

Links between soilborne pathogens, plant parasitic nematodes, farm management and biophysical constraints in a southern Australian rainfed cropping system

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ABSTRACT

Context. Rotations in rainfed farming systems of southwest Australia have shifted towards intensified cropping and it is necessary to reassess soilborne pathogens and plant parasitic nematodes within this context. Aims. We tested the hypothesis that these recent changes in rotations and agronomy have altered the efficacy with which rotations reduce the incidence of common root pathogens and plant parasitic nematodes. Methods. We tracked changes in common pathogen DNA in soil and the incidence and severity of crop root damage in 184 paddocks, over 6 years from 2010 to 2015, and related this to farmer practices. Key results. Overall, severe root damage was rare, with 72% of plant samples showing no damage or only a trace and only 1% severely damaged. We found that the reduction of paddocks in pasture and resultant very low weed populations, combined with early sowing, reduced persistence of pathogens and nematode pests. But some aspects of crop management had the opposite effect: high rates of herbicide, increased frequency of cereals and canola at the expense of lupin and increased N fertiliser use. Conclusions. Current agronomic practices and the frequency of non-host crops in rotations appear to be effective in controlling common root pathogens and plant parasitic nematodes. But the aspects of agronomic management that increased populations of pathogens should be applied cautiously. Implications. Studies such as this that link multiple productivity constraints, such as pathogens and nematode pests, weeds and nutrients, to management practices are important to understand the sustainability of current or proposed production methods.

Keywords: agronomy, crop pathogens, crop rotation, crown rot, rainfed, rhizoctonia bare patch, root lesion nematode, take all.

Introduction

The most widespread and economically important soil root pathogens or plant parasitic nematodes of grain production in southwest Western Australia (WA) are Fusarium pseudograminearum and Fusarium culmorum complex (crown rot), Gaeumannomyces graminis var. tritici (take all), Pratylenchus neglectus, Pythium clade F. and Rhizoctonia solani Anastomosis Group (AG) 8 (rhizoctonia bare patch), (Riley and Kelly 2002; Vanstone 2002; Murray and Brennan 2009a, 2009b; Thomas et al. 2010; Khangura et al. 2013). These pathogens and nematode pests have been estimated to cause yield losses in wheat (Triticum aestivum) of AUD234 million per annum and AUD60 million per annum in barley (Hordeum vulgare) (Murray and Brennan 2009a, 2010) throughout Australia.

The 14 million hectares of mixed crop and pasture farms in southwest Australia, with a rainfed Mediterranean-type climate, supplied ~30% of Australia's broadacre grain over the period of this study (2010-2015) (ABS 2016).

Increasingly in dryland cropping areas throughout the world, including southwest Australia, the practise of stubble retention has been adopted. Some of the reasons this occurred were because herbicide (FAO 2020b) and nitrogen fertiliser (FAO 2020a) usage increased and tillage was utilised less for weed control and to mineralise nitrogen.

This trend has continued with various forms of reduced tillage seeding machinery being widely adopted (Llewellyn *et al.* 2012; Llewellyn and Ouzman 2019) and due to increasing environmental concerns and regulation around the burning of crop residues, as shown by Abdurrahman *et al.* (2020).

Increased stubble retention has resulted in increased water use efficiency and provided a range of other benefits such as reduced soil erosion and improved soil structure (Derpsch et al. 2010; Fisher and Hobbs 2019), but has also been reported to increase the prevalence of root and stubble borne plant pathogens (Bockus and Shroyer 1998; Paulitz et al. 2002, 2006; Kirkegaard et al. 2011). There are several documented cases of minor pathogens becoming prominent under these faming systems throughout the 1970s and 1980s, i.e. R. solani (MacNish 1985; Weller et al. 1986; Pumphrey et al. 1987; Paulitz 2006), G. graminis (Cotterill and Sivasithamparam 1989), tan spot (Septoria tritici) (Bockus and Shroyer 1998) and Pythium spp. (Cook et al. 1980).

Historically crop and pasture rotations have also been a major influence on soilborne pathogens and nematode pests. A pertinent example is the southern Australian ley farming systems of the 1970s, when intensive cereal production intermixed with grassy pasture resulted in *G. graminis* outbreaks causing ~40% yield loss in wheat in higher rainfall regions (>350 mm long term average growing season rainfall) (Cotterill and Sivasithamparam 1989; Kirkegaard *et al.* 2011). This continued until the disease cycle was broken by using grass selective herbicides and more diverse rotations, including legume break crops (Anderson *et al.* 2005).

More recently a shift towards cropping rather than sheep production, due to commodity price fluctuations, improved economies of scale and technological advances in crop production (Kirkegaard *et al.* 2011), triggered a heavy reliance on herbicides, leading to the evolution of weeds resistant to herbicides (Heap 2020). The widespread occurrence of herbicide resistant weeds in southwest Australia (Walsh *et al.* 2007; Owen and Powles 2009; Owen *et al.* 2014; Heap 2020) has made weed control more difficult to achieve and one response by farmers has been to increase production of crops in which weeds can be more effectively controlled (Harries *et al.* 2020).

Between 2000 and 2015, the area per farm dedicated to pasture declined by up to 30% in some agroecological zones of southwest Australia and sheep numbers declined from 26 to 14 million head (Planfarm and Bankwest 2016). The area sown to wheat, barley and canola (*Brassica napus*) increased in the period 2000 to 2016 by 0.7, 0.3 and 0.7 million hectares respectively, while grain legume crop area declined by 0.73 million hectares. This has resulted in substantial changes to rotations (Harries *et al.* 2015) and associated agronomy.

These changes in rotations not only directly impact soil pathogen populations, due to changes in the frequency of production of host crops, but also indirectly impact pathogen populations as a result of changes to other aspects of the agroecosystem, i.e. alternative host populations and nitrogen and water supply. The investigation of these interrelationships is often constrained by a lack of data linking biophysical changes to agronomic management at the field level (Lacoste 2017; Peterson *et al.* 2018).

We tested the hypothesis that these recent changes in rotations and agronomy have altered the efficacy with which rotations reduce the incidence of common root pathogens and nematode pests. We do this by tracking changes in common pathogen DNA in soil and the incidence and severity of root damage in paddocks, over 6 years from 2010 to 2015, and relating this to farmer practices within these paddocks.

Data sources

Data were accessed from the Focus Paddock dataset, which paired records of biophysical measurements of weeds, soilborne diseases and parasitic nematodes, and soil chemical and physical properties to land management actions from the same paddocks from 2010 to 2015. Paddocks were selected by targeting two or three soil types on each farm, which were common to the area. At face-toface interviews instructions were given to farmers that they should identify paddocks that reflected the majority of paddocks on the farm, not to select either their poorest or best performing paddocks. In total 184 paddocks were selected, providing 1017 paddock-years, after accounting for missing data; geographically 346 in the Central Agricultural Region (CAR), 416 in the Northern Agricultural Region (NAR) and 255 in the Southern Agricultural Region (SAR) (Fig. 1).

All field measurements were from a geo-referenced one-hectare area within each paddock. Farmers who managed the paddocks were interviewed annually, providing information on land use and agronomic inputs, and insights into management rationale. Wheat was grown in all paddocks in the first year of monitoring, followed by farmer-specified land uses in the following years. Climate data were obtained for each paddock using the SILO (Scientific Information for Land Owners) database (Jeffrey *et al.* 2001).

Soilborne pathogen DNA concentrations within soil

To assess levels of fungal plant pathogens and plant parasitic nematodes within the soil, the one-hectare area was divided into four nested replicates of 25 m by 100 m and soil was sampled in a zig-zag transect through each. Samples were taken on the previous crop row, where evident, twice per year, prior to seeding (February–April) and at anthesis (Zadoks 65) (August–October) (Zadoks *et al.* 1974), with 44 cores (11 from each replicate pooled) taken to a depth

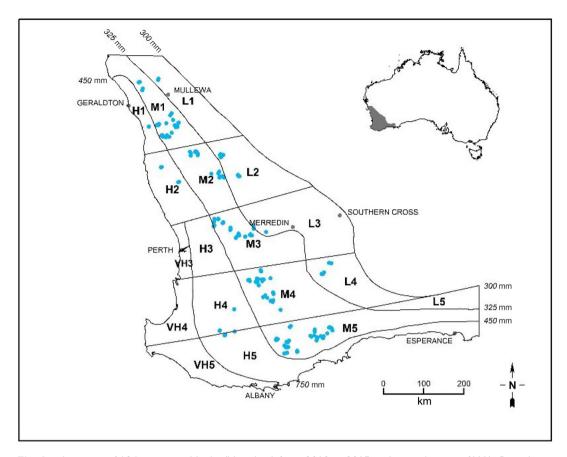


Fig. 1. Location of 184 survey paddocks (blue dots) from 2010 to 2015 in the south-west of WA. Boundaries depict Western Australian Department of Primary Industries and Regional Development (DPIRD) agroecological zones according to rainfall. Letters refer to rainfall zones: VH, very high; H, high; M, medium; L, low. Numbers refer to regions Northern (1 and 2), Central (3 and 4) and Southern (5) Agricultural Regions. Note the 300 mm isohyet does not represent the geographic extent of crop production, i.e. paddocks in L1 and L2 were at the eastern fringe of the production area. Very high rainfall areas support different, more intensive, farming systems.

of 10 cm, without clearing the soil surface of stubble, using a 1 cm diameter Accucore[®] soil probe. This sampling procedure ensured that soil samples contained some plant residues and roots. Overall, 1751 DNA assays of each pathogen were matched to land uses, with 947 assays taken in autumn (pre-sowing) and 804 in spring (in crop or pasture). Samples were taken prior to 59 barley crops, 137 canola crops, 68 lupin (Lupinus angustifolius) crops, 122 pastures, 533 wheat crops and 28 other land uses, which comprised of chickpea (Cicer arietinum), faba bean (Vicia faba), fallow (chemical fallow sprayed in spring), field pea (Pisum sativum), oat (Avena sativa), oaten hay and vetch (Vicia spp.). These soil samples were air dried in a laboratory, if wet, and sent immediately to a commercial laboratory (the South Australian Research and Development Institute, Urrbrae, South Australia) for DNA analysis, using the widely tested and used PREDICTA B® assay (Hollaway et al. 2003; Ophel-Keller et al. 2008; Wicks et al. 2011; Poole et al. 2015; Hay et al. 2016). We present data of ten pathogens and nematode pests or complexes analysed for DNA content in soil: *Didymella pinodes* and *Phoma pinodella*, (black spot of field pea), *Ditylenchus dipsaci* (stem nematode), *F. pseudograminearum* and *F. culmorum* (crown rot), *G. graminis* var. *tritici* (take all), *Heterodera avenae* (cereal cyst nematode), *P. neglectus*, *P. quasitereoides*, *P. thornei*, *Pythium* Clade F., and *R. solani* (AG-8).

Soil DNA results are presented in three ways. First, results are reported as frequency of results within disease risk categories defined for the PREDICTA $B^{\mathbb{G}}$ assay, which predicts crop yield loss based on autumn DNA concentrations in soil, $\log_{10}(x+1)$ transformed, for fungal pathogens and eggs of the cyst nematode, or on copies per gram of soil for root-lesion nematodes (Table 1). Second, results are shown as incidence of assays above the DNA detection limit, low risk or above (Table 1). Third, results are indicated using the DNA concentration reported from the assay, to obtain more precise analysis of pathogen DNA soil concentrations.

Table 1. Risk category for potential yield loss in the following sown crop based on PREDICTA B assay (SARDI 2020).

Pathogen/nematode pest	Amount of pathogen or nematode detected and (potential % yield loss)								
Risk category	Below detection	Low	Medium	High					
D. dipsaci ^B (nematodes/g)	<0.5	<5.0	<10	>10					
D. pinodes, P. pinodella (log pg DNA/g)	<1.2 (0-5)	1.2-2.0 (5-10)	2.0-2.5 (10-20)	>2.5 (>20)					
Fusarium spp. (log pg DNA/g)	<0.6 (0-5)	0.6-2.0 (0-10)	2.0-2.5 (5-30)	>2.5 (15–60)					
G. graminis var. tritici ^A (log pg DNA/g)	<0.8 (<1)	0.8-1.1 (10)	1.1–2.0 (10–44)	>2.0 (>44)					
H. avenae (eggs/g)	<0.05 (0–5)	1.0-5.0 (5-25)	5.0-10 (25-50)	>10 (>40)					
P. neglectus (nematodes/g)	<0.1 (0)	0.1-5.0 (<10)	5.0-25 (5-20)	>25 (10–40)					
P. quasitereoides (nematodes/g)	0.1	0.1-20	20–60	>60					
P. thornei ^C (nematodes/g)	0.1	0.1-15	15–60	>60					
Pythium clade F. ^C (log pg DNA/g)	<0.6	0.6–1.4	1.4-2.0	>2.0					
R. solani AG-8 (log pg DNA/g)	<0.5 (0)	0.5-1.5 (0-10)	1.5-2.0 (5-20)	>2.0 (10–50)					

Note that predicted crop yield loss is for wheat except for *D. pinodes* and *P. pinodella*, where it is for field pea (*Pisum sativum*). Values in parenthesis, beside nematode/g or log pg DNA/g values, indicate the range in yield loss expected (%) for the respective risk category, i.e. for *G. graminis* var. *tritici* 0.8–1.1 log pg DNA/g is estimated to cause 10% yield loss in 10–30% of paddocks. For crown rot separate qPCR tests results for *F. pseudograminearum* (Test 1 and Test 2) and *F. culmorum* were summed prior to log transformation.

Visual assessment of pathogen damage to crop and pasture roots

To assess plant root and crown damage caused by root pathogens and nematode pests, 40 whole plants (10 per nested replicate) were taken from the hectare area in the same zig-zag pattern described above for soil samples. This was done twice each year from 2010 to 2014 inclusive: firstly in autumn or winter when plants were in the vegetative stage (Zadoks 1 for wheat), or the equivalent growth stage for other species, and secondly in spring, at anthesis (Zadoks 65 or equivalent). The number of plants from each paddock displaying root or crown damage symptomatic of Fusarium spp., G. graminis var. tritici, P. neglectus and R. solani (AG-8) were recorded. An overall rating of percentage severity of root damage (SRD) caused by all pathogens and nematode pests combined was given on a 0–5 scale: 0 (no disease), 1 = 1-5%(trace disease), 2 = 6-25% (low amount of brown lesions), 3 = 26-50% (medium amount of brown lesions, similar amounts of healthy and necrotic), 4 = 51-75% (most of the roots covered in brown lesions, little healthy root left) and 5 = 76-100% (all or nearly all roots covered in brown lesions or short brown stumps), similar to the method of McDonald and Rovira (1985).

Overall plant samples were taken from 1289 field visits, with 634 taken at the vegetative development stage from 51 barley crops, 72 canola crops, 52 lupin crops, five pastures, 439 wheat crops and 15 other land uses, and the remaining 655 samples taken at anthesis from a similar break-up of land uses.

Plant observations are presented in three ways. Firstly, the incidence of symptoms caused by *Fusarium* spp., *G. graminis*,

P. neglectus and *R. solani* (AG-8) is reported, expressed as % of field visits from which symptoms were observed on roots of at least one of the 40 plants sampled. Secondly, the frequency of diseased plants in each 40-plant sample is shown, expressed as percentage of plants. Thirdly, the severity of disease is presented, expressed as SRD, as described above.

Statistical analysis

Binomial logistic regressions were conducted as single regressions, one predictor at a time, to test whether the incidence of positive DNA test results and incidence of paddock-years with root disease observed were related to each of the variates presented in Table 2. For the economically important pathogens and nematode pests, for which we had both DNA and root disease symptom observations (Fusarium spp., G. graminis var. tritici, P. neglectus and R. solani), binomial generalised linear models, with multiple predictors, were developed to predict the likelihood of paddocks having DNA above the detection limit or root disease symptoms in spring. We used data collected in spring for these analyses to capture effects of crop management. Optimisation of models was based on the lowest Akaike Information Criterion via the R step function. The incidence of positive DNA test results, from both the Z1 and Z65 sampling times combined, was also assessed with Chi-squared tests of goodness of fit, to determine whether the incidence of DNA assays above detection of each of these pathogens and nematode pests were the same across the three regions, and 6 years, of the survey.

Differences in concentration of DNA in soil among independent variates (Table 2) in both autumn and spring

^AYield losses are expected from these DNA levels in 10-30% of paddocks.

^BYield loss of 5–20% for broadleaf crops and of 5–80% for oats.

^CTests under development and reported as relative population density categories, not yield risk categories.

Table 2. Independent variables used in binomial logistic regressions of incidence of paddocks with DNA above detection or plant root symptoms of *R. solani* (AG-8), *G. graminis* var. *tritici*, *Fusarium* spp. and *P. neglectus*.

Variate	Unit
Summer rain	mm
Annual rain	mm
Growing season rain	mm
January–March rain	mm
April-June rain	mm
July-September rain	mm
Growing season temperature	°C
January-March temperature	°C
April-June temperature	°C
July-September temperature	°C
Sow day	Julian day of year
Number of herbicides applied	n
Weed density in spring	(plants/m²)
Fertiliser N	(kg/ha)
Soil mineral N (0-10 cm)	(mg/kg)
Soil P (0–10 cm)	(mg/kg)
Soil K (0–10 cm)	(mg/kg)
Organic carbon	(%)
Electrical conductivity (0–10 cm)	dS/m
pH (0–10 cm)	CaCl ₂
Soil texture	(1-5) ^A

ASoil texture bolus ribbon length method: I = sand little ribbon coherence, 1.5 loamy sand 5–15 mm ribbon, 2.0 loam 20–25 mm ribbon, 2.5 clay loam 45–50 mm ribbon, 3.0 clay 60–65 mm ribbon, 3.5 = heavy clay 75 mm + ribbon (Schoknecht and Pathan 2013).

were assessed using ANOVA. To account for positive skewed distribution, DNA data for *D. pinodes* and *P. pinodella*, *D. dipsaci*, *Fusarium* spp., *G. graminis var. tritici*, *Pythium* Clade F., and *R. solani* (AG-8) were transformed using $\log_{10}(x+1)$ prior to ANOVA. If ANOVA indicated overall difference ($P \leq 0.05$), *t*-tests and their pairwise comparisons or TukeyHSD tests were applied. Paired *t*-tests, based on individual paddocks, were made to determine if changes in soil DNA concentration from autumn to spring were statistically significant. Root and crown disease data were assessed in the same manner as soil DNA concentration, using ANOVA and Tukey HSD tests.

Results

Climatic conditions

Western Australia has a Mediterranean-type climate in which the grain growing season occurs between May and November. There were large differences in rainfall between years and regions with 2010 and 2011 being the years with greatest contrast (Fig. 2); annual rainfall ranging from 196 mm for the CAR in 2010, to 546 mm for the SAR in 2011 (Fig. 3).

DNA assay results

DNA concentrations within PREDICTA B risk levels

Averaged across all pathogens and nematode pests, 70% of assays were below the detection limit, 20% low, 7% medium and 3% high disease risk (Fig. 4). Because *H. avenae* and *D. dipsaci* were not detected and <1% of *P. thornei* and *P. quasitereoides* were within medium and high-risk categories, statistical analyses of these pathogens and nematode pests were limited. Incidence of DNA in the high yield loss category was greatest (13%) for *D. pinodes/P. pinodella*, pathogens that cause blackspot of field pea. Approximately 7% of *Fusarium* spp. and *R. solani* (AG-8) autumn DNA tests were in the high yield loss category, while all other pathogens and nematode pests were below 3.4% (Fig. 4). The incidence of paddocks with DNA below detection for each pathogen or parasitic nematodes in spring were similar to autumn (data not presented).

Incidence of DNA assays above detection limit

There were large differences in the incidence of DNA assays above detection between pathogens and nematode pests for the total of autumn and spring samples, i.e. *D. dipsaci* and *H. avenae* were not detected, compared to *Pythium* spp. detected in 86% of samples. Apart from *D. dipsaci* and *H. avenae* the incidence of DNA detected of each pathogen, except *Pythium* spp., differed between regions (Table 3). For six of the eight species detected incidence was lowest in the NAR, and for six highest incidence occurred in the SAR. Hence, in general, SAR paddocks had a higher incidence of soil DNA concentrations above detection, although there were some exceptions, including the CAR with the highest detections of *P. quasitereoides* and *P. thornei*.

The incidence of most pathogens and nematode pests remained stable over the years of the survey, with the exceptions of highly significant increases for *Fusarium* spp. and *G. graminis* var. *tritici*, and there was also an increasing trend for *P. neglectus* but this was not significant (Fig. 5).

Binomial logistic regressions of incidence of pathogen DNA in spring against environmental and management variates showed that for *Fusarium* spp., *G. graminis* var. *tritici*, *P. neglectus* and *R. solani* (AG-8) there were highly significant (P < 0.001) effects of air temperature and soil organic carbon (%). The negative coefficients in the regressions of temperature variates meant that lower temperature was related to a higher probability of DNA levels being above detection limit, while the positive coefficient for organic carbon indicate more organic carbon was related to higher probability of DNA above detection (Table 4).

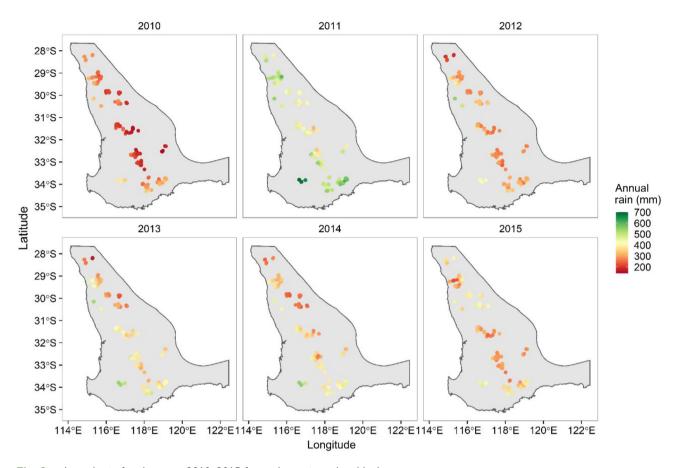


Fig. 2. Annual rain for the years 2010–2015 for each monitored paddock.

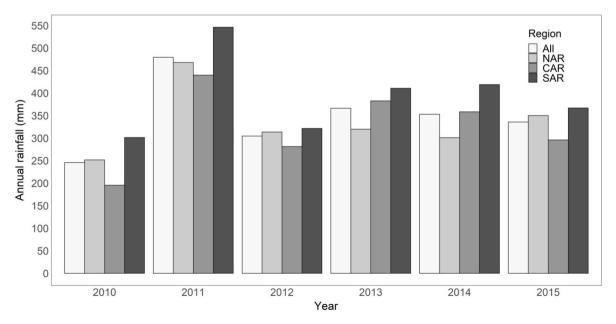


Fig. 3. Annual rainfall (mm) for southwest Australia (all regions combined), and regions within southwest Australia, including the Northern Agricultural Region (NAR), Central Agricultural Region (CAR) and Southern Agricultural Region (SAR), for the years 2010–2015.

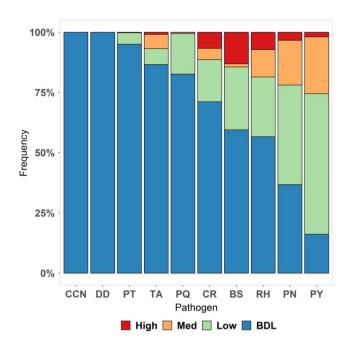


Fig. 4. Frequency of pathogen DNA concentration assays, taken at Visit I (autumn), within PREDICTA B® disease risk yield loss categories (BDL = below detection limit, Low, Med = medium, High), for CCN (cereal cyst nematode, *H. avenae*), DD (stem nematode, *D. dipsaci*), PT (*P. thornei*), TA (take all, *G. graminis* var. *tritici*), PQ (*P. quasitereoides*), CR (crown rot, *Fusarium* spp.), BS (black spot, *D. pinodes/P. pinodella*), RH (*R. solani* AG-8), PN (*P. neglectus*) and PY (*Pythium* Clade F). Note Pythium (PY) and (PT) *P. thornei* tests are under development and categories represent population density not disease risk.

More summer rain, in the period between growing seasons, was associated with increased frequency of DNA of *Fusarium* spp., *P. neglectus* and *R. solani* (AG-8) but not *G. graminis* var. *tritici.*, while January–March rain was not significant (P > 0.242). This occurred because summer rain was

calculated from the date of crop maturity in the previous year and averaged 84 mm, compared to January–March rain which averaged 48 mm. Hence rain in October–December increased the frequency of DNA detection. Soil texture was also significant (P < 0.05); *G. graminis* var. *tritici* and *R. solani* (AG-8) DNA was more frequently detected on finer textured soils, and *Fusarium* spp. and *P. neglectus* on sandier soils. Other factors of note were that higher soil N, P and S concentration resulted in more frequent *P. neglectus* DNA and in paddocks with more weeds there was more frequent detection of *Fusarium* spp., *R. solani* (AG-8) and *P. neglectus* DNA (Table 4).

DNA concentration

When sampled in autumn the soil concentrations of all pathogens and P. neglectus were greater ($P \le 0.05$) in the SAR than the CAR and NAR (Fig. 6). The same was found from spring sampling, with the exceptions of P. neglectus in the NAR not being different to the SAR (P = 0.076) and D. pinodes/P. pinodella in the CAR not being different to the SAR (P = 0.370), data not presented. There were no differences (P > 0.05) in soil DNA concentration of G. graminis, Fusarium spp. and R. solani between the NAR and CAR in both autumn and spring. There were differences between these regions ($P \le 0.05$) for Pythium spp. and D. pinodes/P. pinodella in both autumn and spring and for P. neglectus there was a difference (P < 0.05) in autumn but not in spring.

Of all the land uses, when sampled in autumn, pastures contained the greatest DNA concentration for each pathogen assessed, with concentrations greater, ($P \le 0.05$) than some of the other land uses for all pathogens and nematode pests (Fig. 7). Interestingly for *P. neglectus*, canola, which is a host, was sown into paddocks with higher autumn DNA concentration than lupin, despite lupin being a non-host, as indicated by the reduction ($P \le 0.024$) of *P. neglectus* DNA

Table 3. Incidence of DNA assays above detection limit (%) for eight pathogens or plant parasitic nematodes within three agricultural regions of southwest WA: northern agricultural region (NAR), central agricultural region (CAR) and southern agricultural region (SAR), for the total of autumn and spring soil samples.

Pathogen/nematode		χ				
	All	NAR	CAR	SAR		
	n = 1788	n = 743	n = 632	n = 413		
D. pinodes, P. pinodella	40	9	59	67	P < 0.001	
Fusarium spp.	30	15	19	72	P < 0.001	
G. graminis var. tritici	15	13	6	31	P < 0.001	
P. neglectus	65	51	66	90	P = 0.004	
P. quasitereoides	17	3	33	19	P < 0.001	
P. thornei	5	2	П	1	P = 0.002	
Pythium clade F.	86	75	91	98	P = 0.206	
R. solani AG-8	47	41	40	69	P = 0.004	

Note: D. dipsaci and H. avenae were not detected.

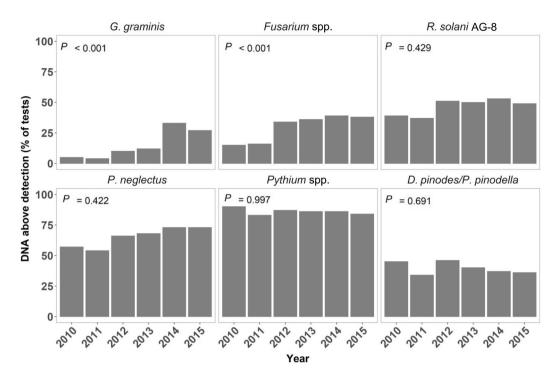


Fig. 5. Incidence of DNA assays above detection limit for five pathogens and a nematode pest for each year of the survey, total of autumn and spring soil samples. Inset Chi-squared *P* values indicate whether differences between years were statistically significant.

Plant observations

Incidence of field visits with disease observed

Plants displaying root disease symptoms (autumn and spring visits combined) of *Fusarium* spp. were observed from 6% of visits, *G. graminis* 24%, *P. neglectus* 58% and *R. solani* (AG-8) 65%. Root damage from all pathogens and nematode pests was more frequent in spring: *Fusarium* spp. observed in 10% of spring samples, *G. graminis* 39%, *P. neglectus* 62% and *R. solani* (AG-8) 72% (Table 5).

For the binomial logistic regression of root disease symptoms (presence/absence) fewer variate/pathogen combinations with a P value < 0.05 than for binomial

logistic regressions of DNA. In common with the DNA analysis there were highly significant (P < 0.001) effects of air temperature; greater incidence of plant root disease with lower temperatures for all pathogens/nematode pests except *Fusarium* spp. Higher soil N, P and S content resulted in greater frequency of paddocks with root damage from *P. neglectus*. In contrast to the DNA, less rainfall in various time periods, associated with negative coefficients in the regressions of rain variates, meant that lower rainfall was related to increased frequency of paddocks containing plants with damage symptoms of each pathogen. Also summer rain only affected the frequency of paddocks with plant damage caused by *G. graminis* var. *tritici* (Table 6).

Frequency of diseased plants in each 40 plant sample

In autumn the proportion of plants within the 40 plant sample with root or crown symptoms was 0%, 1.1%, 18.7% and 9.7% for *Fusarium* spp., *G. graminis*, *P. neglectus* and *R. solani* (AG-8) respectively. Root or crown damage occurred on more plants in spring; 10%, 39%, 62% and 72% of the 40 plant sample for *Fusarium* spp., *G. graminis*, *P. neglectus* and *R. solani* (AG-8) respectively. Hence for all pathogens few samples contained a large proportion of plants displaying symptoms (Supplementary material S3). The percentage of plants with symptoms of *Fusarium* spp., *P. neglectus* and *R. solani* (AG-8) increased with the number of wheat crops grown in succession, consequently the incidence of plants

Table 4. Binomial logistic regressions of pathogen DNA in soil in spring (absent or present) for environmental and agronomic variables.

Independent variate	R. solani	(AG-8)	P. neglectus		Fusarium spp.		G. graminis var. tritici	
	P value	Coef.	P value	Coef.	P value	Coef.	P value	Coef.
Rain								
Summer rain (mm)	0.018	0.004	0.001	0.007	0.000	0.008	0.170	0.004
Annual rain (mm)	0.574	0.000	0.579	0.000	0.163	0.001	0.988	0.000
Growing season rain (mm)	0.782	0.000	0.008	-0.002	0.320	-0.001	0.427	0.001
January–March rain (mm)	0.977	0.000	0.242	0.003	0.637	-0.001	0.793	-0.001
April–June rain (mm)	0.084	-0.004	0.001	-0.007	0.249	-0.002	0.364	-0.003
July-September rain (mm)	0.294	0.002	0.001	-0.005	0.018	-0.004	0.005	0.007
Temperature								
Growing season temperature (°C)	0.000	-0.164	0.000	-0.263	0.000	-0.379	0.000	-0.221
January-March temperature (°C)	0.000	-0.187	0.000	-0.306	0.000	-0.432	0.000	-0.230
April-June temperature (°C)	0.000	-0.174	0.000	-0.485	0.000	-0.532	0.001	-0.229
July-September temperature (°C)	0.002	-0.148	0.000	-0.354	0.000	-0.344	0.006	-0.189
Management								
Sow day	0.742	0.002	0.000	0.021	0.032	0.011	0.624	0.004
Number of herbicides applied	0.055	0.061	0.001	-0.111	0.053	-0.062	0.160	0.078
Weed density in spring (p/m ²)	0.001	0.001	0.022	0.001	0.000	0.001	0.337	0.000
Fertiliser N (kg/ha)	0.097	-0.006	0.913	0.000	0.002	-0.012	0.543	-0.004
Soil								
Soil mineral N (mg/kg 0-10 cm)	0.674	0.002	0.033	0.010	0.116	0.007	0.070	0.014
Soil P (mg/kg 0–10 cm)	0.003	0.013	0.000	0.041	0.000	0.039	0.183	0.009
Soil K (mg/kg 0–10 cm)	0.037	-0.00 I	0.490	0.000	0.012	0.001	0.214	0.001
Soil S (mg/kg 0–10 cm)	0.428	0.002	0.020	0.010	0.021	0.006	0.728	-0.001
Organic carbon (%)	0.000	0.395	0.000	0.797	0.000	0.819	0.000	1.265
Electrical conductivity (dS/m 0-10 cm)	0.140	1.409	0.000	5.436	0.000	5.121	0.801	0.372
pH (CaCl ₂ 0–10 cm)	0.601	-0.06 I	0.077	-0.216	0.027	-0.273	0.093	0.334
Soil texture (I-5) ^A	0.030	-0.362	0.032	0.404	0.012	0.419	0.047	-0.454

P values and coefficients (coef.) presented. Grey background indicates a significant effect at $P \le 0.05$.

ASoil texture: I = coarse texture (sand), 5 = fine texture (clay). Sow day = days since I January in each year, for volunteer pastures the first occurrence of 15 mm of rain over two or less days after I April was considered sow day. Summer rain = rain between crops or pastures. Models are presented in Supplementary material (S2).

with symptoms of at least one root pathogen also increased when paddocks were successively sown to wheat (Fig. 8).

Severity of root disease (SRD)

Most samples were rated as having low disease severity: 25% displayed no disease symptoms, 47% a trace, with only 1% with most roots diseased and none with all roots diseased, as per the 0–5 rating scale. Mean SRD from all samples (autumn and spring visits) was 0.69. The severity of root diseased was greater in wheat (0.84 \pm s.e.m. 0.03) and barley (0.84 \pm 0.09) than canola (0.11 \pm 0.03) and lupin (0.22 \pm 0.04); lower in the SAR (0.52 \pm 0.05) than the CAR (0.73 \pm 0.04) and NAR (0.74 \pm 0.03); and declined over the survey period, with a reduction in each subsequent year: 2010 (1.5 \pm 0.03), 2011 (0.95 \pm 0.12), 2012 (0.63 \pm 0.04), 2013 (0.43 \pm 0.04) and 2014

 (0.24 ± 0.02) . Severity of root damage did not increase in the second or third wheat crops in succession (Fig. 8).

Discussion

Overall incidence and severity of disease

Overall, our results showed that farmers are managing soilborne pathogens and plant parasitic nematodes effectively, with few instances of severe root disease. However, these organisms were distributed widely throughout the survey area, particularly *R. solani* (AG-8) and *P. neglectus*, and recent changes in rotations and agronomy have altered the efficacy with which rotations can be used to manage common soil pathogens.

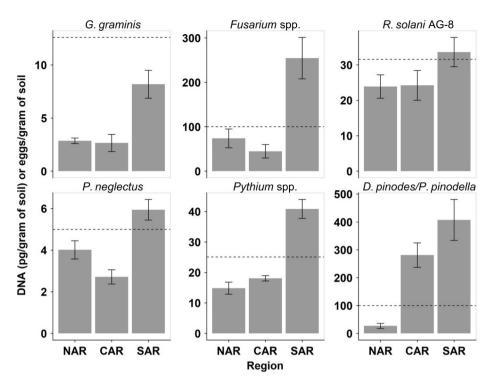


Fig. 6. Amount of DNA of *Fusarium* spp., *R. solani* (AG-8), *G. graminis* var. *tritici*, *Pythium* Clade F, D. *pinodes/P. pinodella*, or eggs of *P. neglectus* in soil when sampled in autumn for the northern agricultural region (NAR), central agricultural region (CAR) and southern agricultural region (SAR). Error bars are I s.e.m. Horizontal dashed lines represent the upper limit of the low yield loss PREDICTA B® category, back transformed from log₁₀ for fungal pathogens.

The incidence of each pathogen or nematode pest are reflective of documented changes in their prominence across southwest Australia, with reports of reduced prominence of G. graminis var. tritici, and H. avenae (Cotterill and Sivasithamparam 1989; Vanstone et al. 2008; Kirkegaard et al. 2011) and increased frequency of R. solani (AG-8) and P. neglectus (Vanstone et al. 2008; Khangura et al. 2013). The incidences of DNA above detection were mostly similar to those previously found in this region: H. avenae and stem nematode undetected (Flower et al. 2019), P. neglectus 70% (Vanstone 2002) and Fusarium spp. (41%), but lower for R. solani (AG-8) (81%) (Khangura et al. 2013). The number of plants per sample with root or crown symptoms of these pathogens and nematodes also reflected the current prominence of these organisms, overall ~15% of plants with R. solani (AG-8) and P. neglectus symptoms, compared to $\sim 1\%$ for G. graminis var. tritici and Fusarium spp.

Pathogen dynamics by land use

Host/non-host relationships were identified by comparing autumn and spring pathogen DNA concentrations in soil. These matched known host ranges for each pathogen, although not always at statistically significant levels. An exception to this was the significant reduction in *R. solani* (AG-8) DNA over the growing season (autumn to spring) in

paddocks sown to canola, which was accompanied by a low proportion (5%) of canola plants with symptoms of *R. solani* (AG-8) damage compared to the other crops (\sim 67%). This contradicts previous management guidelines, that R. solani (AG-8) has such a wide host range that it cannot be controlled using rotations (MacLeod et al. 2008), and adds to a growing body of evidence suggesting canola is a poor host of R. solani AG-8 (Gupta et al. 2010; Babiker et al. 2013; Hüberli et al. 2013; Flower et al. 2019). Interestingly P. neglectus DNA increased within canola crops and this carried through to following wheat crops, but only a small proportion of canola plants (2%) showed P. neglectus symptoms, which indicates canola is a tolerant host, as previously reported (Smiley et al. 2014; Flower et al. 2019) and visual assessment of symptoms is not a good indicator of susceptibility.

Rotations

Cereals accounted for 66% of paddock-years in the Focus Paddock dataset (Harries *et al.* 2020) and remain the most frequently grown crops in southwest Australia, but importantly canola production has increased from 0.4 to 1.4 million hectares over the period 2005 to 2015 (ABS 2016) and inclusion of canola at the expense of lupin is likely to result in the build-up of *P. neglectus* throughout

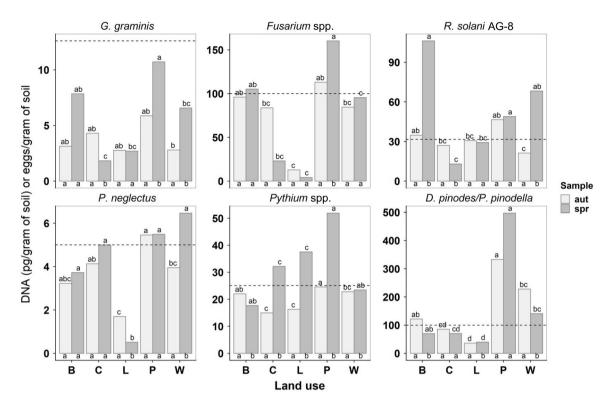


Fig. 7. Amount of DNA of Fusarium spp., R. solani (AG-8), G. graminis var. tritici, Pythium Clade F, D. pinodes/P. pinodella, or eggs of P. neglectus, in soil when sampled in autumn (aut) and spring (spr) for the land uses of barley (B), canola (C), lupin (L), pasture (P), and wheat (W). Letters above bars represent significant differences ($P \le 0.05$) between land uses within each sample season (aut or spr). Letters below bars represent significant differences ($P \le 0.05$) within years, between each sample season (aut and spr). Horizontal dashed lines represent the upper limit of the low yield loss PREDICTA B® category, back transformed from \log_{10} for fungal pathogens.

the survey area (Riley and Kelly 2002). Indeed, paddocks sown to canola had higher *P. neglectus* soil DNA concentration than those sown to lupin, indicating that this may have already occurred. Conversely, inclusion of canola in place of pasture reduces the inoculum load of *Fusarium* spp. and *G. graminis* var. *tritici*, *R. solani* (AG-8) and *D. pinodes/P. pinodella*, within subsequent wheat and barley crops. In contrast, the recent increase in frequency of cereal production needs to be managed carefully because we found increased incidence of plant symptoms caused by several pathogens and increasing overall incidence of root disease symptoms in longer sequences of wheat monoculture and increased incidence of DNA assays of *Fusarium* spp. and *G. graminis* var. *tritici* over the period of the survey.

Management factors

Weed density and herbicide applications

One reason for the increased use of canola is the excellent weed control obtained in this crop. Harries *et al.* (2020) conducted detailed analyses of weed dynamics with the Focus Paddocks observing that glyphosate tolerant canola crops averaged 4 grass weeds/m² in spring compared to

14/m² for wheat and 562/m² for pasture. The low density of weeds/alternative pathogen hosts in canola may be an important factor in the reduction in R. solani (AG-8) DNA within the canola years that we reported. This idea is supported by the fact that logistic regression indicated more weeds per square metre were associated with increased incidence of Fusarium spp., P. neglectus and R. solani (AG-8) DNA and incidence of R. solani (AG-8) root disease. This shows weeds are hosting pathogens, as has been previously reported in WA (Vanstone and Russ 2001a, 2001b) and nematode pests and/or weed competition may be impacting root growth and soil pathogen interactions; stunting root growth so that roots take longer to grow into the sub-soil, beyond the soil depth where pathogens and nematodes are most prolific. Additionally, longer sequences of monoculture wheat led to greater grass weed populations; with mean weed density in the fourth successive wheat crop (35 grass weeds/m²) triple that of the first wheat (Harries et al. 2020). Hence, the reduced frequency of pasture and increase in canola, a non-host crop in which weeds can be controlled, are important factors keeping cereal pathogens and nematode pests in check within the current cereal dominated rotations.

Table 5. Incidence of field visits in which one or more plants with root or crown symptoms of *G. graminis*, *Fusarium* spp., *P. neglectus* and *R. solani* (AG-8) in autumn and spring were detected.

All samples									
Pathogen		Autumn	observed		Spring observed				
	NAR	CAR	SAR	TOTA	NAR	CAR	SAR	TOT ^A	
Fusarium spp.	I	0	3	I	12	7	12	10	
G. graminis var. tritici	10	9	4	9	39	41	35	39	
P. neglectus	53	60	40	53	60	64	60	62	
R. solani AG-8	58	62	46	58	70	72	74	72	
				Wheat (Tritic	cum aestivum)				
Fusarium spp.	1	0	4	I	16	9	15	13	
G. graminis var. tritici	14	12	6	12	52	55	44	52	
P. neglectus	70	75	57	70	79	84	85	81	
R. solani AG-8	67	70	56	67	90	91	90	90	
				Barley (Horo	deum vulgare)				
Fusarium spp.	0	5	4	4	33	14	19	18	
G. graminis var. tritici	0	9	4	6	0	52	48	47	
P. neglectus	75	59	56	59	100	86	70	78	
R. solani AG-8	100	68	64	69	67	90	93	90	
				Canola (Bro	issica napus)				
P. neglectus	2	0	0	I	5	0	0	2	
R. solani AG-8	5	0	0	2	5	3	0	3	
				Lupin (Lupinu	s angustifolius)				
P. neglectus	3	0	0	2	6	0	0	4	
R. solani AG-8	66	57	86	66	34	29	100	40	

Note root disease symptoms were assessed as accurately as possible, but we acknowledge that there are some limitations of symptom attribution by pathogen. *R. solani* (AG-8) and *P. neglectus* can be difficult to differentiate, particularly when together on the same plant. *R. solani* (AG-8) may prune roots, hindering the rating of other pathogens and nematode pests. Also the timing of sampling was not ideal for *Fusarium* spp., because distinctive symptoms are observed at or after plant maturity. ATOT (overall percentage of field visits with one or more plants with symptoms) is not equal to the mean of regional values because the number of observations in each region differs.

While low grass weed numbers are a benefit for suppression of cereal diseases the use of herbicides can stunt plant growth and predispose plants to pathogens and nematode pests. This may explain why in our optimised models for *Fusarium* spp., *G. graminis* var. *tritici* and *R. solani* (AG-8) we found the incidence of root damage increased if more herbicides were applied to a paddock. Several studies document increased *R. solani* (AG-8) damage in cereals and soybean with the application of ALS (acetolactate synthase) inhibitor herbicides (Rovira 1986; Bradley *et al.* 2002; Lee *et al.* 2012; Rose *et al.* 2016). ALS-inhibitors were some of the most commonly used herbicides within the Focus Paddock data set (Harries *et al.* 2020).

Plant nutrition

Plant nutrition was also an influential management factor, although more so for *P. neglectus* than the other pathogens. Greater soil concentration of one or more of the macro nutrients (N, P, K and S) resulted in a greater incidence of

Fusarium spp., P. neglectus and R. solani (AG-8) DNA and P. neglectus root damage. Also, our optimised models of P. neglectus included increasing fertiliser N as a predictor of increased incidence of both DNA above detection and root disease. This is noteworthy because mean amount of N fertiliser applied to rainfed wheat in Australia increased from 30 kg N/ha to 45 kg N/ha from 2000 to 2017 (Angus 2001; Angus and Grace 2017), type and amount of nitrogen fertiliser is documented to impact Fusarium spp. (Duffy and Défago 1999) and increasing rates of N fertiliser have been reported to increase nematode population densities and favour plant parasitic species such as Pratylenchus spp. (Todd 1996; Sarathchandra et al. 2001; Thompson et al. 2008; Forge et al. 2020). These findings are consistent with N being a common constraint in dryland farming systems (Faroog and Siddique 2017); the logical consequence of ameliorating the N constraint is an increase in root and shoot biomass and in species that parasitise these roots and crowns, as was reported by Wilkinson et al. (2018).

Table 6. Binomial logistic regressions of pathogen root disease observed in spring (absent or present) for environmental and agronomic variables.

Independent variate	R. solani	(AG-8)	P. neg	P. neglectus		Fusarium spp.		G. graminis var. tritici	
	P value	Coef.	P value	Coef.	P value	Coef.	P value	Coef.	
Rain									
Summer rain (mm)	0.075	-0.004	0.484	-0.001	0.508	0.002	0.005	-0.006	
Annual rain (mm)	0.000	-0.004	0.000	-0.003	0.346	-0.001	0.000	-0.005	
Growing season rain (mm)	0.000	-0.005	0.000	-0.004	0.003	-0.005	0.000	-0.007	
January–March rain (mm)	0.632	-0.00 I	0.329	0.003	0.288	-0.005	0.805	-0.001	
April–June rain (mm)	0.000	-0.011	0.000	-0.010	0.199	0.005	0.000	-0.014	
July-September rain (mm)	0.000	-0.007	0.000	-0.006	0.000	-0.014	0.000	-0.009	
Temperature									
Growing season temperature (°C)	0.836	-0.008	0.914	0.004	0.651	-0.024	0.144	0.049	
January-March temperature (°C)	0.507	-0.024	0.945	-0.002	0.965	0.002	0.194	0.043	
April-June temperature (°C)	0.022	-0.131	0.027	-0.117	0.003	0.249	0.036	-0.112	
July-September temperature (°C)	0.000	-0.200	0.000	-0.196	0.820	0.019	0.000	-0.228	
Management									
Sow day	0.000	0.082	0.000	0.071	0.009	0.024	0.000	0.048	
Number of herbicides applied	0.003	0.138	0.223	0.048	0.012	0.142	0.120	0.060	
Weed density in spring (p/m²)	0.032	0.010	0.208	0.004	0.522	-0.003	0.248	0.002	
Fertiliser N (kg/ha)	0.437	-0.004	0.366	0.004	0.883	-0.001	0.687	0.002	
Soil									
Soil mineral N (mg/kg 0–10 cm)	0.877	-0.00 I	0.093	0.009	0.042	0.014	0.199	-0.006	
Soil P (mg/kg 0-10 cm)	0.381	0.005	0.031	0.011	0.750	-0.003	0.315	0.005	
Soil K (mg/kg 0–10 cm)	0.567	0.000	0.048	0.001	0.240	0.001	0.631	0.000	
Soil S (mg/kg 0–10 cm)	0.718	0.001	0.043	0.008	0.635	0.002	0.848	-0.001	
Organic carbon (%)	0.120	0.183	0.205	0.131	0.227	-0.227	0.854	0.018	
Electrical conductivity (dS/m 0–10 cm)	0.395	0.989	0.014	2.786	0.140	2.150	0.479	-0.737	
pH (CaCl ₂ 0-10 cm)	0.685	-0.058	0.441	-0.102	0.251	0.233	0.544	0.080	
Soil texture (I-5) ^A	0.092	0.355	0.084	0.325	0.408	0.226	0.077	0.314	

P values and coefficients (coef.) presented. Grey background indicates a significant effect at $P \le 0.05$.

ASoil texture: I = coarse texture (sand), 5 = fine texture (clay). Sow day = days since I January in each year, for volunteer pastures the first occurrence of 15 mm of rain over two or less days after I April was considered sow day. Summer rain = rain between crops or pastures. The models are presented in Supplementary material (S2).

It should also be acknowledged that fertiliser inputs generally increase yield in dryland farming systems and this needs to be balanced against our findings of associated increase in disease.

Sowing date

Sowing later in the year, increasing sow day, increased the incidence of root disease caused by *Fusarium* spp., *R. solani* (AG-8), *P. neglectus* and *G. graminis* var. *tritici*, with sow day a variate within the optimised models for each of these pathogens, except *G. graminis* var. *tritici*. The median sowing date became earlier over the survey period, being 25th of May in 2010 compared to 11th of May in 2014 (Harries *et al.* 2020), a continuing trend reported from other surveys (Stephens and Lyons 1998; Fletcher *et al.* 2015; Fletcher *et al.* 2016; Anderson *et al.* 2017). The reduced root

damage from earlier sowing is likely to be due to more rapid root growth in warmer soil, as evidenced by the negative coefficients in most temperature variates for each pathogen in the binomial logistic regressions.

Environmental factors

The strong geographic difference in pathogen/nematode pest DNA incidence and concentration in soil, where SAR had the greatest and NAR least for most organisms tested, was not evident in plant root observations. For the DNA assays, lower temperature was related to higher probability of DNA levels being above detection limit. Likewise, root disease incidence increased as temperature decreased, but also as rain decreased. Hence, in environmental conditions with greater water stress, the higher latitude NAR and CAR

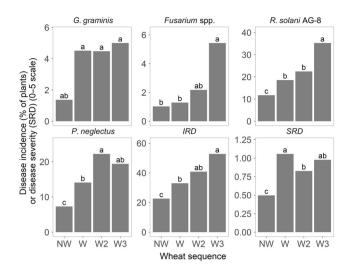


Fig. 8. Mean percentage of plants taken in spring with diseased symptoms from *Fusarium* spp., *R. solani* (AG-8), *G. graminis* var. *tritici* and *P. neglectus* or with symptoms of at least one root pathogen, incidence of root damage (IRD). Mean percentage of severity of root damage (SRD) from spring samples assessed using a 0–5 rating scale: 0 (no disease), I = I-5% (trace disease), 2 = 6-25% (low amount of brown lesions), 3 = 26-50% (medium amount of brown lesions, similar amounts of healthy and necrotic), 4 = 5I-75% (most of the roots covered in brown lesions, little healthy root left) and 5 = 75-100% (all or nearly all roots covered in brown lesions or short brown stumps). NW = Non-wheat, W = first wheat crop, W2 = second wheat in succession, W3 = third wheat in succession.

regions (Harries *et al.* 2021), there was more root damage despite less soil DNA compared to the SAR. This is consistent with findings of Poole *et al.* (2015) who analysed a sub-set of the Focus Paddock data to report that temperature and rainfall parameters explained most of the variation in root health but this was not always strongly correlated to soil DNA levels.

Several factors driven by climate and soil differences between regions may be involved, i.e. we found greater rainfall and more fertile soils in the SAR meant plants produced more above ground biomass (Harries et al. 2021), and presumably below ground biomass although this was not measured, which may enable plants to cope with higher background pathogens and nematode pests DNA levels. Also, soils vary in suppressiveness of soilborne disease and nematode pest symptoms. For example, greater rotational diversity has been associated with increased microbiota biomass, diversity and suppression of crop pathogens and plant parasitic nematode levels (Postma et al. 2008; McDaniel et al. 2014), although this will depend on crops used and pathogen/nematode pest issues (Flower et al. 2019). However, we did not have the data to test these relationships.

We found that the climate influenced nematode pest and soilborne disease expression. Given reports of substantial and continuing climate change in southwest Australia, with increased summer fallow rainfall, reduced growing season rainfall and increased temperatures (BOM 2018; Scanlon and Doncon 2020), it is important to investigate these effects on the interaction between soil pathogen/nematode pest and their host plants, across the whole of the cropping region of southwest WA.

Conclusions

Overall, the inclusion of non-host crops at the current level coupled with current agronomic practices meant severe root damage was rare. We found that the reduction of paddocks in pasture and resultant very low weed populations, combined with early sowing will, in general, reduce the persistence of the soil pathogens and nematode pests in paddocks of southwest Australia. Some aspects of management had the opposite effect, including increased frequency of herbicide use, cereals and canola replacing lupin and increased N fertiliser use, and these must be applied cautiously.

These agronomic changes have mostly been made in response to production constraints other than root pathogens and nematode pests, for example to reduce soil erosion, improve soil water conservation and yield potential and improve weed control and soil fertility. Studies like ours, that link management practices to multiple productivity constraints, such as pathogens, nematode pests, weeds, and nutrients, are important to understand the sustainability of current or proposed production methods.

Supplementary material

Supplementary material is available online.

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Conflicts of interest. The authors declare no conflicts of interest.

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