln(Pt + 1000)
Mb (0.45–0.9 m) bulked soil	Uniform	ln(Mb + 1000)
Np	Uniform	ln(Np + 100)
Soil water (0–0.6 m)	Unstructured	–
Soil water (0–1.5 m)	Unstructured	–
Soil nitrate (0–1.5 m) bulked soil	Power (heterogeneity)	Square-root

Grain yield of first-year crops

Grain yield of first-year crops showed a significant interaction between crop and aldicarb. Grain yield of wheat (mean 3681 kg/ha) and linseed (mean 1101 kg/ha) showed no response to aldicarb, but there was a significant response in canola (nil aldicarb 1251 kg/ha, plus aldicarb 1845 kg/ha; l.s.d. ($P = 0.05$) = 274).

Pratylenchus thornei *after first-year treatments*

After the first-year treatments, *P. thornei* was present in the soil profile to 1.2 m depth both with and without aldicarb treatment (Fig. 1*a–b*). The highest populations of *P. thornei* were after wheat cv. Janz, with 11 600/kg soil at 0.45–0.6 m soil depth. There were significant ($P < 0.001$) interactions of depth × crop treatment × aldicarb for populations of *P. thornei* in the top 0–0.45 m soil depth. Wheat Janz (plus or minus aldicarb) had significantly greater *P. thornei* populations than other first-year treatments for the three depths (0–0.15, 0.15–0.3, 0.3–0.45 m). Aldicarb significantly reduced *P. thornei* populations under wheat (0–0.3 m) to 1109/kg soil compared with 3970/kg soil without aldicarb, but below this depth, populations of *P. thornei* under wheat did not differ with aldicarb treatment. Populations of *P. thornei* for canola and linseed treatments were significantly reduced by aldicarb within the 0.3–0.45 m soil interval. Populations of *P. thornei* for treatments other than wheat ranged from 187/kg soil after canaryseed (0–0.15 m) to 1866/kg soil after canola (0.3–0.45 m), with populations after canaryseed being 86–94% lower than wheat without aldicarb for all intervals in the top 0.45 m.

In the deeper soil profile, 0.45–0.9 m, there were significant ($P < 0.001$) effects of depth and crop treatment on *P. thornei* populations, with no significant interaction between variables. Populations of *P. thornei* within this depth interval were not reduced by the aldicarb treatment and were greatest after wheat (11645/kg soil at 0.45–0.60 m) compared with all other treatments. There was no significant difference in *P. thornei* numbers for remaining treatments within this soil interval.

Only very low levels of the ectoparasitic nematode *M. brevidens* were detected at the site, with the highest mean population (69/kg soil) at 0.45–0.6 m depth. There was no difference between first-year treatments, and aldicarb had no

Table 2. Monthly rainfall data for the field site at Formartin over the 2-year experiment compared with the average rainfall data from site records (65 years) and the long-term average rainfall data (121 years) from the nearest Bureau of Meteorology (BOM) site number 041008 at Bowenville, Queensland

	J	F	M	A	M	J	J	A	S	O	N	D	Total
1997	4	69	0	4	55	0	91	0	44	75	101	40	394
1998	74	70	0	70	53	37	62	56	121	6	86	33	667
Site records	79	72	42	33	35	30	30	25	28	53	67	80	572
BOM	86	64	61	35	38	37	35	29	36	56	75	95	634

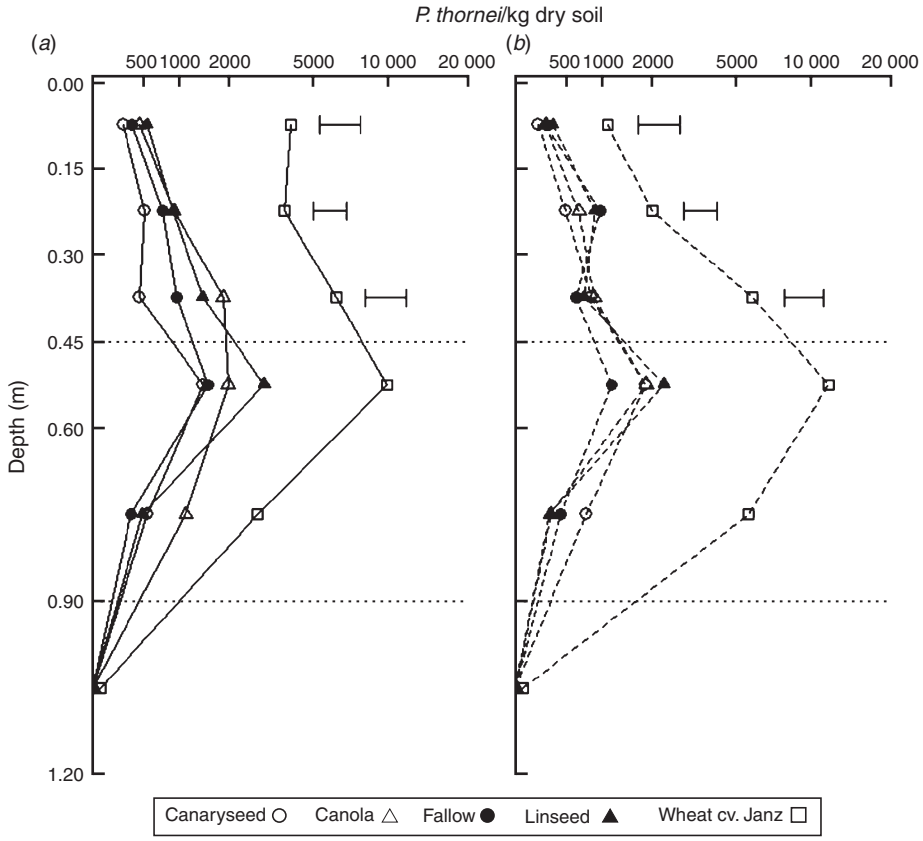

Fig. 1. Distribution of *Pratylenchus thornei*/kg soil in the soil profile (*a*) without aldicarb and (*b*) with aldicarb following first-year treatments that were sampled before planting chickpea and wheat in the following year. Bar markers are l.s.d. ($P = 0.05$) for 0–0.45 m depth. Horizontal lines separate 0–0.45 m (ANOVA with five samples per treatment per depth) from 0.45–0.9 m depths (samples bulked across five duplicate plots per block per depth). For the 0.45–0.6 and 0.6–0.9 m soil depths, first-year treatment and depth were statistically significant with no significant interactions. Wheat had significantly higher numbers of *P. thornei* than other treatments and there was no significant difference between remaining treatments for numbers of *P. thornei.* Aldicarb treatment was not significant at 0.45–0.9 m depth. The *x*-axis is on a logarithmic scale and the means from $\ln(x + 1000)$ are back-transformations in ANOVA. The points are $\ln(x + 1000)$ means from ANOVA with appropriate l.s.d. bars and back-transformed scale on the horizontal axis.

effect on populations (data not shown). Non-plant-parasitic nematodes, mainly fungal and bacterial feeders, showed significant ($P < 0.001$) differences with depth and crop treatment within the 0–0.45 m soil depth. The highest mean population (409/kg soil) was at 0–0.15 m soil depth. Linseed had significantly higher populations (275/kg soil) than canaryseed (174/kg), wheat (161/kg) or fallow (82/kg). Few non-plant-parasitic nematodes (<184/kg soil) were found deeper in the soil (0.45–1.2 m), and there were no significant differences between treatments. Aldicarb had no significant effect on non-plant-parasitic populations at any depth (data not shown).

Soil water and nitrate following first-year treatments

Gravimetric soil water following the first-year treatments showed a significant ($P < 0.001$) depth × crop treatment interaction (Fig. 2). At 0–0.15 m soil depth, the mean soil water for wheat (50.5%) was significantly higher than for linseed (49.5%). There was no significant effect of cropping treatments on water within the 0.15–0.6 m soil profile, whereas deeper in the soil (0.6–1.2 m), there was significantly less soil water following canola than the other treatments. In general, soil water was greater in the upper soil profile (0–0.6 m, mean 51.2%) than the deeper profile (0.6–1.5 m, mean 45.8%). Aldicarb treatment had no significant effect on soil water content.

Similar trends were seen for available water content ,whereby there was little difference between crop treatments for the upper soil profile (0–0.6 m), ranging from 114 mm after canaryseed to 117 mm after fallow. Deeper in the soil profile (0.6–1.5 m), canola resulted in 84 mm of available water, which was 37 mm less than the mean of the other treatments. Throughout the whole soil profile (0–1.5 m), available water was least after canola (200 mm) and greatest after fallow (243 mm), followed by canaryseed (239 mm) wheat (236 mm) and linseed (232 mm).

Soil nitrate concentration following the first-year treatments showed a significant ($P < 0.001$) depth × crop treatment interaction (Fig. 3). Nitrate increased with soil depth, with peak concentrations in the 0.6–1.2 m depth interval. There was

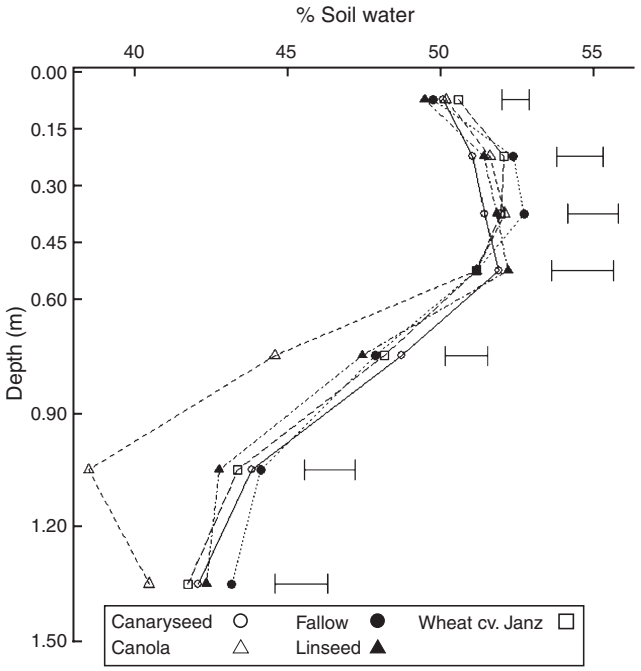

Fig. 2. Gravimetric water content in the soil profile (0–1.5 m) following first-year crop treatments sampled 6 months after harvest (4 days before planting second-year chickpea and wheat) at Formartin, Queensland. Bar markers are l.s.d. ($P = 0.05$).

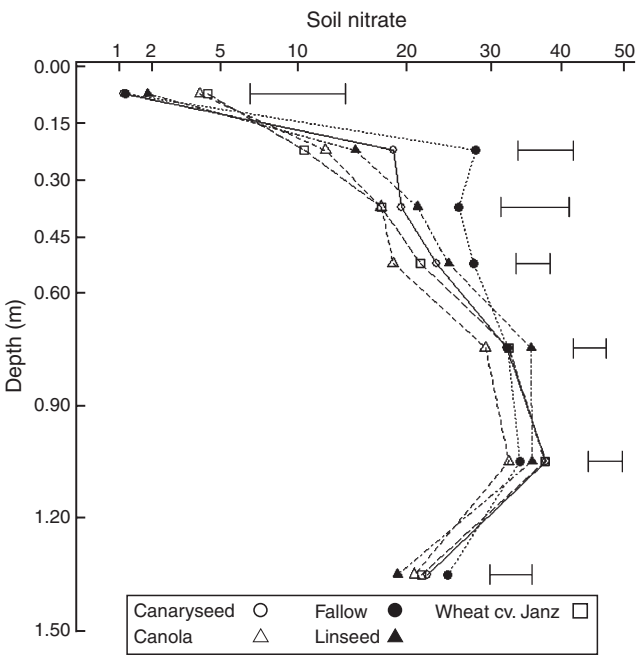

Fig. 3. Soil nitrate (mg/kg) concentration in the soil profile (0–1.5 m) after first-year crop treatments sampled 4 days before planting second-year crops, 6 months after harvest at Formartin, Queensland. Bar markers are l.s.d. ($P = 0.05$).

no significant difference between treatments for nitrate concentrations in the 0–0.15 and 0.9–1.2 m soil intervals. Nitrate concentrations were significantly higher after fallow (28 mg NO_3-N/kg) than after all other treatments at 0.15–0.3 m, and higher than canola and wheat at 0.3–0.45 m and wheat, canola and canaryseed at 0.45–0.6 m. Linseed was the only treatment significantly different at 0.6–0.9 m soil depth, having higher levels of soil nitrate than canola. Aldicarb had no significant effect on soil nitrate concentration.

Plant biomass of second-year crops

Plant biomass (Table 3) of the second-year chickpea and wheat cv. Gatcher (averaged across cultivars and aldicarb treatment) was significantly ($P < 0.001$) greater after canaryseed, and significantly ($P < 0.001$) less after canola. Biomass increased 23% after canaryseed and 13% after linseed compared with biomass after first-year wheat cv. Janz. Application of aldicarb significantly ($P < 0.01$) increased overall plant biomass by 8%. No significant interactions occurred between first-year treatments, second-year crops and aldicarb application; however, interactions between the first-year treatments and second-year crops (averaged for plus and minus aldicarb) approached significance ($P = 0.059$). This trend showed chickpea cultivars increasing up to 24% and wheat cv. Gatcher 88% more after canaryseed than after wheat cv. Janz. All chickpea cultivars had less biomass when grown after canola and fallow treatments, whereas wheat biomass increased 31% when grown after canola, 70% after fallow and 76% after linseed, compared with wheat biomass after wheat (data not shown).

Grain yield of second-year crops

Grain yield of the second-year chickpea and wheat (cv. Gatcher) crops was greater after canaryseed than after other treatments, resulting in a significant ($P < 0.001$), 14% increase compared with yields after wheat cv. Janz. Grain yield after linseed was 4% greater than after wheat, and grain yields following canola, fallow and wheat were lower than yield after linseed. Applying aldicarb increased overall grain yield by 6% ($P < 0.001$) (Table 4). No significant interactions occurred between first-year treatments, second-year crops and aldicarb; however, interactions between first-year treatments and second-year crops (averaged across plus and minus aldicarb) approached significance ($P = 0.06$). This interaction showed yields after canaryseed increase 15% and 13% for chickpea cvv. Tyson and Norwin and 38% for wheat cv. Gatcher compared with grain yields after wheat (cv. Janz). All chickpea cultivars had lower grain yield after canola and fallow than after other treatments, whereas grain yield of wheat cv. Gatcher increased 19% after canola and 37% after fallow compared with grain yield after wheat (cv. Janz) (Fig. 4).

Grain-yield losses derived from comparison of yields after canaryseed and wheat without aldicarb and derived tolerance indices show chickpea cultivars having grain-yield losses up to 20% and wheat 35% (Table 5).

First-year crop effect on AMF

Total AMF spore numbers were significantly ($P < 0.001$) lower after fallow and canola treatments than after wheat, linseed and canaryseed, all of which had similar levels of AMF spores (Fig. 5). Aldicarb had no effect on AMF spore numbers.

Table 3. Biomass (kg/ha) of chickpea and wheat after first-year treatments at Formartin, Queensland

	Aldicarb	Chickpea cvv.				Wheat cv.	Mean after first-year
		Norwin	Tyson	Barwon	Lasseter	Gatcher	treatment
First-year treatment:							
Canaryseed	–	7761	6795	9037	6445	5993	7079
	+	8042	5931	7799	7164	5816	
Linseed	–	6735	5031	6140	7316	5010	6478
	+	7412	5759	8077	7242	6056	
Wheat cv. Janz	–	6120	4284	5566	7578	1950	5750
	+	6681	6231	8057	6693	4350	
Canola	–	4453	3943	4781	6081	4207	4737
	+	4805	5273	5371	4399	4061	
Fallow	–	5421	4926	5109	6451	5840	5814
	+	6621	5370	7224	6313	4867	
Second-year crop means		6405	5354	6716	6568	4814	
Aldicarb means:							
Nil	5719						
Plus	6224						
l.s.d. ($P = 0.05$):							
First-year treatment					599		
Second-year crop					599		
Aldicarb					379		
First-year treatment × second-year cultivar					1340		

Table 4. Grain yield (kg/ha) of chickpea and wheat grown after first-year treatments at Formartin, Queensland

	Aldicarb	Chickpea cvv.				Wheat cv.	Mean after first-year
		Norwin	Tyson	Barwon	Lasseter	Gatcher	treatment
First-year treatment:							
Canaryseed	–	2725	2546	2670	2224	1636	2358
	+	2650	2488	2595	2294	1752	
Linseed	–	2408	2075	2560	2174	1201	2159
	+	2450	2449	2459	2155	1658	
Wheat cv. Janz	–	2394	2038	2307	2113	1057	2074
	+	2350	2327	2674	2068	1408	
Canola	–	2313	1779	2342	1876	1477	2016
	+	2244	1983	2597	2086	1459	
Fallow	–	2187	1910	2436	1945	1509	2096
	+	2360	2050	2490	2205	1867	
Second-year crop mean		2408	2164	2513	2114	1502	
Aldicarb means:							
Nil	2076						
Plus	2205						
l.s.d. ($P = 0.05$):							
First-year treatment					115		
First-year crop					115		
Aldicarb					73		
First-year treatment × second-year cultivar					257		

Multiple regression analysis

Regression analyses (Table 6) show the effects on chickpea and wheat plant biomass and grain yield of the variables *P. thornei* population density, AMF spores, available water and nitrate. Plant biomass of chickpea was positively related to AMF spores (0–0.15 m) and available water in the subsoil (0.6–1.2 m), but negatively related to water in the topsoil (0–0.15 m). Wheat biomass was negatively related to *P. thornei* populations in the soil profile (0–0.9 m) and positively related to nitrate (0.15–0.6 m).

The grain yield of chickpea was negatively related to populations of *P. thornei* in the soil profile (0–0.9 m) and nitrate in the upper profile (0.15–0.6 m), but positively related to density of AMF spores in the topsoil (0–0.15 m), available water (0.6–1.2 m) and nitrate in the lower profile (0.6–1.2 m) (Fig. 6). The strong negative relationship between chickpea grain yield and populations of *P. thornei* showed that yield decreased by 180 kg/ha per unit of ln(*P. thornei*/kg soil + 1), resulting in a difference of 540 kg/ha from the highest to the lowest mean *P. thornei* population in this experiment. The grain

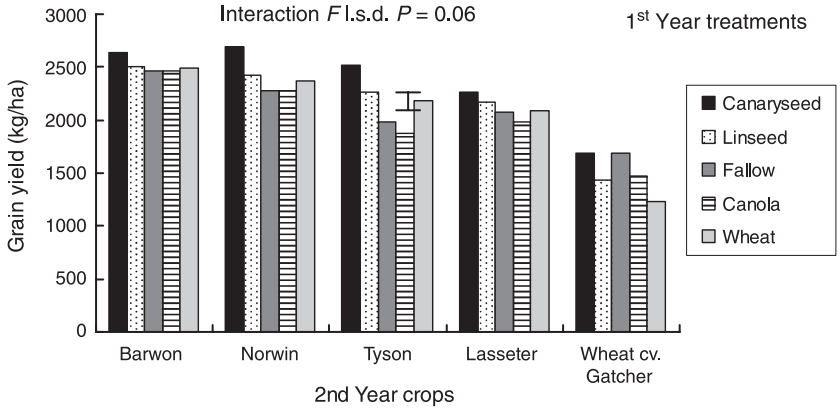

Fig. 4. Grain yield (kg/ha) of chickpea cultivars and wheat cv. Gatcher averaged across plus and minus aldicarb treatments at Formartin, Queensland, following first-year treatments.

Table 5. Tolerance index for chickpea and wheat cultivars derived from grain yield (kg/ha) following low populations of *P. thornei* (canaryseed without aldicarb) and high populations of *P. thornei* (wheat without aldicarb) where tolerance index = 100 × (yield after canaryseed – yield after wheat)/yield after canaryseed

MT, Moderately tolerant; MI, moderately intolerant; I, intolerant

Crop	Cultivar	Grain yield (kg/ha)		Tolerance index (%)	Proposed classification	Yield loss (%)
		After canaryseed	After wheat			
Chickpea	Norwin	2725	2394	88	MT-MI	12
	Tyson	2546	2038	80	MI	20
	Barwon	2669	2307	86	MT-MI	14
	Lasseter	2224	2113	95	T-MT	5
Wheat	Gatcher	1636	1057	65	MI-I	35

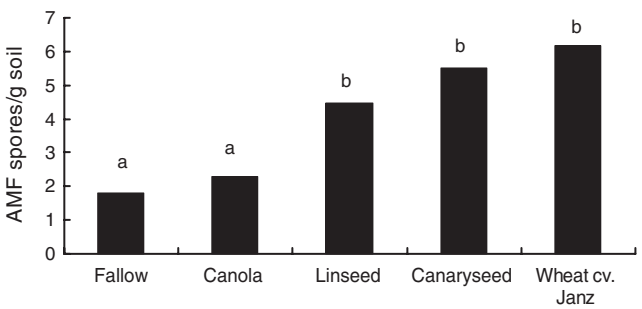

Fig. 5. Back-transformed means for total number of arbuscular mycorrhizal fungal (AMF) spores/g soil collected on sieves ≥38 µm mesh size at 0–0.15 m following first-year treatments sampled 4 days before planting second-year crops (6 months after harvest) at Formartin, Queensland. Bars with the same subscript are not significantly different at $P = 0.05$.

yield of wheat was negatively related to *P. thornei* populations in the soil profile (0–0.9 m), which reduced yield by 174 kg/ha for every unit of ln(*P. thornei*/kg soil + 1) (Fig. 7).

Discussion

This study shows for the first time that pre-cropping with resistant canaryseed and susceptible wheat to create low and high population densities of *P. thornei* is an effective alternative to using nematicide when assessing tolerance of chickpea cultivars to *P. thornei*. Importantly, our results showed aldicarb ineffective at controlling *P. thornei* populations deeper in the soil profile. However, cropping with canaryseed without aldicarb reduced numbers of *P. thornei* by up to 94% in the soil profile compared with wheat cv. Janz, and left adequate levels of mycorrhizal spores that did not compromise the yields of subsequent chickpea or wheat cv. Gatcher. Our research indicated the dependence of chickpea on AMF, as seen by the significantly lower chickpea yields after a non-mycorrhizal crop such as canola and the fallow treatment, further validated by multiple regressions showing positive associations with mycorrhizal spore numbers and chickpea yield. The combined effect of lower *P. thornei* populations and sufficient levels of soil mycorrhiza resulting from rotations with resistant canaryseed without aldicarb contributed to chickpea increasing up to 25% and wheat yields 55%, which is consistent with previous studies in this region (Thompson *et al.* 1997; Owen *et al.* 2010).

About 67% of fields tested in the Australian northern grain region are infested with *P. thornei*, and although chickpea–wheat rotations are commonly practiced in this region, they contribute to increasing *P. thornei* populations within the soil (Thompson *et al.* 2010). In our study, *P. thornei* was present throughout the 1.2 m soil depth, with the highest populations found within the 0.3–0.6 m soil interval, which is consistent with other studies conducted within this region (Doyle *et al.* 1987; Thompson *et al.* 1999). Aldicarb failed to reduce *P. thornei* populations deeper than 0.3 m for wheat, and 0.45 m for other crops and fallow, and consequently was ineffective for assessing yield loss and

Table 6. Regression equations and R^2 values relating measures of *P. thornei*, arbscular mycorrhizal fungi, soil nitrate and water after the first-year treatments, to biomass and grain yield of second-year chickpea and wheat

BM, Biomass (kg/ha); GY, grain yield (kg/ha); Pt, ln(*P. thornei*/kg soil + 1); AW, available water (mm); N, nitrate-N(kg/ha); AMF, arbuscular mycorrhiza fungal spores/g soil

	Equation	*P*-value	*n*	R^2 value
	Biomass			
Wheat cv. Gatcher	BM = 359 – 33(Pt at 0–0.9 m) + 1.2(N at 0.15–0.6 m)	<0.001	29	0.40
Chickpea	BM = 592 + 7.18(AMF at 0–0.15 m) – 17.9(AW at 0–0.15 m) + 1.9(AW at 0.6–1.2 m)	<0.001	30	0.59
	Grain yield			
Wheat cv. Gatcher	GY = 2745 – 174.2(Pt at 0–0.9 m)	0.003	30	0.25
Chickpea	GY = 2955 + 21.27(AMF at 0–0.15 m) – 180(Pt at 0–0.9 m) + 7.99(AW at 0.6–1.2 m) – 6.23(N at 0.15–0.6 m) + 1.98(N at 0.6–1.0 m)	<0.001	24	0.77

tolerance to *P. thornei*. Similar research has shown that aldicarb controlled *Pratylenchus* populations in the upper layers of soil only, but populations increased deeper in the profile (Beane 1985; Doyle *et al*.1987).

On the other hand, low populations of *P. thornei* were found throughout the soil profile after growing canaryseed, linseed, canola and the clean fallow treatment. Canaryseed was the most effective treatment; on average, *P. thornei* populations were 88% lower throughout the 0–0.9 m soil profile than after susceptible wheat cv. Janz. Lower *P. thornei* populations after canaryseed resulted in the following wheat (cv. Gatcher) and all chickpea cultivars (except Barwon) having greater differences in grain yield between treatments pre-cropped with resistant canaryseed and susceptible wheat than between treatments pre-cropped with susceptible wheat with and without aldicarb. It is noteworthy that no additional reduction in *P. thornei* populations occurred when using aldicarb with resistant canaryseed, or the fallow treatment. However, there was a further reduction in *P. thornei* populations under canola and linseed within the 0.3–0.45 m depth and a 32% increase in yield of canola in the first year due to aldicarb. An explanation is that, although populations of *P. thornei* were lower after canola and linseed than after wheat, both crops without aldicarb treatment had *P. thornei* populations approaching the estimated wheat damage threshold of 2000/kg soil (Thompson *et al*. 2010). Other studies have classified canola as moderately resistant to *P. thornei* (Hollaway *et al*. 2000; Owen *et al*. 2010; Vanstone *et al*. 2008) but cultivars can vary in their host status (Webb 1996). Crop tolerance is also independent of resistance (Trudgill 1991), and canola cv. Hyola 41 may not be tolerant. Although canola is often used in rotations with wheat in the southern part of the northern grain region of Australia, commercial cultivars are not routinely screened for RLN tolerance or resistance. Obtaining this information for new canola cultivars would assist growers to manage *P. thornei* in their farming systems.

The failure of aldicarb to control *P. thornei* populations in the deeper soil layers in our study could be linked to the relatively high clay content and water-holding capacities of the soil, which slow movement and dilute the concentration of the nematicide faster with depth (Awad *et al*. 1984; Noling 2002). Aldicarb dispersion in the soil is dependent on water movement (Noling 2002), and in our trial, adequate rain fell during both years after nematicide application. It has also been suggested that, through aldicarb controlling nematodes in the upper soil layer and thereby increasing plant vigour, root growth may increase, allowing nematode multiplication in unprotected roots deeper in the soil profile (Beane 1985; Barker *et al*. 1988).

Tolerance testing

For determining levels of genetic tolerance of chickpea in our study, pre-cropping with susceptible wheat with and without aldicarb clearly underestimated yield loss, as opposed to the strategy of comparing yields after canaryseed and wheat without aldicarb. With the strategy of comparing yields after canaryseed and wheat without aldicarb, chickpea cvv. Barwon and Norwin could be ascribed as moderately tolerant, having smaller yield loss (12–14%) than Tyson, which was moderately intolerant, suffering a yield loss of 20%. The small difference in grain yield response of cv. Lasseter (2–5%) determined by both methods indicates tolerance, whereas the low grain yield is likely related to Lasseter's adaptation to the southern Australian region rather than the northern grain region (Siddique *et al*. 2000). Of interest, the yield difference of chickpea cv. Barwon following wheat with and without aldicarb was similar to the yield difference following canaryseed and susceptible wheat without aldicarb (14%), unlike the other cultivars. Wheat cv. Gatcher was shown to be intolerant with the canaryseed–wheat strategy, suffering a yield loss of 35% as opposed to 25% using the wheat–aldicarb strategy. The percentage loss of chickpea yields under high *P. thornei* pressure at this site was lower than that of the intolerant wheat cv. Gatcher, indicating that chickpea cultivars in this study were more tolerant than wheat cv. Gatcher. However, in a Syrian study, with >2000 *P. thornei*/kg soil (assessed by a centrifugation method), a yield loss of 58% was recorded in chickpea cv. Ghab 1 (Di Vito *et al*. 1992).

Although tolerant chickpea cultivars produce greater yields, the levels of resistance to *P. thornei* also play an important role in management (Thompson *et al*. 1999, 2012; Starr *et al*. 2002). Of the four chickpea cultivars tested, Norwin has a higher level of resistance than both Barwon and Lasseter, which are moderately susceptible, whereas Tyson is highly susceptible to *P. thornei* (Thompson *et al*. 2008, 2011). Cultivars with moderate resistance and tolerance, such as Norwin, are valuable in crop sequences because they suppress *P. thornei* reproduction while maintaining their yield.

Mycorrhiza influence

Fifteen weeks after planting the second-year crops, chickpeas growing in plots previously planted with canola or after fallow had noticeably poorer growth than chickpeas in plots previously

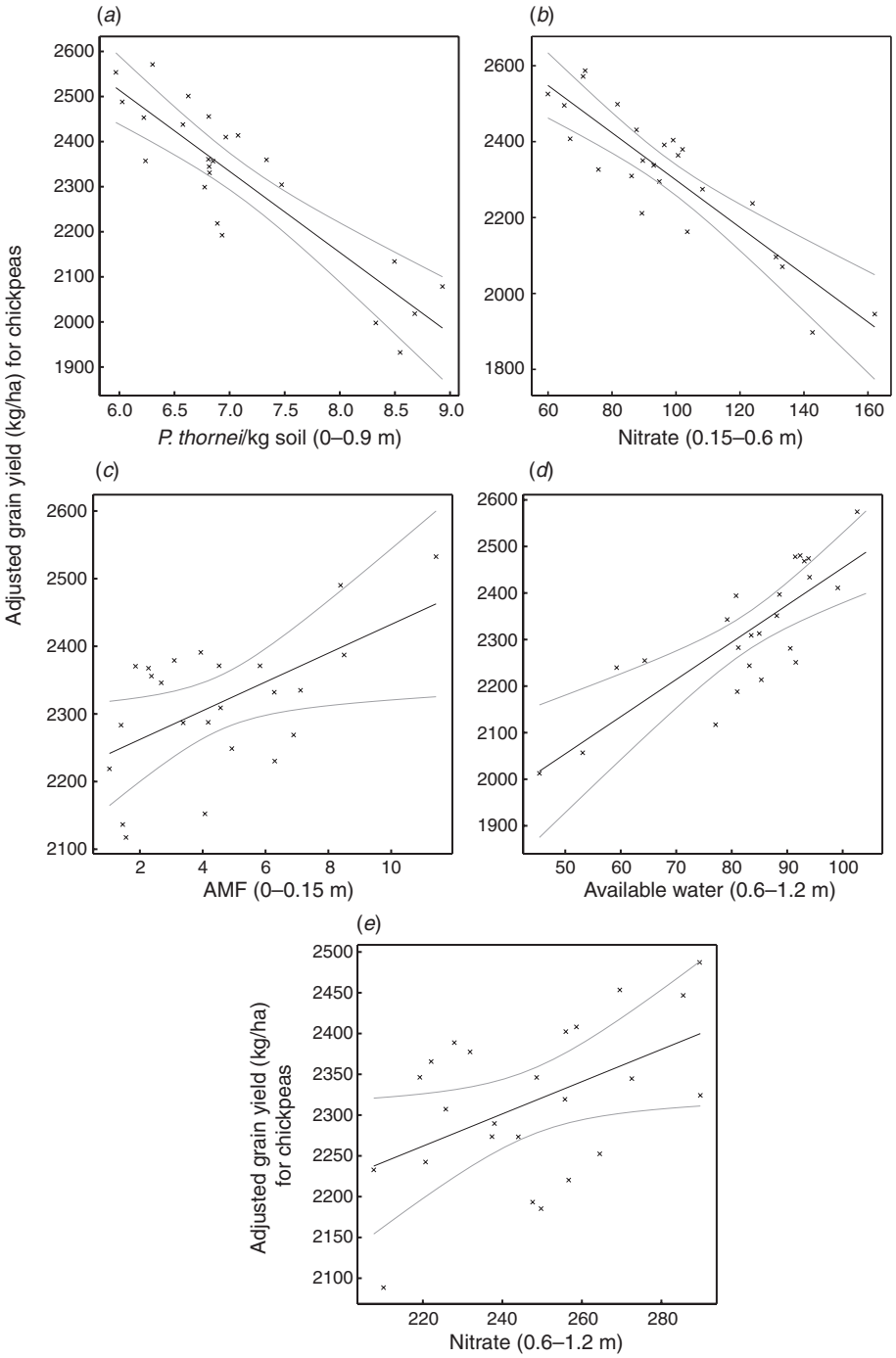

Fig. 6. Correlation of parameters used in a multiple regression to determine effect on final chickpeas grain yield following first-year treatments ($R^2 = 0.76$): (*a*) population density of *P. thornei* at 0–0.9 m, (*b*) nitrate at 0.15–0.6 m, (*c*) numbers of AMF spores at 0–0.15 m, (*d*) available water at 0.60–1.2 m, (*e*) nitrate at 0.6–1.2 m.

planted with canaryseed or linseed. This suggested that the chickpeas could be suffering from long-fallow disorder due to insufficient AMF (Thompson 1987). This observation was further validated by multiple regression analysis, in which AMF spore numbers in the soil before planting were shown to have a positive effect on chickpea plant biomass and final grain yields. Arbuscular mycorrhizae are dependent on a host plant, and during periods of clean fallow their propagules decline in viability, resulting in deficiencies of P and Zn in subsequent crops (i.e. long-fallow disorder) (Thompson 1987, 1991). Canola is one of the few crop species that is a non-host or very poor host of AMF (Ryan and Angus 2003). Similar to our findings, other field

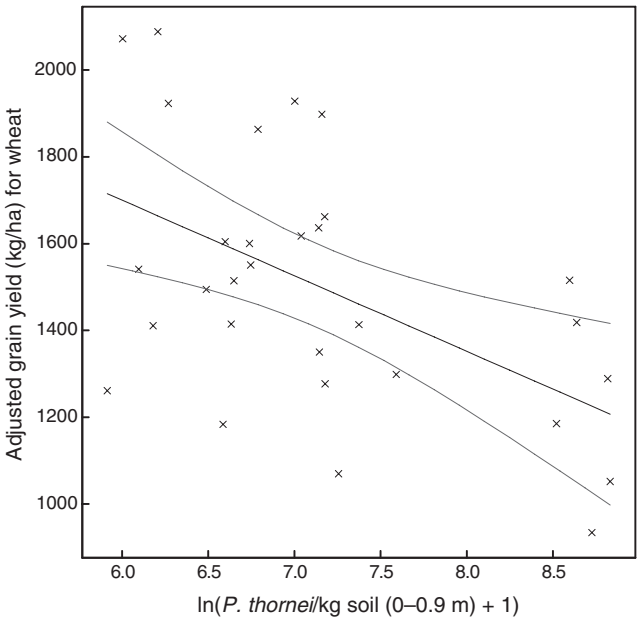

Fig. 7. Relationship between grain yield for wheat cv. Gatcher in the second year of the experiment and *P. thornei* population density at 0–0.9 m soil depth following first-year crops; $R^2 = 0.25$, $n = 30$, $P = 0.003$.

studies by Erman *et al*. (2011) and Ortas (2012) found that AMF increased chickpea yields, and several studies in controlled environments found that AMF increased P uptake, with increased chickpea yields ensuing (Zaidi *et al*. 2003; Zaidi and Khan 2007; Farzaneh *et al*. 2011). Furthermore, increasing plant P concentration improves tolerance to nematodes but can also enhance nematode reproduction (Hussey and Roncadori 1982; Anwar and Zaki 2005). Results from the present study demonstrated that chickpeas grown after canola yielded less than after other crops. Using crop species that support AMF colonisation and the subsequent improvement in P extraction is a desirable management strategy, given that Australian soils have generally low levels of P and that P fertiliser is a non-renewable resource (Cordell *et al*. 2012).

Wheat

Wheat is not as dependent on mycorrhizae as chickpea (Marschner 1986; Thompson 1987), and although AMF can reduce root infection by *Pratylenchus* in wheat (Anwar and Zaki 2005), wheat biomass and grain yield in our study were not correlated with AMF spore numbers. Previous research at the same site in a very dry season showed that pre-cropping with canola reduced *P. thornei* populations and AMF, resulting in decreased yields of the intolerant wheat cv. Batavia that followed, rather than the increase expected from lowering *P. thornei* populations (Owen *et al*. 2010). Decreased crop yields depend on the degree of reduction of AMF inoculum, levels of P and Zn in the soil, and the varying levels of AM responsiveness within species of each crop (Smith and Smith 2011). The low impact of AMF on yield of wheat cv. Gatcher in our experiment may be explained by possible varietal response to AMF (Deepak *et al*. 2006) and high disease pressure by *P. thornei*, as wheat Gatcher is highly intolerant to *P. thornei*.

Influence of soil nutrients and available water on biomass and yield

Whereas prior treatments of various crop species or fallow can set up different population densities of RLN, they can also create differential levels of soil water and nitrate, which might also influence subsequent crop growth and yield. For this reason, we determined water and nitrate levels in the soil profile and included them in multiple regression analyses.

Multiple regression analysis showed that both soil nitrate and available water were associated with plant biomass and grain yield of subsequent chickpea and wheat in the second year. Soil nitrate was positively and negatively associated with chickpea grain yield and positively influenced the biomass of wheat. Lower levels of soil nitrate (0.45–0.6 m) and soil water at depth (0.6–1.2 m) were evident after pre-cropping with canola and were most likely due to the taproot system extending deeper into the soil profile than was the case for the fibrous-rooted crops. Higher nitrate levels found within the root growing zone (0.15–0.6 m) after fallow plots was due to the absence of crops. The lower crop biomass and grain yield following canola and fallow was more evident in chickpea than wheat, reflecting the greater relative mycorrhizal dependency of chickpea than of wheat, rather than differences in water and nitrate. The positive relationship between chickpea grain yield and nitrate in the 0.6–1.2 m soil depth could be linked to lower *P. thornei* populations causing less root damage, as *P. thornei* will reduce the capability of N_2-fixing nodules (Castillo *et al*. 2008). Demand for N by chickpea is affected by season, other pests, associations with rhizobia and supply of other nutrients (Angus 2001). The amount of plant N accumulated by chickpea, or level of soil N, also has no effect on grain yield (Doughton *et al*. 1993; Turpin *et al*. 2002); thus, the negative relationship of N and chickpea yield in our study suggests that this is an effect of low numbers of AMF spores in the soil, which was evident after both fallow and canola, because numbers of *P. thornei* after fallow treatment were low and soil nitrate levels high but grain yields low.

Unlike chickpea, wheat biomass after fallow treatments was relatively high and grain yield similar to wheat following canaryseed, indicating that higher soil nitrate levels following the fallow treatments was more important for the growth of this non-N_2-fixing crop. Regression analysis showed that both nitrate and *P. thornei* were associated with biomass yield, with nitrate positively affecting yield. This agrees with previous studies at this site showing that wheat cv. Gatcher was responsive to N fertiliser in the presence of *P. thornei* (Thompson *et al*. 2012).

Interestingly was the low grain yield of wheat following linseed in view that wheat biomass was relatively high. Studies on linola (*Linum usitatissimum*; similar to linseed) found subsequent wheat yields decreased when an excessive amount of residual soil N resulted in greater vegetative mass and rapid depletion of soil water (Kirkegaard *et al*. 1997). However this did not appear to be the case in our study and the low wheat yields after linseed may be explained by damaging populations of *P. thornei* numbers at depth (0.45–0.6 m). Numbers of *P. thornei* following linseed with or without aldicarb were 2341 and 3024/kg soil respectively.

In the absence of a soil constraint such as RLN, a key determinant of grain yield for chickpea in the northern grain region of Australia is the amount of plant-available water at

sowing, with the critical level being ~100 mm (Whish *et al*. 2007). In the Darling Downs region, chickpeas are known to produce seed under a wide range of soil water contents (Beech and Leach 1988), and in Vertosols, chickpea roots can penetrate deeper than 1.2 m (Singh 1997) with the ability to extract up to 356 mm of water during a wet year (Benjamin and Nielsen 2006). In our trial, chickpea biomass and grain yield were positively associated with available water in the deeper soil profile (0.6–1.2 m), and although canola left less water deeper in the soil profile than other first-year treatments, there was still >200 mm of available water following all treatments before planting chickpea and wheat. Using our actual plant-available water data in the Agricultural Production Systems Simulator (APSIM) legume growth model (Robertson *et al*. 2002), it was demonstrated that having less water after canola than after other first-year treatments had no influence on following chickpea biomass or yields because of the amount of in-crop rainfall. The range in predicated chickpea grain yields after the five pre-crop treatments was slight, at only 2 kg/ha, with a mean yield of 3726 kg/ha. There was no relationship between available soil water and wheat yields in our trial, and this agrees with long-term studies on a Vertosol, which found that *P. thornei* limited the response of intolerant wheat to extra water accumulated in the soil from zero tillage with stubble retention (Thompson *et al*. 1995).

Future research

In Australia, *P. thornei* ranks second in importance of the five major diseases affecting chickpea yield (Murray and Brennan 2012), and with the absence of *P. thornei*-resistant chickpea cultivars worldwide, use of tolerant cultivars combined with crop rotation is a critical part of the management strategy to limit chickpea yield losses. Adopting the strategy outlined in this paper will facilitate plant breeders to screen chickpea germplasm successfully for yield tolerance to *P. thornei.* This strategy was effective for estimating *P. thornei* tolerance in chickpea; however, the potential of this approach could be further extended to assess tolerance in other *P. thornei*-susceptible crops such as faba bean and mungbean (Sheedy *et al*. 2009; Di Vito *et al*. 2000).

Good progress has already being made in Australia to identify sources of resistances to RLN in the wild relatives of chickpea *C. echinospermum* and *C. reticulatum* (Reen *et al.* 2011; Thompson *et al*. 2011); however, further research and development is critical to incorporate this resistance successfully into commercial varieties. The incorporation of resistance into cultivars will lower nematode numbers, but the mainstay in future breeding programs needs to be on nematode tolerance as measured by yield response (Starr *et al*. 2002). The tolerance trait to nematode damage has proved valuable for chickpea (Ansari *et al*. 2004; Sharma *et al*. 1995), and incorporating tolerance with partial resistance has a dual benefit, as seen in wheat, where incorporating partial resistance and high levels of tolerance into spring wheat cultivars increased yields by up to 17% compared with commercial cultivars that are merely tolerant (Sheedy and Thompson 2009).

In conclusion, the present study highlights how population densities of *P. thornei* can be greatly affected by rotational choices and provides valuable crop sequence information regarding chickpea. It demonstrates the importance of AMF for chickpea production, and growers should consider this when growing non-mycorrhizal crops such as canola. Growing resistant canaryseed and susceptible wheat to manipulate population densities of *P. thornei* proved a more effective tool than aldicarb for measuring yield loss and cultivar tolerance in chickpea. Moreover, having a reliable and non-nematicidal strategy for identifying chickpea cultivar tolerance to *P. thornei* will contribute to future collective research efforts for incorporating tolerance genes into commercial cultivars. The incorporation of combined tolerance and resistance genes into commercial chickpea cultivars will benefit both the chickpea and wheat industries in reducing yield losses to *P. thornei*, particularly in systems rotating the two crops.

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