2 A triumph of tolerance: Managing the threat to wheat production by the root lesion nematode *Pratylenchus thornei* in the subtropical grain region of eastern Australia

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Introduction

The root lesion nematode *Pratylenchus thornei* is a severe and widespread threat to wheat (*Triticum aestivum*) production in the subtropical grain production region of eastern Australia. Yield loss of up to 65% has been counteracted by research efforts to produce integrated nematode management (INM) through understanding the biology and host range of *P. thornei* in farming systems, plant breeding and characterization of genotypes for tolerance and resistance traits, and communication with the farming community. The widespread adoption and success of INM has been driven by the release and on-going improvement of wheat cultivars with tolerance to *P. thornei* which deliver immediate economic benefits to grain growers.

Economic importance

Pratylenchus thornei was first detected in the subtropical grain region of eastern Australia in the 1960s. Its distribution closely followed the expansion of wheat production which began in 1860 in southern Queensland (described in Thompson *et al.*, 2010). Thompson *et al.* (2010) hypothesized that the change to barley (*Hordeum vulgare*) production from wheat in the 1930s was related to crop tolerance to *P. thornei* rather than a decline in soil nitrogen fertility, as originally suggested.

In the late 1970s, Queensland grain grower, Mr Alex Gwynne, asked Dr John Thompson to determine the cause of poor yield of wheat when grown as the second crop after long fallow, compared to barley which yielded up to three times that of wheat (J.P. Thompson, Toowoomba, 2020, personal communication). Subsequently, *P. thornei* was shown to be the cause — building up on the first wheat crop to severely damage the second. Mr Gywnne's insight revealed differences in tolerance between cultivars of wheat and barley and to this day he and his family continue to support research on their farm to help counteract the economic consequences of *P. thornei.* Mr Gwynne's advice to all growers in the region is 'Assume that you have these

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© CAB International 2022. *Integrated Nematode Management: State-of-the-art and visions for the future* (eds R.A. Sikora *et al.*)
DOI: 10.1079/9781789247541.0002

nematodes and grow the most tolerant wheat cultivar available' (A. Gywnne, West Prairie, 2012, personal communication).

In 2009, the estimated annual potential cost of lost wheat yields in the region was AU$104 million (Murray and Brennan, 2009). The use of tolerant cultivars and crop rotation reduced the estimated actual cost to AU$38million. In 2018, a new economic analysis (Brennan and Murray, unpublished) estimated this cost to be AU$31 million based on the increased use and availability of tolerant wheat cultivars. For example, in 2010, 21% of bread wheat cultivars recommended for the region were moderately tolerant whereas in 2020, 52% were moderately tolerant or more so.

There is a negative linear relationship between yield of wheat cultivars and *P. thornei* population densities measured at sowing (Thompson *et al.*, 2012; Owen *et al.*, 2014). The degree of yield loss is greatest for cultivars that are intolerant and susceptible compared to cultivars that are tolerant and moderately resistant (Whish *et al.*, 2017). Yield loss of intolerant wheat cultivars is expected in all seasons, but the extent varies with site and seasonal conditions.

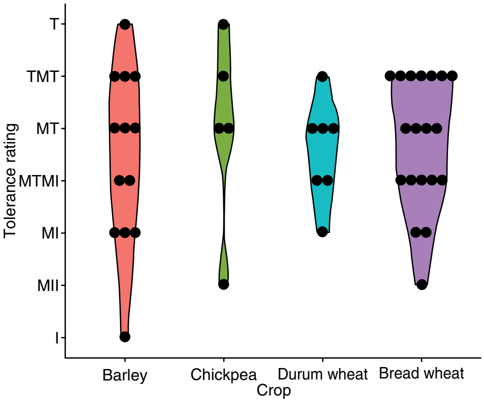


Fig. 2.1. The range and number (indicated by black circles) of cultivars within each *Pratylenchus thornei* tolerance category of commercial cultivars of barley, chickpea, durum wheat and bread wheat recommended for Queensland within the subtropical grain region of eastern Australia in 2020 (Albatross Rural Consulting (2019) 2020 Queensland winter crop sowing guide, available at www.nvtonline.com.au, accessed 13 August 2020). Categories are based on relative tolerance within a crop. T, tolerant; MT, moderately tolerant; MTMI, moderately tolerant–moderately intolerant; MI, moderately intolerant; I, intolerant. Author's own figure.

Host range

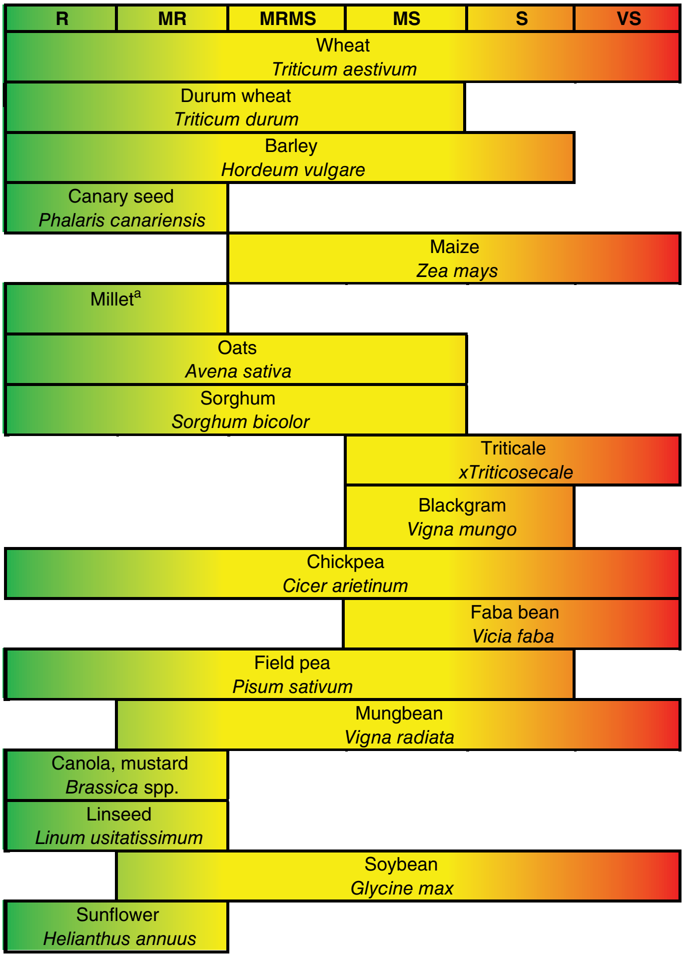
Pratylenchus thornei has a wide host range. The response of cultivars to infestation can be classified by their level of tolerance and resistance which are genetically independent traits. Each trait should be classified separately to maximize the effectiveness of INM. Tolerance is generally assessed in major crops and where there are tangible economic losses.

The diversity of both summer and winter crops grown in the subtropical grain region of eastern Australia is a double-edged sword for INM. Growers can plant non-host crops, such as grain sorghum, sunflower or oats, but susceptibility is high in most cultivars of many other profitable cereal and pulse crops, such as barley, chickpea or mungbean. Resistance and tolerance vary between cultivars within many crop species (Table 2.1 and Fig. 2.1). In response to these challenges, the Grains Research and Development Corporation funds a national programme of comparative crop variety testing called National Variety Trials. Ratings of tolerance and/or resistance to *P. thornei* of current cultivars and advanced lines of wheat, durum wheat, barley, chickpea, faba bean, field pea and oats are derived from repeated experiments and updated annually in consultation with breeding companies and researchers.

Distribution

The subtropical grain production region of eastern Australia covers an area of approximately 4 million ha between latitude 20–32°S (described in Thompson *et al.*, 2010). Typically, the soils are deep cracking clays called vertisols with a neutral to alkaline pH. In a survey of nearly 800 wheat fields in the region, *P. thornei* was more prevalent and abundant than *P. neglectus*. It was found in 67% of fields whereas *P. neglectus* was found in 32% (Thompson *et al.*, 2010).

Table 2.1. The range of resistance responses to *Pratylenchus thornei* of cultivars of grain crops grown in the subtropical grain region of eastern Australia. Author's own table.



		R	MR	MRMS	MS	S	VS
Cereals	Wheat *Triticum aestivum*	■	■	■	■	■	■
	Durum wheat *Triticum durum*	■	■	■	■		
	Barley *Hordeum vulgare*	■	■	■	■	■	
	Canary seed *Phalaris canariensis*	■	■				
	Maize *Zea mays*			■	■	■	■
	Millet[a]	■	■				
	Oats *Avena sativa*	■	■	■	■		
	Sorghum *Sorghum bicolor*	■	■	■	■		
	Triticale *xTriticosecale*				■	■	■
Pulses	Blackgram *Vigna mungo*				■	■	
	Chickpea *Cicer arietinum*	■	■	■	■	■	■
	Faba bean *Vicia faba*				■	■	■
	Field pea *Pisum sativum*	■	■	■	■	■	
	Mungbean *Vigna radiata*		■	■	■	■	■
Oilseeds	Canola, mustard *Brassica* spp.	■	■				
	Linseed *Linum usitatissimum*	■	■				
	Soybean *Glycine max*		■	■	■	■	■
	Sunflower *Helianthus annuus*	■	■				

R, resistant; MR, moderately resistant; MRMS, moderately resistant–moderately susceptible; MS, moderately susceptible; S, susceptible; VS, very susceptible.

[a] *Panicum miliaceum*, *Echinochloa* spp., *Pennisetum glaucum*, *Setaria italica*.

Symptoms of damage

In wheat, *P. thornei* causes symptoms of lower leaf yellowing, decreased tillering, poor canopy closure and generally unthrifty plants (Fig. 2.2). These symptoms are associated with intolerance/tolerance responses, decreased N and P concentrations of the plant tops, decreased tillering and biomass, and grain yield loss (Thompson *et al*., 2012). Recently, the normalized difference vegetation index of plant greenness was shown to be highly correlated with tolerance to *P. thornei* when measured at approximately 'early boot' development stage (Robinson *et al*., 2019).

Biology and life cycle

The survival and reproduction of *P. thornei* is favoured by the soil types and cropping systems of the subtropical grain region of eastern Australia. Rainfall is summer dominant; however, both

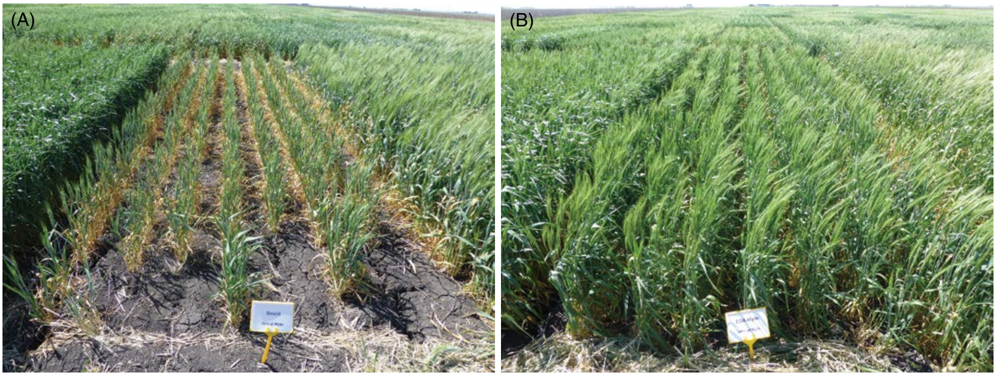


Fig. 2.2. Symptoms of *Pratylenchus thornei* infestation of **(A)** an intolerant wheat cultivar compared to **(B)** a tolerant cultivar. Author's own photographs.

summer and winter crops can be grown because the soils have a high capacity for storing water during weed-free fallow periods. *Pratylenchus thornei* passes through several generations during growth of a wheat crop. The rate of reproduction in the roots and final population densities are controlled by genotype and the environment (Thompson *et al.*, 2015). The maximal intrinsic rate of nematode population growth is genetically controlled in wheat and resistance mechanisms are likely to be produced constitutively and act post-penetration of *P. thornei*. Soil temperature strongly influences the reproduction rate of *P. thornei* with the optimum between 20–25°C, very slow reproduction at 15°C and none at 30°C (Thompson *et al.*, 2015). By modelling soil temperatures, Thompson (2015) demonstrated that sowing as early as possible, within the recommended sowing window, would allow wheat roots to establish before nematode infestation; the yield of an intolerant cultivar was predicted to increase 61% by sowing 4 weeks earlier.

Pratylenchus thornei can occur throughout the soil profile, with peak population densities found at differing depth intervals dependent on prior cropping history and seasonal conditions (Owen *et al.*, 2010; Whish *et al.*, 2017). Population densities averaged over 0–90 cm soil depth are a more reliable predictor of grain yield loss than shallower or deeper samples (Owen *et al.*, 2014). Increases in populations deep in the soil profile after fallow periods may be due to nematode movement in percolating water after substantial rainfall (Owen *et al.*, 2014; Whish *et al.*, 2017).

Populations decrease more quickly in the topsoil than deeper in the soil profile during fallows or when non-hosts are grown (Whish *et al.*, 2014). The decline of *P. thornei* is related to the rate at which soil dries and temperature (Thompson *et al.*, 2015). In soil subjected to quick drying, a greater proportion of J4 nematodes survived compared to other nematode life stages (Thompson *et al.*, 2017).

Interactions with other nematodes and pathogens

Understanding the interaction of *P. thornei* with soil-borne pathogens and arbuscular mycorrhizal fungi (AMF) is an emerging discipline in the region. Yield loss of wheat was exacerbated when crown rot (caused by *Fusarium pseudograminearum* and *F. culmorum*) was also present with *P. thornei* (J.P. Thompson, Toowoomba, 2005, personal communication; S. Simpfendorfer, Tamworth, 2012, personal communication). In contrast, the biomass and yield of wheat was dependent on AMF colonization in a very dry season despite *P. thornei* being present at damaging levels of up to 5/g soil (Owen *et al.*, 2010).

Recommended integrated nematode management

There are five strategies recommended for the management of *P. thornei* in the subtropical grain region of eastern Australia.

1. Identify genus, species and population density of plant parasitic nematodes in soil samples.

Retesting is recommended at the end of a cropping sequence if flooding has occurred or if susceptible crop species have been grown. Currently, a quantitative molecular test is available from a commercial testing service, PREDICTA®B. *Pratylenchus thornei* levels are determined from a 500 g sample consisting of soil and roots collected from approximately 15 locations in a field or production zone at 0–15 cm soil depth.

2. Grow a cultivar with the highest level of tolerance and resistance available, especially for wheat.

3. Grow two or more resistant crops consecutively to reduce population densities to <1/g soil.

4. Sow wheat as early as possible within the recommended sowing window.

5. Promote adoption of INM through regularly updated free crop growing guides providing cultivar ratings of tolerance and/or resistance, and presentations at industry symposia, workshops and field days attended by growers and agronomists.

There is high uptake of the recommended strategies for INM of *P. thornei*, particularly growing of tolerant wheat cultivars because of the immediate economic benefit, the reliability and stability of the tolerance trait and the low cost of cultivar selection. Through extension, growers and their advisers understand the importance of testing soil because of the unique responses of cultivars within each crop to each *Pratylenchus* species found in the region. Additionally, there is an openness and acceptance of a common problem that all growers face because *P. thornei* is widespread.

Disadvantages of the current INM that can decrease acceptance are:

- extended time taken to reduce nematode population densities by growing resistant crops;
- broad host range of *P. thornei* and the limited number of resistant cultivars of crops that can be profitably marketed;
- susceptibility of all major pulse crops;
- cost of the soil tests;
- sporadic publication of ratings of resistance/ tolerance of crops such as sorghum, maize and sunflower;
- subtle or no symptoms in susceptible crops and relatively minor yield loss (<10%); and
- absence of registered, effective and economical nematicides for rapid control of *P. thornei* throughout the soil profile.

Optimization of nematode management

None of the current INM strategies eliminate *P. thornei*, especially where there is a reliance on tolerant, but susceptible, cultivars. Ideally, breeding programmes should be expanded to include all crops grown in the region, particularly chickpea, faba bean and mungbean, and should mimic the success of wheat breeding to release cultivars with tolerance and resistance to *P. thornei*. Complementary research seeking novel sources of resistance, improved markers to select for these traits and optimization of phenotyping methods are needed. Additionally, ratings of tolerance/ resistance should be produced for all new and current cultivars of all crops grown in the region.

Expansion of markets to encourage diversity of crops with resistance to *P. thornei* are required. For example, crops with a limited local requirement but potential export markets, such as millet and panicum, pigeon pea (*Cajanus cajan*), linseed (*Linum usitatissimum*) and safflower (*Carthamus tinctorius*).

Agronomic approaches should also be considered. Cover crops with resistance to *P. thornei* and low water use should be incorporated into fallow periods to increase the diversity of the soil biology to take advantage of natural antagonists of *P. thornei*, greater levels of soil carbon and maintenance of AMF. Improving the frost tolerance of wheat would allow earlier sowing so that roots grow in cool soils (ideally <15°C). Additional strategies to immediately decrease *P. thornei* population densities and improve plant health are needed. This may include products which are already available for other nematode/ crop systems that prime plant defence mechanisms and protect entire root systems.

Future research requirements

Wheat breeding has been the saviour of the industry for management of *P. thornei* in the low input farming systems of the region and therefore should continue to be expanded. Effective genes for resistance to *P. thornei* in landraces, synthetic hexaploids and wild relatives of wheat have been discovered and these need to be bred into cultivars. The incorporation of other traits which offer drought tolerance may further improve tolerance and resistance to *P. thornei*, for example, selection of germplasm which favours root colonization by AMF. Understanding the mechanism of tolerance and resistance in wheat could offer new genes for selection of breeding material. Release of cultivars with tolerance and resistance to *P. thornei* and major soil-borne diseases, such as crown rot (*F. pseudograminearum* and *F. culmorum*) and common root rot (*Bipolaris sorokiniana*) will further improve wheat production.

Other relatively low-cost options to supplement current INM should include seed treatments or in-furrow application of products that are developed specifically for migratory nematodes such as *P. thornei*. These products may activate plant defences, stimulate root growth, and promote diversity of soil biology. Protection of plants throughout the season is critical in the design of future products.

Adaptation of extension material to take advantage of technology to improve ease of use is required. Linking results from soil tests to apps using models which incorporate temperature, rainfall, other diseases and the presence of abiotic stressors could be used to optimize strategies for specific farming systems within fields.

Outlook: anticipating future developments (2050+)

Climate change is likely to cause increased temperatures and drought, and fewer frost events which will impact wheat production in rain-fed farming systems of Australia. Higher temperatures, particularly for winter-grown crops, may increase the reproduction of *P. thornei* but decrease survival in hot topsoils (Thompson *et al.*, 2018). With fewer frosts, the recommended sowing window may expand to earlier in the season; however, if soil temperatures increase, sowing wheat early in the season may become a less effective strategy.

The distribution and impact of *P. thornei* in Australian wheat regions may increase in the cooler, temperate southern regions. Currently, yield loss from *P. thornei* in wheat in these regions is less severe and infrequent compared to the subtropical region despite population densities being similar, if not greater, than in the subtropical region.

Conservation agriculture, which incorporates stubble retention, zero and minimum tillage and herbicides is widely practiced in rain-fed faming systems of Australia. However, globally there is a desire to decrease chemical usage in agriculture. Without herbicides, fallow periods may become weedier, resulting in increased tillage and burning to control weeds. Adaption of INM to new farming systems may be required, particularly if weeds are susceptible to *P. thornei* and soil carbon and biology are negatively affected. Alternatively, if pasture phases were introduced, there may be changes in population dynamics of *P. thornei*, depending on the host status of pasture species, and the subsequent positive effects on soil chemistry and biology.

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