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Spatial spread of Ditylenchus gigas and its interaction with Botrytis fabae on Vicia faba

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Isadeha, A., Shaw, M. W. ORCID: https://orcid.org/0000-0002-6993-048X and Pembroke, B. (2025) Spatial spread of Ditylenchus gigas and its interaction with Botrytis fabae on Vicia faba. Annals of Applied Biology, 186 (2). pp. 125-131. ISSN 1744-7348 doi: 10.1111/aab.12945 Available at https://centaur.reading.ac.uk/118805/

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Publisher: Wiley

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Received: 26 June 2023 | Revised: 15 April 2024 | Accepted: 17 July 2024

DOI: 10.1111/aab.12945

Annals of Applied Biology
An international journal of the aab

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ORIGINAL ARTICLE

Spatial spread of *Ditylenchus gigas* and its interaction with *Botrytis fabae* on *Vicia faba*

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Abstract

Ditylenchus gigas Vovlas is the dominant species of *Ditylenchus* nematode on faba bean in the UK. It is normally reported with *Botrytis fabae* Sardiña, which causes chocolate spot of faba bean. The aim of the work reported here was to estimate how fast isolated infections of *D. gigas* may spread spatially and how background infection of the host with *B. fabae* alters multiplication of *D. gigas*. Spatial spread in field conditions was measured in plants growing in square grids. After establishment, single plants at the centre of each grid were spray inoculated with *D. gigas*. In summer 2017, *D. gigas* spread to a distance of at least 1 m, the edge of each 2 m × 2 m plot. Incidence on shoots decreased very slowly with distance beyond 0.4 m. In a repeat experiment harvested in autumn 2018, *D. gigas* was detected at distances of up to 160 cm in 4 m × 4 m plots. The yield effect and reproduction rate of *D. gigas* were measured in glasshouse experiments, alone and following brush inoculation with low (10^3) or high (10^6 conidia/mL) doses of *B. fabae*. At low doses of *D. gigas* inoculum multiplied by approximately 75-fold, with lower rates of multiplication as the inoculum dose increased. The reproduction rate of *D. gigas* was reduced in plants inoculated with *B. fabae*, especially at high doses of *D. gigas*. The reduction was approximately proportional to log (*B. fabae* dose). Seed yield from inoculated plants decreased approximately in proportion to the logarithms of the initial dose of *D. gigas* and of *B. fabae*.

KEYWORDS
antagonism, *B. fabae*, *D. gigas*, faba bean, spatial spread, synergy

1 | INTRODUCTION

Ditylenchus gigas (Vovlas, 2011) is the dominant species of *Ditylenchus* in the UK (Stawniak, 2011). *D. gigas* was formerly referred to as the giant race of *D. dipsaci*. It is a migratory endo-parasitic nematode which causes stem lesions in faba bean (*Vicia faba*), alongside *D. dipsaci*. Both species may be seedborne. It is more destructive on *Vicia fabae* (faba bean) than *D. dipsaci* (Sikora & Greco, 1990; Sturhan & Brzeski, 1991) which is classified as an A2 quarantine pest by the European and Mediterranean Plant Protection Organisation (EPPO). Certification schemes against both species are in place (EPPO, 2021).

Ditylenchus spp. are naturally present in temperate and subtropical countries where they affect faba bean, onions, garlic, alfalfa and many others (Jones et al., 2013). They are rarely reported in tropical countries. However, some recent reports have recorded the presence of *D. gigas* and other *Ditylenchus* spp. in areas where they were formerly thought not to occur (e.g., Indarti et al., 2018; Maafi, Taheri, &

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Subbotin, 2013) despite their ability to survive extreme conditions (Jones et al., 2013). Stawniak (2011) reported a 14-fold increase in the population of *D. gigas* on *V. fabae* cv. Fuego following inoculation of a single plant. It seems likely that seed is an important means of dissemination of the nematode to new geographic regions.

Botrytis fabae Sardiña is a necrotrophic fungus very common on faba bean on the field. It is seed-borne on faba bean. Thus, seed movement can be a route by which both *B. fabae* and *D. gigas* disperse on regional scales.

Interaction between *B. fabae* and *D. gigas* is likely because of their similar niches on the host plant and opposing nutritional requirements: both can infect stems and leaves, but *B. fabae* is necrotrophic (Van Kan, 2014), whilst *Ditylenchus* is biotrophic (Jones et al., 2013). *B. fabae* excretes toxins which kill invaded tissues and therefore counteracts active defences, whilst *D. gigas* requires living tissue to multiply and evades or inactivates defences.

Information on how *D. dipsaci* spreads in the field has been published (Kort, 1972; Perry & Moens, 2013), but little is known about the field-scale spread of *D. gigas*. Because *B. fabae* is very common, spread of *D. gigas* is likely to be affected by *B. fabae* severity. The experiments reported here quantified (1) the distance spread by *D. gigas* over a season, (2) the extent of multiplication in relation to initial inoculum, and (3) the effect of background infection by *B. fabae* on multiplication and severity of *D. gigas*.

2 | MATERIALS AND METHODS

2.1 | Spatial spread experiments

Two spatial spread experiments were conducted in 2017 (April–July) and 2018 (July–November). The second experiment was intended to validate the first. The difference in the sowing dates was because in spring 2018 inoculated plants did not establish on the experimental field, because of prolonged drought.

To verify that the sites were free of *D. gigas* before the experiment was established, soil samples were collected separately 1 m apart from each plot. Half a metre was avoided from the edge of each plot on all sides. For each sample about 1 kg soil was collected at a depth of 20–30 cm using a hand trowel. Six samples were collected in an area of 4 m^2 and 12 samples in an area of 16 m^2. The soil samples were bulked and used to fill 1 L pots (top diameter: 13 cm, bottom diameter: 10 cm, depth: 11 cm). One faba bean (cv. Fuego) seed was planted in each pot. The pots were kept in a glasshouse and observed for nematode symptoms. At maturity, plants were harvested and modified Baermann extraction trays (Coyne et al., 2007) set up for nematode extraction.

At the experimental site, faba bean (cv. Fuego) was sown in three replicates of a square grid pattern. Each replicate grid had sides of 2 m (2017) or 4 m (2018). Plants were spaced 20 cm apart within and between rows. Two weeks after emergence, a 2-week-old seedling grown in a glasshouse and previously inoculated at the growing tip with 300 nematodes/plant was transplanted into the centre of each plot. At physiological maturity (19–20 weeks following inoculation in 2017, 17–18 weeks in 2018) plants along transects oriented north, east, south and west from the centre were uprooted. Nematodes were extracted from the plants using the modified Baermann extraction method. Meteorological data was obtained from the University of Reading Atmospheric Observatory.

2.2 | Seasonal multiplication of *D. gigas*

Faba bean seeds cv. Fuego were sown in 12 L plastic pots (top diameter: 28 cm, bottom diameter: 23 cm, depth: 25 cm) filled with John Innes No. 2 compost. The plants were kept in a glasshouse, where temperature ranged between 14 and 21°C. The experiment in 2017 was sown on 14 March and terminated on 6 July, whilst that of 2018 was sown on 7 March and terminated 2 July. In 2017, 2 weeks after planting (two leaf stage) the growing tips of the plants were inoculated with 1 mL mixed life stages of five *D. gigas* suspensions (to give 0, 30, 100, 300, 1000 or 3000 nematodes per plant). The concentrations of inoculum were adjusted to their respective doses using a counting dish under a binocular microscope with 25× magnification.

In 2018, plants were also inoculated with suspensions of *B. fabae* conidia (0, 2×10^3/mL and 2×10^6/mL) in a factorial design with five populations of *D. gigas* (0, 30, 100, 300, 1000 or 3000 nematodes). One milliliter of inoculum of *B. fabae* or water was applied with a paint brush to the surface of the second true leaf. The inoculated plants were covered with polythene bags for 24 h to maintain humidity for infection. The experiments were laid out in a randomised complete block design with five replications, blocked parallel to the glasshouse axis, north-east to south-west. Sachets of *Amblyseius cucumeris*, Oudemans (BioLine, Syngenta) were used to limit infestation by western flower thrips (*Frankliniella occidentalis* [Pergande]) and bamboo sticks were used to support individual plants.

Plants were harvested at full maturity, when stems turned black, pods were dry and black, and seed were fully hardened. Plants were removed for nematode extraction at the junction of the stem and root. The soil in the pot was thoroughly mixed and 200 mL samples taken for assessment of the nematode population in the soil as before. Data collected from the above ground samples were: number of tillers; percentage chocolate spot severity on inoculated leaves; stem lesion length; lesion girth; symptom severity as below; nematode population extracted as before; and grain yield. The *D. gigas* reproduction rate was calculated in each pot by dividing the final nematode population by the initial nematode dose.

A scale of 1–9 (Hanounik & Sikora, 1980) was used in assessing severity symptoms of *D. gigas* (SSI) with index points: 1 = no visible attack of the plant; 3 = traces of necrosis at base of the stem; 5 = leaves and stem deformed on 10%–25% plant; 7 = stem with necrosis, swelling and distortion reaching 75% plant; 9 = plant dead or heavily infested.

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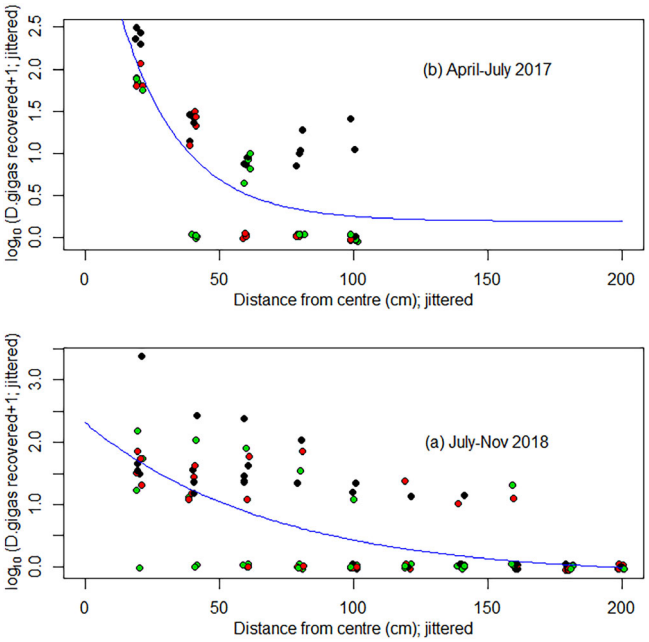

FIGURE 1 Concentration of *Ditylenchus gigas* in washings of *Vicia faba* cv. Fuego at harvest in relation to distance from an inoculated source plant at the centre of a grid of plants (a) spring–summer 2017, 4 m^2 plots; (b) summer–autumn 2018, 16 m^2 plots. Lines show best fitting exponential decline of recovery with distance. Distance jittered for clarity.

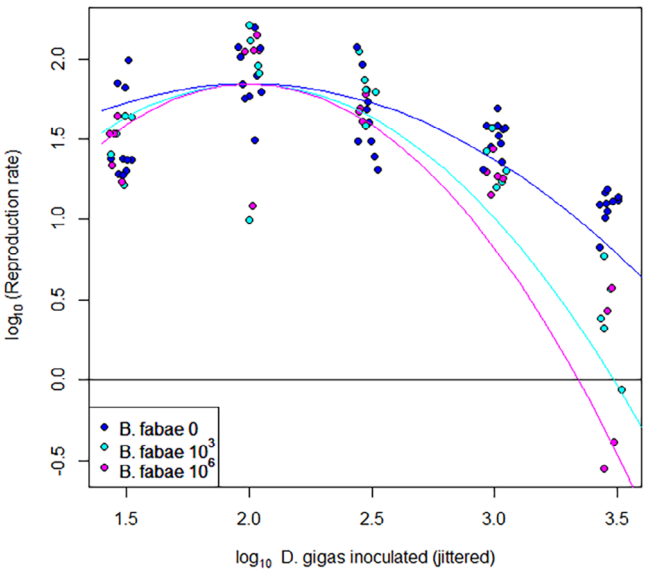

FIGURE 2 Reproductive rate ($\log_{10}$ [nematode concentration in washing at maturity/nematode concentration in inoculum]) of *Ditylenchus gigas* on *Vicia faba* cv. Fuego growing in a greenhouse, in relation to *D. gigas* inoculum applied and prior inoculation with *B. fabae*. Lines show best fitting quadratic relation for each level of *B. fabae* used. Peak reproductive rate was at $\log_{10}$ (*D. gigas* dose) = 2.177. Without *B. fabae*, the peak $\log_{10}$ reproductive rate was 1.85–0.47 $\log_{10}$ (*D. gigas* dose), curvature $p < .001$. With *B. fabae* at 3×10^3 spores mL^{-1}, $\log_{10}$ (*D. gigas* reproductive rate) = 1.85–0.83 $\log_{10}$ (*D. gigas* dose), curvature $p < .001$; with *B. fabae* at: 3×10^6 $\log_{10}$ (reproductive rate) = 1.85–1.02 $\log_{10}$ (*D. gigas* dose), curvature $p < .001$. The black horizontal line represents the line where the *D. gigas* recovery would be the same as the dose applied. Horizontal axis coordinates jittered for clarity.

2.3 | Statistical analysis

Analysis used GenStat 18th edition (VSN International, 2015) and R v3.5.1 (R Core Team, 2023). A linear model including direction and distance and their interactions was fitted to the $\log_{10}$ transformed nematode counts in the spread experiments using Genstat. Each grid was regarded as a block; the 2 years' data were analysed separately. A non-linear curve ($a - b(1 - e^{-c\ \text{distance}})$ where a, b, and c were fitted parameters) was also fitted to the spatial spread data using nls() in R after allowing for inter-block differences.

For the *D. gigas* reproduction experiments, *D. gigas* dose inoculated and reproduction rate in each pot were transformed to $\log_{10}(x + 1)$ before analysis, using lm() in R. Significance tests of model terms were made against the block level sums of squares. Inoculation with *B. fabae* was treated as a three-level treatment factor. A single location of the zero of the quadratic function describing the relations of *D. gigas* reproduction to inoculation dose was used because differences for each *B. fabae* level were very small and far from significance. For the same reason, linear terms in the function were deleted from the models. The final model therefore used separate quadratic functions to describe the relation between reproduction rate and inoculated dose for each dose of *B. fabae*.

The relationship between *D. gigas* recovery and symptom score was analysed by ANOVA using untransformed *D. gigas* recovery data and treating symptom scores as levels of an unordered factor, treating blocks as a random factor.

The relationship between $\log_{10}$ (*D. gigas* inoculum concentration) and seed weight was analysed by lm() in R with linear, quadratic and cubic contrasts in $\log_{10}$ (*D. gigas* inoculum concentration) and linear and quadratic contrasts in $\log_{10}$ (*B. fabae* inoculum concentration), treating blocks as a random factor.

3 | RESULTS

3.1 | Spread of *D. gigas* from single source plants

No infection was detected in the initial soil in either year.

In 2017 *D. gigas* spread from the infected source plant to a maximum distance of 20 cm on the seed, 40 cm on the pods, 60 cm on the roots and 100 cm (the edge of the plot) on the shoots. The mean incidence of infected plants in a 4 m^2 plot was 71%. The pattern of dispersal differed between replicates. The fit of the best fitting exponential decline with distance was poor (Figure 1a), with a half-distance (after allowing for differences between replicates in the mean spread) of 16^{+7}_{-4} cm (with 1SE upper and lower confidence limits indicated).

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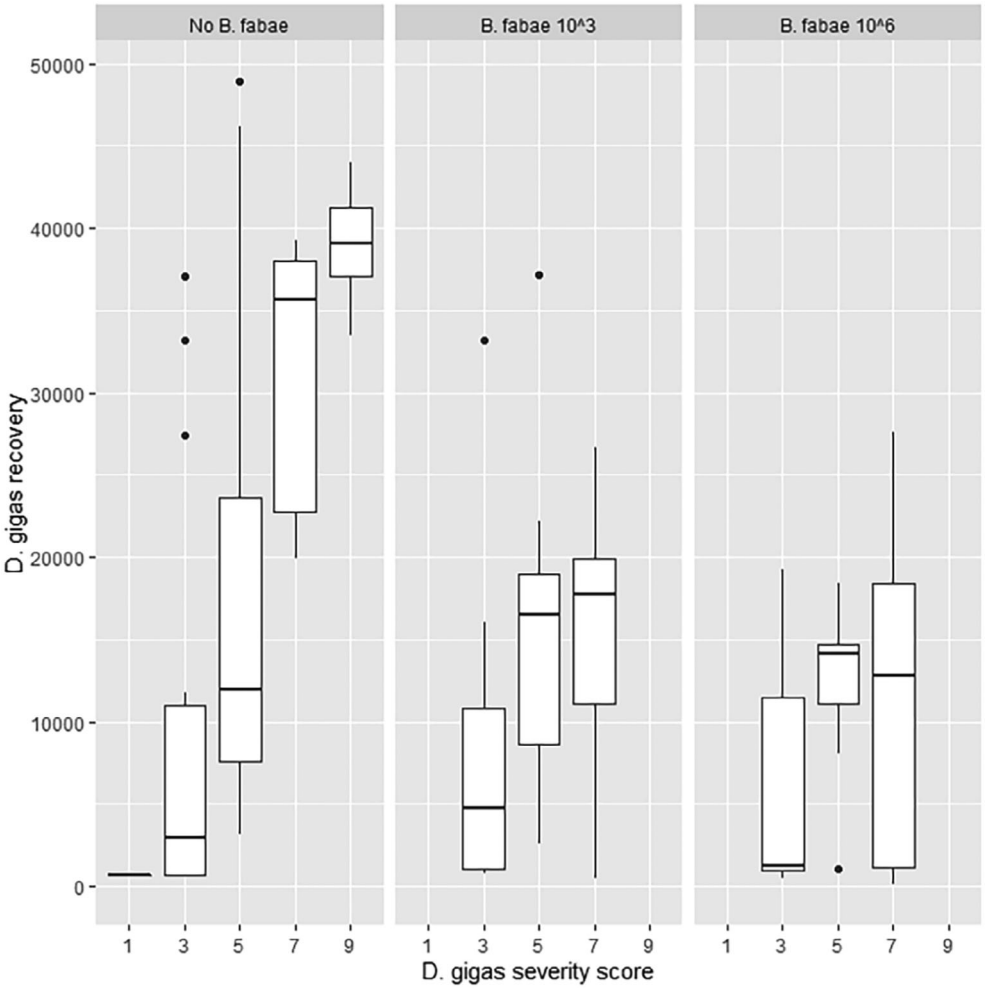

FIGURE 3 *Ditylenchus* nematode concentration in 200 mL modified Baermann washings in relation to severity score (1–9 ordered qualitative scale with increments of 2) of *Vicia faba* cv. Fuego plants at maturity. Black line: mean, box ends: upper and lower quartiles; dashed lines maximum and minimum; circles: outliers. Box above each tick mark on the *x*-axis represents *D. gigas* recovery from plants with a group of severity scores: B0, without *B. fabae*; B3, inoculated with 2×10^3 *B. fabae* spores mL^{-1}; B6, inoculated with 2×10^6 *B. fabae* spores mL^{-1}.

The 2018 experiment was conducted between July and November, so the plants did not pod. *D. gigas* was detected up to a distance of 160 cm on the shoots, and 80 cm on the root (Figure 1b). The maximum number of *D. gigas* was recorded at a distance of 20 cm from the source; as in 2017 the fit to an exponential or power–law dispersal curve was again poor, with a best fitting half distance of 48^{+28}_{-13} cm. The 95% confidence limits for half-distances in 2017 and 2018 overlap. The mean incidence of infected plants in an entire 16 m^2 plot was 35%, and in the central 4 m^2 (comparable with the 2017 data), 60%.

In 2017, differences between directions were not detected ($p = .9$). In 2018, significantly more nematodes were recovered from the north and south transects than along the east and west ($p < .001$). There was no obvious relation to prevailing wind direction in any month (Appendix S1, Figures S1–S4).

3.2 | Reproduction rate of *D. gigas*

The pattern of final recovery of *D. gigas* in the replication without *B. fabae* was consistent across experiments (Appendix S1, Figures S1–S4). The nematode population extracted from the soil was about 1/1000 of the population extracted from the above ground parts ($p < .01$), although the data were very variable.

Reproduction rate fell with increasing *D. gigas* dose from a (back-transformed) maximum of $\times 70^{+88}_{-39}$ (error limits are based on back-transformed 1SEM) for inoculations with 100 *D. gigas*. The decline of reproduction rate with log dose was approximately quadratic for all doses of *B. fabae* (Figure 2). *B. fabae* inoculation, at either density, significantly ($p = .01$) reduced the reproduction rate of *D. gigas* at high initial doses (3×10^6 conidia/mL) (Figure 2). The reduction in the reproduction rate at the higher *D. gigas* doses was greatest at the higher concentration of *B. fabae* inoculum. However, at low *D. gigas* inoculum *B. fabae* had no measurable effect on the reproduction rate of *D. gigas*.

The pattern in the number of *D. gigas* extracted from soil was similar to that from stem material, although about 1/1000 of the absolute numbers (Figure S5).

3.3 | Symptom severity and yield effects

D. gigas recovery increased approximately proportionately with increasing severity score in the absence of *B. fabae* inoculation

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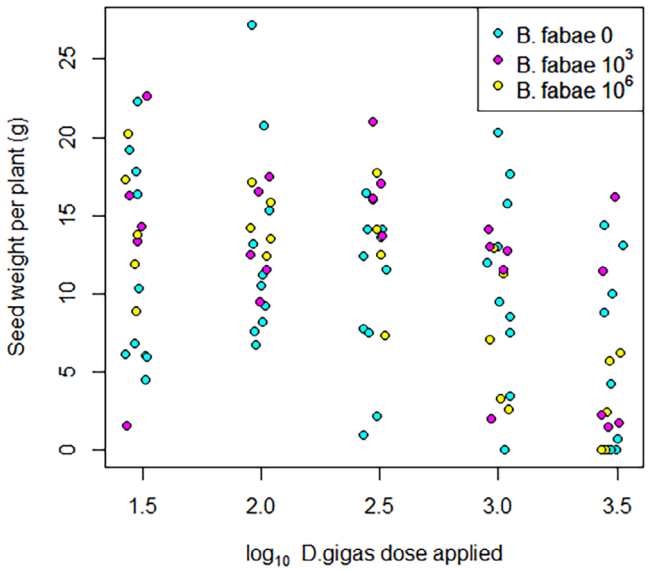

FIGURE 4 Grain yield per pot grown plant at harvest, 8–9 weeks following inoculation, from *Vicia faba* cv. Fuego inoculated with various concentrations of *B. fabae* and *D. gigas*. 0: uninoculated with *B. fabae*; 3: inoculated with 2×10^3 *B. fabae* spores; 6: inoculated with 2×10^6 *B. fabae* spores. Anova of effect on yield: linear effect of log *D. gigas* dose $p < .001$, quadratic deviation from linear effect $p = .006$; linear effect of log *B. fabae* dose $p = .04$; interaction of log *D. gigas* inoculation dose and log *B. fabae* dose $p > .9$).

(Figure 3). With *B. fabae* inoculation at either level there was a jump in recovery between severity scores of 3 and 5 (Figure 3). The area density of chocolate spot symptoms was not significantly altered by applying any of the concentrations of *D. gigas* ($p > .9$), but there was an approximately 10% increase in chocolate spot severity at the higher dose of *B. fabae*, from 79% to 86% (Figure S6; anova, $p = .03$).

Seed weight per plant declined with increasing log dose of *D. gigas*, with losses of 86% at an inoculum dose of 3000 nematodes. Losses were slightly increased by *B. fabae* infection (Figure 4; ANOVA: linear effect on yield of log *D. gigas* dose $p < .001$, quadratic deviation from linear effect on yield $p = .006$; linear effect of log *B. fabae* dose $p = .04$; interaction of *D. gigas* inoculation dose and log *B. fabae* dose on yield $p > .9$).

4 | DISCUSSION

D. gigas infection spread to a distance of 1.6 m from the source within the 2018 season. This is consistent with the 2017 data in which the nematode spread to the edge of the plots (1.0 m). The maximum distance of spread was detected on the shoot in both seasons. On the root, the nematode was detected at about 50 cm from the source. There was no directional effect of the spread of the nematode in 2017, whilst the nematode spread more towards the south and north in 2018. The nematode may have been spread by different means in the field, including run-off and rain splash. The life cycle of the nematode takes about 19–23 days under favourable conditions (Yuksel, 1960; *D. gigas* is presumably similar), so the observed spread represents several population cycles; this amplifies the random dispersal. Since *D. gigas* does not reproduce parthenogenetically, it requires individual nematodes of both sexes to start a new reproducing colony. This will result in uneven and aggregated distribution of nematodes in the field, as witnessed in this study.

Previous estimates of reproduction rate vary between 14 (Stawniak, 2011) and 18,000 (Hesling, 1970; *D. dipsaci* on *Narcissus*). Our estimate is consistent with, though greater than, that of Stawniak. At 25 plants/m^2 or 250,000 plants per hectare, approximately the densities used here, if one infested seed were planted per m^2, there would initially be about 10,000 infested plants/ha. By the end of the second season of farm-saved seed essentially all plants in the field would be likely to have some detectable level of infestation.

D. gigas may have spread from the infected source to other plants in several ways. Firstly, spread may have occurred when plant leaves touched one another. *D. gigas* are migratory endo-parasites and can move in films of water within and outside the plant tissue. Although the spacing in this experiment was 20 cm, the plant leaves were able to touch one another later in the growing season.

Secondly, it is possible for the nematode to have been spread through movement in soil water. Kort (1972) reported that *D. dipsaci* can traverse 10 cm of soil in 2 h. A random walk at this speed would lead to substantial log-distance dispersal, but field levels in an otherwise healthy crop would be likely to be much lower. Dispersal by farm machinery probably dominates movement within a season.

Thirdly, although *D. gigas* does not permanently inhabit the root, it may enter the plant via the root and the plant and free-living nematodes can be recovered from soil water. For example, Thorne (1962) noted that *D. dipsaci* can be moved in irrigation water: approximately 25 *Ditylenchus* nematodes per liter were recovered in wastewater from an infected field in Utah.

Finally, the nematodes may have been dispersed by wind or on birds. McKenry and Roberts (1985) noted that *D. dipsaci* can be blown in soil particles or infested propagules. Godfrey (1924) hypothesised that the prevalent occurrence of *D. dipsaci* on the Pacific Coast of the U.S. was a result of wind-blown infected seed of *Hypochaeris radicata*.

Faba bean seeds can harbour large number of nematodes. The nematodes are capable of surviving and can remain viable in extreme conditions, hence stored seeds remain an important inoculum source. Green and Sime (1979) established that a single infected faba bean seed can harbour up to 19,000 *D. dipsaci*. Even at low nematode populations, *Ditylenchus* can cause mild, but detectable symptoms. In the present study, as few as 30 *D. gigas* per plant caused mild but detectable symptoms on faba bean.

Most nematodes were recovered from the shoot, whilst the fewest came from the seeds. This may be because the nematode usually enters the plant through the stomata and moves, feeds (on parenchymatous tissue, i.e., in the shoot) and reproduces within plant cells, moving to other parts of the plant when the population builds up.

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In 2018, the plants did not pod, because the experiment was conducted between the months of July to November and the cultivar tested (cv. Fuego) is a spring variety. This cultivar is normally cultivated between late February and July. The experiment in 2017 was conducted in the spring (March–July) and flowered at about 7–8 weeks after sowing. The conditions in the 2018 experiment were unsuitable for seed production (Appendix S1, Figures S1–S4), although the 2018 experiment flowered almost at the same growing time as that of 2017. However, flowers in 2018 were few and there was much abscission. As a result, not unexpectedly, no pods were produced.

In the interaction experiments, *B. fabae* inoculation primarily affected the multiplication of *D. gigas* when the dose of nematodes received by the host plants was high. The symptom severity scores of *D. gigas* were higher when *D. gigas* was inoculated alone rather than when co-inoculated with *B. fabae*. *D. gigas* did not increase the severity of chocolate spot induced by *B. fabae*.

Reduction in grain yield was greater when both organisms were inoculated than with either organism alone.

The reproduction rate of *D. gigas* alone and with co-inoculation with *B. fabae* fell with increasing dose of *D. gigas* only if the *D. gigas* dose was above 100 nematodes per plant. The slightly lower reproduction rate of *D. gigas* inoculated at low doses suggests plant defences which are effective initially but exhausted as inoculum dose rises. By contrast, reduced reproduction rates of *D. gigas* when initial nematode doses were high may be because of competition amongst the nematodes. Similar low reproduction rates at high inoculum doses were reported by Seinhorst (1970) and Greco and di Vito (2009).

Susceptible genotypes to *D. gigas* in faba bean are characterised by increased stem swelling and brownish stem lesions (Caubel & Leclercq, 1989). Severity symptom index and rate of reproduction are used as a measure of resistance in faba bean (Hooper, 1984) but severity is much quicker to measure than reproduction rate. In the present study, the strong correlation between severity and recovery of *D. gigas* suggests that symptom severity is a useful proxy for multiplication rate.

D. gigas did not change the severity of chocolate spot induced by *B. fabae* (Figure S6). By contrast, Griffin (1990) reported that *D. dipsaci* increased the severity of wilt induced by *Fusarium oxysporum* f. sp. *medicaginis* on alfalfa. One likely reason for non-increase in the severity of chocolate spot by *D. gigas* is that *B. fabae* causes cell death and colonises dead substrate. *Ditylenchus* can only propagate in a living host and not in dead tissue (Perry & Moens, 2013).

In conclusion, this study showed that *D. gigas* could spread at least 1.6 m from an infected source to adjacent plants up to in a season and multiplied up to 75-fold in a season, with implications for regulatory control. The population of the nematode can persist in the soil, thus affecting future crops. *D. gigas* did not alter the severity of chocolate spot induced by *B. fabae*, but in a controlled environment *B. fabae* partly suppressed the reproduction of *D. gigas* on faba bean. Seed yield of faba bean was least when plants were infected with both organisms at high doses.

ACKNOWLEDGEMENTS

Funded by Federal University of Agriculture Makurdi, Nigeria and University of Reading. Becky Howard of the Processors and Growers Research Organisation Peterborough kindly donated the initial *D. gigas* culture.

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How to cite this article: Isadeha, A., Shaw, M. W., & Pembroke, B. (2024). Spatial spread of *Ditylenchus gigas* and its interaction with *Botrytis fabae* on *Vicia faba*. *Annals of Applied Biology*, 1–7. https://doi.org/10.1111/aab.12945

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