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Arbuscular mycorrhizal fungi enhance the efficacy of Solanum trap crops against potato cyst nematodes

Hadil KBAR [1], Michael LEWIS [2], Nyambura MWANGI [2], M. Willow H. MAXWELL [1],
Matthew BACK [2,*] and Chris A. BELL [1,*]

[1] *School of Biology, Faculty of Biological Sciences, University of Leeds, Leeds, UK*
[2] *Agriculture and Environment Department, Harper Adams University, Newport, UK*
ORCID iDs: Maxwell: 0009-0004-3886-6296; Back: 0000-0003-4774-5491; Bell: 0000-0002-7437-2793

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Summary – Potato cyst nematodes cause significant yield losses in potato crops worldwide. Trap cropping with non-host solanaceous species offers a sustainable alternative to chemical control by inducing nematode hatching without supporting lifecycle completion. However, trap crop efficacy is often limited by poor establishment under nutrient-deficient conditions. Arbuscular mycorrhizal (AM) fungi, known to enhance plant growth through improved nutrient acquisition, may strengthen trap crop performance. This study investigated whether AM fungi colonise Solanum trap crops (*S. chenopodioides* and *S. scabrum*) and assessed their impact on *Globodera pallida* suppression. Both plant species were colonised by AM fungi, resulting in increased root biomass. In sterile and field soils, AM fungal inoculation significantly enhanced the ability of trap crops to reduce *G. pallida* populations compared to AM-free plants. Furthermore, root leachates from AM-colonised trap crops induced greater expression of the nematode hatching gene *Gp-nep-1*, suggesting amplified hatch stimulation. These findings demonstrate that AM fungi improve both growth and biological efficacy of Solanum trap crops, positioning AM-enhanced trap cropping as a potential strategy for integrated *G. pallida* management.

Keywords – *Globodera pallida*, *Gp-nep-1*, hatching, *Solanum chenopodioides*, *Solanum scabrum*.

Over 380 million tonnes of potato were produced in 2023, placing it as the most produced non-cereal food crop (FAOSTAT 2023). Like all plants, *Solanum tuberosum* is subject to various pathogens and pests, ranging from insects and nematodes to fungi and viruses. *Globodera pallida*, the white potato cyst nematode, is a widespread biotrophic endoparasite that along with the closely related *G. rostochiensis*, causes major damage to potato crops worldwide (approximately 9% crop losses per annum; Kantor *et al.*, 2022). In the UK alone, potato cyst nematodes cause over £30 million in economic losses per annum (Price *et al.*, 2021). Although *G. pallida* and *G. rostochiensis* exclusively infect Solanaceous species, the historically reduced availability of commercially viable resistant cultivars has resulted in their increased persistence in agricultural soils (Gartner *et al.*, 2021). A major contributor to their persistence is the ability of *Globodera* eggs to lay dormant in soils until they perceive exudates, specifically the exuded hatching factors, from Solanaceae plant roots (Price *et al.*, 2021). Hatching factors alter the permeability of the eggshell membrane resulting in rehydration of the nematode within and contributing to its hatching (Perry & Beane, 1989). Several hatch-inducing compounds have been identified although they remain poorly characterised (Devine *et al.*, 1996; Schenk *et al.*, 1999; Byrne *et al.*, 2001; Shimizu *et al.*, 2020; Bell *et al.*, 2021a; Price *et al.*, 2021). Additionally, the molecular aspect to the hatching process is yet to be fully characterised. A *Globodera* neprilysin gene, which encodes a metalloprotease, was identified as the first transcript to be upregulated in eggs treated with host root exudate and was suggested to activate or inactivate peptide hormones that may then cascade events to facilitate hatching (Duceppe *et al.*, 2017). It is unknown whether the regulation of these signal cascades is responsive to different hatching factors, or root exudates, thereby resulting in differential hatching rates.

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* Corresponding authors, e-mails: c.a.bell@leeds.ac.uk; mback@harper-adams.ac.uk

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Plants that can induce hatching of *Globodera*, but are not actual hosts themselves, are referred to as 'trap crops' (Mhatre *et al.*, 2021). Typical trap crops are members of the Solanaceae family that likely exude similar hatch-inducing compounds as potato, but do not allow the nematode to complete its life cycle within the root, thereby leading to a reduced nematode egg population within the soil (Dandurand *et al.*, 2019; Gómez-Armesto *et al.*, 2025). Solanaceous trap crops such as *S. chenopodioides* (tall nightshade), *S. scabrum* (African nightshade) and *S. sisymbriifolium* (sticky nightshade) have been suggested as control options in certain scenarios and environments, due to their strong hatch-inducing potential coupled with their non-host status towards *G. pallida* (Chitambo *et al.*, 2019; Hickman & Dandurand, 2023). The efficacy of these trap crops has been evidenced in both glasshouse and field trials (Timmermans *et al.*, 2007; Hickman & Dandurand, 2023). For example, *S. scabrum* may reduce *Globodera* populations by up to 80% (Chitambo *et al.*, 2019). Unfortunately, the relative success of these trap crops is highly dependent on how well they can establish in the field, which is largely dictated by the growing climate and plant nutrition (Timmermans *et al.*, 2007). Efforts to improve trap crop vigour would greatly improve their deployment as part of integrated pest management systems.

Plant nutrition may be enhanced through mutualistic relationships with beneficial soil organisms. Arbuscular mycorrhizal (AM) fungi can form symbiotic relationships with potato roots, where they deliver soil nutrients such as N and P to the roots in exchange for plant-fixed carbon (Smith & Read, 2008; Bell *et al.*, 2022). As these nutrients are a major limiting factor for plant growth (Agren *et al.*, 2012), AM fungal associations can often lead to increased plant vigour, including in *S. tuberosum* where AM fungal colonisation may increase root biomass as well as overall nutrition, increasing host tolerance to *G. pallida* (Bell *et al.*, 2023a, b). Although AM-colonised *S. tuberosum* exhibit increased tolerance to *G. pallida*, they are simultaneously more susceptible to their infection, potentially due to the enhanced nutrition of AM fungal-colonised host plants (Bell *et al.*, 2022). This implies that although AM fungi may impart some benefits to plant growth, they could concurrently increase the soil populations of parasitic nematodes.

Here, we investigated whether *Solanum* trap crops are hosts for AM fungi and if fungal colonisation impacts plant susceptibility to *G. pallida*, thereby affecting the function of trap crops in depleting the soil nematode population. To validate the hatching signal cascades induced by trap crop leachates and potential AM fungal interactions, we quantified the responsiveness of the *Globodera* hatching-indicator gene, *Gp-nep-1*.

Materials and methods

AM FUNGAL INOCULATION AND PLANT GROWTH

Firstly, the host status of *S. scabrum* and *S. chenopodioides* to AM fungi was determined. *Solanum scabrum* and *S. chenopodioides* plants were established in 12 cm pots (five replicates of each) containing sand:topsoil (50:50, RHS Silver Sand:Bailey Norfolk Topsoil; heat-sterilised; nutritional information previously determined Bell *et al.*, 2023a). Pots were inoculated with either *Rhizophagus irregularis* at a rate of 30 g pot^{-1} (PlantWorks UK) or blank inoculum (*i.e.*, AM fungi-free), to account for any nutrients in the carrier mix. The carrier mix was composed of pumice:zeolite 1:1 consisting of approximately 7000 spores plus hyphae. Plants were grown at 19°C under 16 h/8 h light/dark cycles for 3 weeks before harvesting.

STAINING OF AM FUNGI

Root samples were cleared in 10% potassium hydroxide on a 90°C heat block for 30 min. AM fungal structures were stained with ink and vinegar (5% pelican brilliant black, 5% acetic acid, 90% distilled water) (Vierheilig *et al.*, 1998) at 90°C for 15 min. Roots were destained in 1% acetic acid and mounted on microscope slides using polyvinyl lacto-glycerol. The AM fungal structures (hyphae, arbuscules, or vesicles) were counted to assess for AM colonisation in the roots using the intersect method (McGonigle *et al.*, 1990).

ASSESSMENT OF TRAP CROP EFFICACY

In Glasshouse Experiment 1, stock *G. pallida* soil was obtained from glasshouse cultures (Lindley PA2/3, originally obtained from UK soils in 2010) and mixed into 20 cm pots (4.3 l) containing sand:topsoil 50:50, prepared as described above, to achieve a final population of 20 eggs (g soil)$^{-1}$. Glasshouse Experiment 2 was conducted using *G. pallida* infested soil obtained from fields located at Adney Yard Field, Shropshire, UK (52°45′56″N, 2°25′54″W) and mixed to create a potting mix of field-soil: sand 50:50 in 20 cm pots. Soil samples (5×10 cm cores) were taken from each pot and dried in an oven. The cysts were extracted using a Fenwick can (1940) before crushing and quantification of eggs, to determine the initial *G. pallida* densities for individual pots (20-52 eggs (g soil)$^{-1}$).

For both glasshouse experiments, seeds of *S. chenopodioides* and *S. scabrum* were sown in the aforementioned *G. pallida* infected soil at 19°C under 16 h/8 h light/dark cycles. In Glasshouse Experiment 1 one plant was grown per pot and in Glasshouse Experiment 2 six seeds were grown in each pot. Treatments consisted of the two solanum species (*S. chenopodioides* and *S. scabrum*) planted in pots treated with aggregate containing *Rhizophagus irregularis* (30 g pot^{-1}) or the blank carrier aggregate (30 g pot^{-1}) and fallow (non-treated and non-planted) pots. Each treatment was replicated six times ($n = 30$). Pots were watered every other day with the same volume of water (200 ml) and plants were grown for 14 weeks until senescence. Pots were treated with tomato feed (Tomorite; NPK 4-3-8) weekly from week 12 to aid crop health, at the manufacturer's recommended dose of 4 ml (l water)$^{-1}$. Upon harvest, roots were washed to remove soil and allowed to air dry before weighing. Roots were stained to confirm AM fungal colonisation of each plant. For each experiment, soils from different pots were pooled and six 100 g aliquots were taken for cyst extraction using a Fenwick can (1940). Cysts were manually crushed to quantify eggs. Final (P_f and initial (P_i) egg quantities were used to determine the reproductive potential of each treatment.

GP-NEP-1 GENE EXPRESSION ANALYSIS

Three weeks after germination of *S. chenopodioides* and *S. scabrum* in both AM fungal inoculated and AM-free soils, plant pots were watered to saturation; 200 ml of excess water was administered and collected from the bottom of the pot, hereafter described as soil leachate. Leachate was also collected from sterilised soils without a plant, as control. Groups of five *G. pallida* cysts were treated with root leachates for 8 days, until juveniles began to hatch. Control treatment was set up with water instead of root leachate and ended at the same timepoint. Total RNA was purified from the treated cysts, firstly by crushing cysts in an Eppendorf using a micropestle and then by using the E.Z.N.A® Plant RNA Kit (Omega Biotek) including a DNase treatment. First-strand cDNA was synthesized from 500 ng RNA using iScript cDNA Synthesis Kit (BioRad) following the manufacturer's instructions. Quantitative reverse transcriptase (qRT)-PCR was carried out on the resulting cDNA using SsoAdvanced™ Universal SYBR® Green Supermix (Bio-Rad) and a CFX Connect instrument (Bio-Rad). Expression of *G. pallida neprilysin-1* (GPLIN_000276000) was studied and normalised to the housekeeping gene *Elongation Factor 1-α* (Nicot *et al.*, 2005). Primers Gpnep1F (5′-TCACGGCATCAGACAACATT-3′), Gpnep1R (5′-CCG TGTCACTTAGCCGATTT-3′), GpEF1aF (5′-AATGACC CGGCAAAGGAGA-3′), and GPEF1aR (5′-GTAGCCGG CTGAGATCTGTC-3′) were used for analysis of *G. pallida neprilysin-1* and *Elongation Factor 1-α*, respectively (Hoysted *et al.*, 2018). Gene expression analysis was performed on seven biological replicates for all treatments, and each reaction was carried out in technical triplicate.

DATA ANALYSIS

The data obtained from this study were analysed using OriginPro. The initial population (P_i) and the final population (P_f) were compared by using P_f/P_i to obtain the change in populations. The histogram of residuals demonstrated that the data were normally distributed; therefore, no transformation of the data was required. One-way analysis of variance (ANOVA) and Tukey *post hoc* tests were used to compare the effect of both *Solanum* trap crops and AM fungal inoculation against controls. Two-way ANOVA coupled with Tukey *post hoc* tests were used to outline the influence and interactions between individual trap crop species and AM fungal inoculation. Data are given as means±standard error.

Gene expression data were analysed using the $2^{-\Delta\Delta CT}$ method (Taylor *et al.*, 2019).

Results

AM FUNGAL COLONISATION OF SOLANUM TRAP CROPS

Three weeks post-inoculation, AM fungal colonisation of both *S. chenopodioides* and *S. scabrum* was observed. *S. chenopodioides* and *S. scabrum* root lengths were colonised 24.6±1.2% and 23.6±7.4%, respectively. Roots from non-AM-inoculated treatments were not colonised.

SOLANUM TRAP CROP ROOT WEIGHT

The biomass of 14-week-old STC roots from Experiment 1 were measured upon harvest to determine an effect of AM fungal colonisation. The presence of AM fungi increased the root biomass of both *S. chenopodioides* and

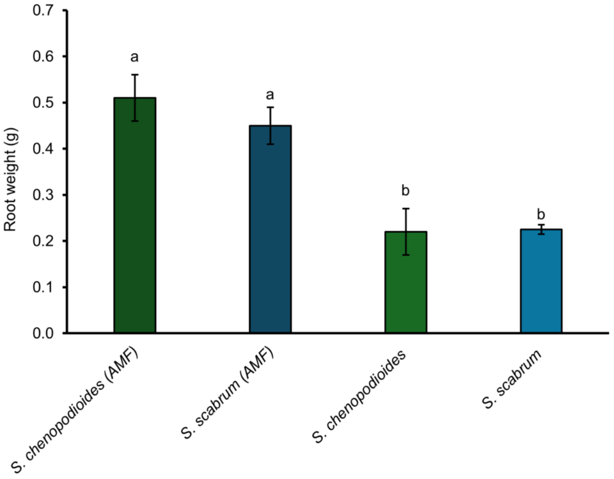

Fig. 1. Biomass of *Solanum chenopodioides* and *S. scabrum* roots grown with and without AM fungi inoculation (Experiment 1). Root biomass taken at harvest at 14 weeks growth. Bars show mean with error bars representing the standard error. N = 12. Letters denote significant difference according to one-way ANOVA plus Tukey's *post hoc* test.

S. scabrum (Fig. 1; $P < 0.05$; one-way ANOVA followed by Tukey *post hoc* test).

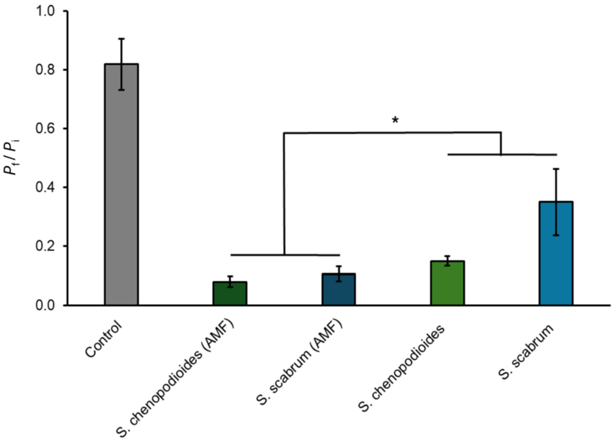

Fig. 2. Effect of arbuscular mycorrhizal (AM) fungi on *Globodera pallida* suppression by Solanum trap crops in sterile soils (Experiment 1). *Globodera pallida* cysts were quantified in pots after 14 weeks-growth of *Solanum chenopodioides* and *S. scabrum.* Pots contained sterilised compost inoculated with cyst-containing soil at known concentrations. AM fungi were inoculated in respective pots upon planting. Final (P_f) and initial (P_i) populations were used to calculate reproductive capacity ($P_\mathrm{f}/P_\mathrm{f}$). Bars show mean with error bars representing the standard error. n = 12. Two-way ANOVA followed by Tukey *post hoc* test with * indicating $P < 0.05$, between +/− AM inoculated pots.

AM FUNGAL COLONISATION INCREASES THE EFFECTIVENESS OF TRAP CROPS AGAINST *G. PALLIDA* IN BOTH STERILE AND FIELD SOILS

To determine whether AM fungal colonisation impacted the hatch-inducing effect of trap crops, the soil *G. pallida* population was quantified post-trap crop growth with AM fungi (Experiment 1). Soils were sterilised pre-AM fungi and *G. pallida* inoculation to test the specific AM fungi-*G. pallida* interaction. Both *S. chenopodioides* and *S. scabrum* triggered hatching of *G. pallida* and led to a reduced soil *G. pallida* population as a result of their non-host status, compared to fallow soils (Fig. 2; $P < 0.05$; one-way ANOVA followed by Tukey *post hoc* test). The effect of AM fungal colonisation of both trap crops (25±4.5%; total root colonisation) on *G. pallida* hatch was broadly similar across plant species ($P = 0.054$; two-way ANOVA followed by Tukey *post hoc* test). The presence of AM fungi regardless of plant species significantly further decreased *G. pallida* soil populations, compared to AM-free trap crops (AM + $P_\mathrm{f}/P_\mathrm{i} = 0.096$, AM − $P_\mathrm{f}/P_\mathrm{i} = 0.236$; $P = 0.03$; two-way ANOVA followed by Tukey *post hoc* test). There was no significant interaction between AM fungal inoculation and plant species ($P = 0.09$; two-way ANOVA followed by Tukey *post hoc* test).

To assess the potential field applicability of AM fungi for enhancing *G. pallida* control through trap crops, non-sterilised field soils were used (Experiment 2) to account for the potential contrasting effects of microbial diversity. Both trap crop species reduced the *G. pallida* soil population in field soils (Fig. 3; $P < 0.05$, one-way ANOVA). Inoculation of pots with *R. irregularis* led to AM fungal colonisation of both *S. scabrum* (31±1.4%) and *S. chenopodioides* (25±2.2%). Both trap crop species grown in field soils containing blank inoculum were not colonised by AM fungi (0±0%). Two-way ANOVA and Tukey *post hoc* analyses indicated that there was no effect of plant species on the reduction of *G. pallida* soil populations as a result of trap crop growth ($P = 0.41$); however, the presence of AM fungi, regardless of trap crop identity, further increased the effect of trap crops on *G. pallida* populations (AM + $P_\mathrm{f}/P_\mathrm{i} = 0.354$, AM - $P_\mathrm{f}/P_\mathrm{i} = 0.470$; $P = 0.02$; two-way ANOVA followed by Tukey *post hoc* test) (Fig. 3). There was no significant interaction between plant species and AM fungal inoculation ($P = 0.47$).

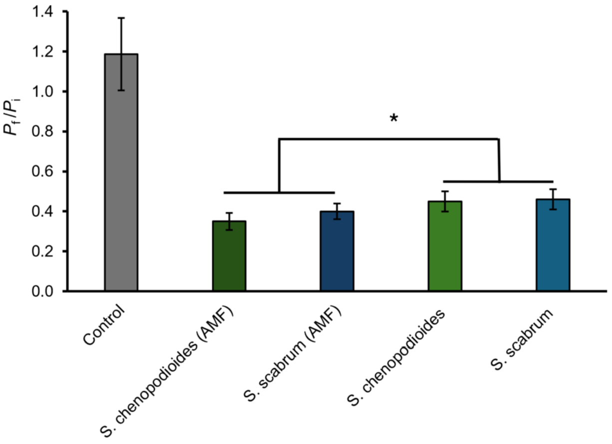

Fig. 3. Influence of arbuscular mycorrhizal (AM) fungal colonisation on *Globodera pallida* suppression by Solanum trap crops grown in field soil. *Globodera pallida* cysts were quantified in pots after 14 weeks-growth of *Solanum chenopodioides* and *S. scabrum*. Plants were grown in field soils with known concentrations of *G. pallida* cysts. AM fungi were inoculated in respective pots upon planting. Final (P_f) and initial (P_i) populations were used to calculate reproductive capacity (P_f/P_i). Bars show mean with error bars representing the standard error. n = 12. Two-way ANOVA followed by Tukey *post hoc* test with * indicating $P < 0.05$, between +/− AM inoculated pots.

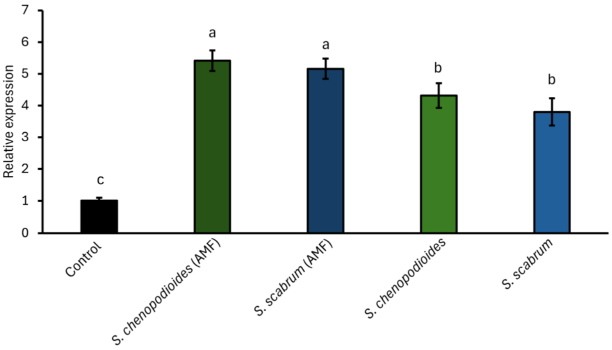

Fig. 4. Expression of a neprilysin gene (*Gp-nep-1*) in *Globodera pallida* cysts treated with trap crop root leachate. *Globodera pallida* cysts were treated with root leachates from pots growing *Solanum chenopodioides* or *S. scabrum* that were +/− colonised by arbuscular mycorrhizal (AM) fungi. Expression was normalised to *Elongation Factor 1-α* and presented relative to expression in cysts treated with leachates collected from sterilised soils. All treatments were applied 8 days before gene expression analysis. Values are means±SE from seven replicates with five cysts per replicate. Letters denote significant differences between treatments (one way ANOVA followed by Tukey *post hoc* test; $P < 0.05$).

Gp-nep-1 GENE EXPRESSION ANALYSIS

We investigated expression of *Gp-nep-1* in *G. pallida* eggs treated with *Solanum* trap crop leachates when roots were either colonised/non-colonised by AM fungi due to the gene's role in hatching in response to compounds secreted by potato roots (Duceppe *et al.*, 2017; Hoysted *et al.*, 2018). Exposure of *G. pallida* cysts to leachates from *Solanum* trap crops induced upregulation of *Gp-nep-1* greater than when treated with leachates from fallow, sterile soils (Fig. 4). Leachates collected from AM fungi-inoculated pots led to greater *Gp-nep-1* induction beyond that observed from AM-free pots (Fig. 4).

Discussion

This study demonstrates that Solanum trap crops are hosts to AM fungi and that this association enhances the efficacy of these trap crops in controlling *G. pallida*. AM fungal colonisation increased the root biomass and hatching potential of both *S. chenopodioides* and *S. scabrum*, leading to a greater reduction in soil *G. pallida* populations. These findings suggest that AM fungi may serve as a valuable co-treatment in integrated pest management strategies targeting *G. pallida*, particularly in environments where trap crop establishment is a limiting factor.

The successful colonisation of *S. chenopodioides* and *S. scabrum* by AM fungi aligns with previous reports that *Solanum* species are compatible hosts for AM symbiosis (Smith & Read, 2008; Songachan & Kayang, 2012; Bell *et al.*, 2021b, 2022, 2023a, b, 2024; Carrara *et al.*, 2023; Demir *et al.*, 2024; Magkourilou *et al.*, 2024; Maxwell *et al.*, 2025). While potato (*S. tuberosum*) is known to benefit from AM associations through improved nutrient uptake and stress tolerance, this study extends those benefits to non-host solanaceous species used as trap crops, through observed increases in root biomass. The colonisation rates observed (∼24%) suggests that these species form symbioses with AM fungi, similar to other nightshade species (Songachan & Kayang, 2012). AM fungal colonisation resulted in an increase in root biomass that in turn yielded an increase in *G. pallida* hatch from these soils. Colonisation of *S. tuberosum* by different arbuscular mycorrhiza species has previously been reported to increase *G. pallida* hatching (Ryan *et al.*, 2000; Deliopoulos *et al.*, 2007). Likewise, greater nutrition of Solanums from their AM association (Bell *et al.*, 2022) may provide greater resources, potentially allowing for greater quantity and perhaps quality of exudation, as seen in other plant species (Sarathambal *et* *al.*, 2023). The dual role of AM fungi, enhancing plant growth while potentially increasing susceptibility to *G. pallida* (Bell *et al.*, 2022), raises important questions about the balance between biomass-driven efficacy and an unintended facilitation of nematode development, when hosts are planted. In trap crops, however, where *G. pallida* lifecycle completion is blocked, this trade-off is presumably less concerning, but it warrants further investigation in mixed cropping systems or rotational designs. The lack of an interaction between trap crop species and AM fungal inoculation suggests that trap crop identity does not influence the observed effects on nematode populations. Rather, AM fungal colonisation generally increased the performance of solanaceous trap crops in suppressing *G. pallida* populations.

The observed upregulation of *Gp-nep-1* in *G. pallida* eggs following exposure to leachates from *S. chenopodioides* and *S. scabrum*, particularly when roots were colonised by arbuscular mycorrhizal (AM) fungi, suggests that these trap crops activate a hatching cascade analogous to that triggered by potato in the absence of AM fungi (Duceppe *et al.*, 2017). *Gp-nep-1* encodes a metalloprotease with responsive gene expression to root exuded chemical cues and is indicated to degrade the eggshell to facilitate hatching (Duceppe *et al.*, 2017; Hoysted *et al.*, 2018). This supports the hypothesis that trap crops can exploit the nematode's innate host-recognition mechanisms to induce hatching and that AM fungal symbiosis may amplify this effect by modulating plant secondary metabolism or root physiology. Greater induction of *Gp-nep-1* following exposure to leachates from AM fungal-colonised pots, compared to AM-free pots, may indicate an earlier induction of hatching and/or a greater percentage of eggs responding to these leachates.

Beyond AM fungal inoculation, several agronomic strategies have been proposed to improve trap crop performance. Fertilisation regimes, particularly nitrogen and phosphorus supplementation, are often required for *S. sisymbriifolium* (Timmermans *et al.*, 2007), which also germinates significantly greater under warmer temperatures, reducing its efficacy in colder climates (Gómez-Armesto *et al.*, 2025). The sowing density, time of year and rainfall can also impact trap crop establishment and subsequent success (Timmermans *et al.*, 2007). The integration of AM fungi into these strategies may offer a scalable and sustainable solution to improve establishment in marginal soils or under nutrient-limited conditions.

Trap cropping presents a biologically targeted and environmentally friendly approach, particularly when enhanced by AM fungi, towards *Globodera* species. Unlike chemical treatments, trap crops do not pose toxicity risks, and unlike resistant cultivars, they do not rely on genetic resistance mechanisms that can be overcome by nematode adaptation (they are non-hosts). The addition of AM fungi further strengthens this strategy by improving plant vigour and hatch induction, potentially shortening the time required to reduce soil nematode populations. Furthermore, the potential saleable quality of species such as *S. scabrum* or their use as green-manure could give secondary benefits (Gómez-Armesto *et al.*, 2025). The efficiency of AM fungi in soils obtained from the field, outlines the robustness of the approach and potentially the lack, or minimal influence, of competition/deleterious interactions with other soil microorganisms. Different *Globodera* populations or pathotypes may react differently the effects observed within this study, potentially reducing efficacy of this approach. However, it is likely that trap crop growth may be a greater variable determining efficacy, given their sensitivity to climate and nutrition (Timmermans *et al.*, 2007). It is interesting that non-inoculated field soils did not yield AM colonisation of the trap crops, suggesting a lack of AM fungi, which are commonly referred to as ubiquitous in soils, capable of colonising these trap crops.

Although AM fungi improved trap crop performance in this study, the practicality of applying AM inoculum at field scale remains uncertain. Current commercially available inoculum would equate to a substantial quantity of product per hectare, raising questions about the weigh trade-off between cost and application logistics, and the *G. pallida* reduction potential compared to other approaches. Future research is required to increase the efficiency of the delivery systems, by using approaches such as seed coatings or low volume formulations. These considerations suggest that the integration of AM fungi into trap cropping based pest management programmes will require further evaluation of both economic feasibility and practical deployment. Furthermore, *Solanum* trap crops can self-seed and may persist as groundkeepers without herbicide applications. Certain *Solanum* species used as trap crops have also been reported to act as reservoirs for other potato pathogens such as spindle viroid (Fowkes *et al.*, 2021). These factors highlight the need to balance nematode management benefits with broader agronomic risks when integrating trap crops into field rotations.

This study reveals that AM fungi significantly enhance the performance of solanaceous trap crops in controlling

G. pallida, a major pest of potato. By colonising the roots of *S. chenopodioides* and *S. scabrum*, AM fungi increased root biomass and amplified the effect of these plants in reducing soil nematode populations. These findings suggest that AM fungi not only improve trap crop growth but also boost their biological efficacy, positioning AM-enhanced trap cropping as a promising sustainable strategy within integrated pest management frameworks for potato cyst nematodes.

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