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Oilseed radish/black oat subsidiary crops can help regulate plant-parasitic nematodes under non-inversion tillage in an organic wheat-potato rotation

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Summary – Soil conservation is one of the major challenges for agriculture in the 21st century. For this reason, non-inversion tillage systems including subsidiary crops have become popular over the last three decades in Europe. However, the adoption of new agricultural practices may change the diversity and abundance of certain pests and diseases. For example, plant-parasitic nematodes that are major threats towards cultivated plants may be promoted if good hosts, such as certain subsidiary crops and weeds, occur more frequently. The indigenous plant-parasitic nematode fauna under organic farming systems is already adapted to diverse crop rotations and usually dominated by nematodes with broad host ranges. These may be further enhanced in organic farming systems if non-inversion tillage is introduced, which generally increases the abundance and biomass of certain weeds. We evaluated the early effects of non-inversion tillage and subsidiary crops in an organic wheat-potato rotation on plant-parasitic nematodes in two field experiments in two successive years. The total densities of plant-parasitic nematodes increased from an initial 1260 nematodes (100 ml soil)$^{-1}$ at the start of the experiment to 1850 and 1700 nematodes (100 ml soil)$^{-1}$ after wheat under non-inversion and conventional tillage, respectively. Plant-parasitic nematode densities then decreased on average to 1100 and 560 nematodes (100 ml soil)$^{-1}$ after subsidiary crops and potatoes, respectively. Parasitic nematode densities tended to be higher under non-inversion than conventional tillage, except where oilseed radish and black oats had been used as cover crops. For the latter, no differences between tillage treatments occurred. In the second experiment, about 1700 free-living nematodes (100 ml soil)$^{-1}$ were found under conventional tillage without mulch while under reduced tillage with mulch their numbers were significantly higher at 3100 nematodes (100 ml soil)$^{-1}$. We conclude that an appropriate choice of subsidiary crops can be an important management factor for the long term sustainability of non-inversion tillage systems.

Keywords – compost, conservation agriculture, crop rotation, nematode dynamics.

The three principles of conservation agriculture are defined as permanent soil cover, crop rotation and minimum tillage (Hobbs, 2007). Within this concept, permanent soil cover can be achieved by subsidiary crops, *i.e.*, cover crops and living mulches used for their ecosystem services. If done correctly, conservation agriculture will provide the nutrients required for the subsequent cash crop and at the same time control pests and diseases. Although no-tillage, minimum tillage and reduced tillage systems are increasingly promoted, organic farming in Europe is mostly based on intensive soil tillage. The main reasons for conventional tillage in organic farming are concerns regarding yield losses due to reduced nutrient mineralisation in non-inversion tillage systems as well as excessive weed infestations (Peigné *et al.*, 2007; Carr *et al.*, 2013).

On the positive side, conservation agriculture increases soil organic matter, microbial activity and soil biodiversity, which in the long term might lead to soil suppressiveness (van Bruggen & Semenov, 2015). Among others, free-living nematodes are especially stimulated, providing a range of ecosystem services such as nutrient mineralisation and disease control (Barker & Koenning, 1998; Briar *et al.*, 2007; Ferris, 2010). In contrast to free-living nematodes, the role of plant-parasitic nematodes in conservation agriculture is still unclear. So far it can only be speculated that they might become more important, espe-

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cially if good hosts, such as certain subsidiary crops and weeds, occur more frequently within rotations.

Both nutrient deficiency and weeds affect plant-parasitic nematodes. Whilst nutrient-deficient plants might be more susceptible to nematode attack, weeds within a non-host crop may serve as alternative hosts allowing nematode reproduction. Similarly, subsidiary crops meant to provide continuous soil cover can serve as a food source for plant-parasitic nematodes in times when otherwise no host plants would be grown (Thomas *et al*., 2005; Hallmann & Kiewnick, 2015). Subsidiary crops and weeds especially promote plant-parasitic nematodes with a broad host spectrum, such as *Meloidogyne*, *Pratylenchus* and several ectoparasitic species (Thomas, 1978; Thomas *et al*., 2005) that can build up high population densities in otherwise apparently sustainable systems (Barker & Koenning, 1998).

To avoid build-up of plant-parasitic nematodes, certain non-host subsidiary crops might also be used in conservation agriculture for nematode control. For example, certain cultivars of *Raphanus sativus* and *Sinapis alba* are resistant to *Heterodera schachtii*, and *Crotalaria* and *Tagetes* spp. have been shown to suppress *Meloidogyne* spp. and *Pratylenchus* spp. (Hirling, 1977; Barker & Koenning, 1998; Hallmann & Kiewnick, 2015). Furthermore, black oat (*Avena strigosa*) is a non-host for *Pratylenchus penetrans* and *Meloidogyne hapla* (Visser & Molendijk, 2015).

In addition to subsidiary crops, conservation agriculture often employs compost and organic mulches for nutrient supply and enhanced soil health (Watson *et al*., 2002). However, under temperate climatic conditions, organic amendments do not lead to a general suppressiveness of plant-parasitic nematodes (McSorley, 2011). In cases where nematode suppression was observed, composts had often been applied at impractically high dosages (McSorley & Gallaher, 1996) or contained toxic rates of nitrate or ammonia (McSorley, 2011). Nonetheless, crop yields generally increased after organic amendments despite having limited nematode control (McSorley, 2011).

In this study, we evaluated the effects of: *i*) a standard organic crop rotation (2 years of grass-clover, wheat and potato); *ii*) subsidiary crops following wheat; and *iii*) minimum tillage on the dynamics of plant-parasitic nematodes. We hypothesised that under minimum tillage leguminous subsidiary crops and weeds will increase plant-parasitic nematode densities, whilst opposite effects are expected from oilseed radish/black oat as subsidiary crops.

The specific objectives of this study were: *i*) to evaluate the spectrum of plant-parasitic nematodes after 2 years of grass-clover and subsequently during the wheat-potato cropping sequence; *ii*) to evaluate the effect of non-inversion tillage and organic mulch on plant-parasitic and free-living nematodes; and *iii*) to evaluate the role of subsidiary crops and weeds on plant-parasitic nematode dynamics.

Materials and methods

Experimental design

The experiments were conducted at the organically managed experimental farm of the University of Kassel near Witzenhausen, Germany (51°22′N, 9°54′E), and were established in successive years, *i.e.*, Experiment 1 from 2010-2014 and Experiment 2 from 2011-2015. The soil was a Typic Hapludalf with 13% clay, 84% silt, and 3% sand with 2% organic matter and a pH of 6.0. Throughout the experimental period, the mean temperature was 9.8°C and the annual rainfall 636 mm.

Both experiments were designed as randomised complete blocks with split-plot arrangements with three factors (two tillage systems (main factor as split plot), four subsidiary crops, and two fertilisation regimes) and four replicates, *i.e.*, 64 plots in total. Each experiment started with 2 years of regularly mulched grass-clover as pre-crop and was followed by winter wheat ‘Achat’. The wheat was either undersown with subterranean clover or white clover that continued to grow after the wheat was harvested or the wheat was followed by a legume or non-legume subsidiary crop. The following spring, all plots were planted with potato ‘Marabel’. Factor I (split) was either: *i*) one and two times chisel ploughing at about 10 cm depth followed by mouldboard ploughing at about 25 cm soil depth (hereafter called CT) before wheat and potato, respectively; or *ii*) two to three times chisel ploughing at about 10 cm soil depth (hereafter called RT) prior to wheat and at about 15 cm soil depth prior to potato. In addition, potatoes in RT received an 8-10 cm mulch layer of a winter pea-rye (2014) or triticale-vetch mixture (2015) of about 12 and 26 t ha^{-1} DM, respectively. Factor II was: *i*) winter wheat undersown with subterranean clover (*Trifolium subterraneum* ‘Dalkeith’); *ii*) winter wheat undersown with white clover (*T. repens* ‘Huia’); *iii*) wheat followed by a legume subsidiary crop (*Vicia sativa* ‘Berninova’); and *iv*) wheat followed by a non-legume subsidiary crop (*R. sativus* var. *oleiformis* ‘Kompass’/*A. strigosa* ‘Pratex’,

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Table 1. Chemical characteristics, including dry matter (DM), bulk density, pH, electrical conductivity (EC), potassium (K), phosphorus (P), total nitrogen (N), carbon (C) and C/N ratio of yard waste composts (⩽20 mm sieved) from municipal trees and shrubbery from the composting plant near Dransfeld (3-month-old) used in 2012 and 2013 before wheat, and from the composting plant near Hannover (Aha, 9-month-old) used before potatoes in 2014 and 2015.

Year	DM (%)	Bulk density ($g\ l^{-1}$)	pH	EC ($\mu S\ cm^{-1}$)	K ($mg\ kg^{-1}$)	P ($mg\ kg^{-1}$)	Total N (%)	Total C (%)	C/N ratio
2012	85	389	7.5	498	3104	541	1.8	29.0	16.0
2013	81	282	6.4	778	NA	807	1.5	37.4	25.5
2014	75	604	7.3	915	5276	547	1.3	20.8	16.2
2015	60	731	8.1	1011	4858	616	1.3	16.9	13.0

mixed 1:4). Due to complete failure of both undersown clover species in both experimental years, living mulches were considered as green fallow. This reduced the number of levels for subsidiary crops to one in wheat and to three for the time thereafter. Factor III was either: *i*) application of 5 and 10 t ha^{-1} DM of a yard waste compost to wheat and potato, respectively, applied manually (YWC); or *ii*) mineral fertilisation consisting of potassium sulphate (K_2SO_4) and phosphorus (rock phosphate) approximately matching the potassium and phosphorus concentration of the composts that were applied to potatoes in 2014 and 2015 (Table 1). Total nitrogen in the compost was below 2% and the C/N ratio ranged from 13 to 25 (Table 1). The pH and electrical conductivity in composts ranged from 6.4 to 8.0 and 500 to 1000 $\mu S\ cm^{-1}$, respectively (Table 1).

Nematode sampling and assessments

Soil samples for nematode extractions were collected four times throughout each experiment: *i*) in August of year 2 from the clover grass just before it was terminated; *ii*) in August of year 3 after wheat; *iii*) in March of year 4 prior to termination of subsidiary crops; and *iv*) in September/October of year 4 after potato. Soil samples were collected from the top 25 cm soil using an auger with 2.4 cm diam. To maintain a representative sample compensating for the heterogeneous distribution of plant-parasitic nematodes within the soil, a total of 20 cores per experimental plot were taken always from the same 4 m^2 sampling area of each plot. The soil was collected in a bucket, thoroughly mixed and each aliquot of 500 ml soil was placed in a plastic bag, labelled and shipped within 1 week to the Julius Kühn-Institut (JKI) in Münster, Germany. At JKI, soil samples were stored at 6°C until evaluation.

Above-ground crop and weed biomass were determined at wheat flowering (BBCH 65) and at fruit development of potatoes (BBCH 75). Subsidiary crops and fallow plots were assessed for soil cover 10 weeks after subsidiary crop sowing. In addition, weeds and subsidiary crops were separated and quantified in the subsidiary crop plots. Biomass samples were oven dried for 24 h at 105°C. Although the weed cover was greater in the weedy fallow than in subsidiary crops, weed species in both treatments were similar, mainly consisting of grasses (*Lolium perenne*, volunteer wheat and *Poa annua*) with similar correlations of soil cover and biomass. Therefore, weed biomass in the fallow treatment was estimated from weed soil cover using the formula:

$$\text{Weed biomass (fallow)} = \text{weed soil cover (fallow)} \times \frac{\text{weed biomass (subsidiary crops)}}{\text{weed soil cover (subsidiary crops)}}.$$

Nematode evaluation

Soil samples were passed through a 1 cm sieve to remove root debris and stones, thoroughly mixed, and 250 ml aliquots were taken for nematode extraction following the centrifugal-flotation method as described in Hooper *et al.* (2005) using $MgSO_4$ at 1.15 specific density. Nematodes collected after the final centrifugation step on a 20 μm sieve were transferred into a measuring cylinder and concentrated in 10 ml tap water. The suspension was thoroughly mixed by agitating with air and 1 ml was transferred into a nematode counting slide. Plant-parasitic nematodes were identified and counted at genus level using a Leitz Labovert FS inverted microscope at 63× magnification. Free-living nematodes were counted in extracts from soil after potatoes in the second experiment but not classified into functional groups. For plant-parasitic nematode

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species identification, a composite sample out of all plots was prepared for each experimental site and sampling date. Nematodes were killed with gentile heat, fixed in a triethanolamine formalin (TAF) solution containing 7 ml formalin (40% formaldehyde), 2 ml triethanolamine and 91 ml distilled water (Courtney *et al*., 1955). Fixed nematode specimen were then processed to anhydrous glycerol over a period of 12 days using the slow evaporation technique at 39 ± 1°C (Hooper *et al*., 2005). Species identification was done after transferring female nematodes into anhydrous glycerol on permanent slide mounts following the method described by Hooper *et al*. (2005). Specimen were examined under a Leitz Diaplan compound microscope equipped with differential interference contrast at 630-1000× magnification.

Statistical analysis and data processing

The statistical analysis was performed with R version 3.2.2 (R Core Team, 2013). Total and individual species densities as well as crop and weed biomass were pooled over both field experiments for statistical analysis. Likewise, green fallow plots with identical treatment combinations (with and without compost) were pooled per split to achieve balanced designs resulting in a total number of plots of 48. To improve variance homogeneity, all data were $\ln(x + 1)$-transformed prior to analysis of variance (ANOVA). The ANOVA that accounted for the split-plot arrangement, where the first main factor (split) is tillage, the second main factor is subsidiary crops, and the third is compost, with experiment and replicates as co-variates, was performed on crop and weed biomass, the total density of nematodes, and the density of each nematode genus after subsidiary crops and potatoes. The same ANOVA design was used for data after wheat but with exclusion of the subsidiary crops that were sown subsequently, and therefore could not have an impact on plant-parasitic nematode composition. Protected Fisher-LSD tests ($P < 0.05$) were used for multiple comparisons of treatments using the R-package *agricolae* (Mendiburu, 2010).

To achieve requirements for multivariate data analysis, nematode data observed at each date were $\ln(x + 1)$-transformed. To assess crop effects on nematode dynamics, final minus initial population densities ($P_f - P_i$ values) of transformed data were calculated for wheat, subsidiary crops including green fallow, and potato. A redundancy analysis (RDA) using the R-package *vegan* (Oksanen *et al*., 2015) was performed after averaging all crop-tillage combinations per replicate. These combinations were used as constraining and experimental years/fields as conditional variables in the RDA following instructions of Dormann & Kühn (2009). Significances of the applied model, factors and axes were analysed *via* permutation test with 999 permutations.

A three-factorial ANOVA accounting for the split-plot arrangement with replicates as covariates was performed to analyse tillage, subsidiary crop and compost effects on free-living nematodes after potatoes in the second experiment (free-living nematodes were not counted in the first experiment).

Results

Both field experiments were run successfully and results were similar, although climatic conditions during the potato season were wet and cool in the first experiment and dry and warm in the second. Therefore, data of both experiments were pooled except for the redundancy analysis. Besides the living mulches that failed in both experiments, only the vetch in the second experiment was sparse due to damage by common voles (*Microtus arvalis*).

The above-ground biomass of all crop species varied considerably ranging from 0.2 t ha^{-1} (vetch) to 6.5 t ha^{-1} (wheat) (Table 2). For all crops, weed biomass was highest under non-inversion tillage, in particular under wheat. By contrast, wheat and oilseed radish/black oat biomasses were highest under conventional tillage, while potato and vetch biomasses were higher under non-inversion tillage.

Wheat yields under conventional tillage were 6.6 t ha^{-1} and 5.5 t ha^{-1} in Experiment 1 and 2, respectively. Yields were 20% lower under non-inversion tillage. Potato yields under conventional tillage were 32.4 t ha^{-1} and 25 t ha^{-1} in Experiment 1 and 2, respectively. Under non-inversion tillage, yields were 12% lower in Experiment 1 but 20% higher in Experiment 2 (OSCAR, 2016). These varying results for potatoes were caused by different weather conditions, *i.e*., a wet and relatively cool late spring 2014 overall favouring potato growth in Experiment 1, compared to an extremely dry and warm spring in 2015 that especially suppressed potato growth in the unmulched ploughed plots in Experiment 2. As indicated above, the undersown clover species in wheat failed in both experiments and, thus, were referred to as green fallow that consisted of annual and perennial grass weeds as well as volunteer wheat. Furthermore, the spring vetch largely failed in Experiment 2 because of common voles that multiplied to high densities due to mild weather conditions. Compost had no effects on the plant-parasitic nematode dynamics and therefore is not shown in detail.

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Table 2. Values of $\ln(x + 1)$-transformed aboveground biomass of main and subsidiary crops including the green fallow and their corresponding weeds (untransformed data in brackets) in t ha^{-1} under conventional (CT) and non-inversion (RT) tillage (df = 7) across the crop rotation. Means from both experiments are shown.

	Wheat	Weeds	Potato	Weeds	Fallow	Weeds[1]	Vetch	Weeds	OR/BO[2]	Weeds
CT	1.943	0.229	0.712	0.052	–	0.334	0.183	0.23	0.342	0.16
	(7.38)	(0.42)	(1.08)	(0.06)		(0.41)	(0.21)	(0.29)	(0.43)	(0.18)
RT	1.729	0.615	0.784	0.081	–	0.445	0.195	0.293	0.253	0.23
	(5.83)	(0.99)	(1.23)	(0.09)		(0.58)	(0.24)	(0.35)	(0.37)	(0.27)
MSE[3]	0.008	0.068	0.047	0.003		0.088	0.012	0.027	0.002	0.015
LSD[4]	0.043	0.126	0.09	0.024		0.175	0.091	0.138	0.04	0.103

[1] Estimated from soil cover values and biomass of weeds under Vetch and OR/BO.
[2] Oilseed radish/black oat mixed 1:4.
[3] Mean Square Errors are results from ANOVA after $\ln(x + 1)$-transformation.
[4] Least Significant Difference of $\ln(x + 1)$-transformed means at $P < 0.05$.

Initial nematode densities

Nematode genera frequently found at the first sampling after grass-clover were *Helicotylenchus* (408 individuals (100 ml soil)$^{-1}$, averaged over both experiments), *Paratylenchus* (446 individuals (100 ml soil)$^{-1}$), *Pratylenchus* (250 individuals (100 ml soil)$^{-1}$), and *Tylenchorhynchus* (148 individuals (100 ml soil)$^{-1}$). Criconematidae and *Meloidogyne* occurred at densities below 20 nematodes (100 ml soil)$^{-1}$ and were summarised as 'other' in the detailed analysis.

Regarding the spectrum of plant-parasitic nematodes, the most prevalent species were *P. neglectus*, *P. flakkensis* and *P. penetrans* that occurred in both years. Other commonly detected species were *H. vulgaris*, *Paratylenchus projectus* and *T. dubius*. Several additional species occurred at low densities or only in one experiment, such as *H. digonicus*, *M. naasi*, *Paratylenchus bukowiniensis*, *Rotylenchulus borealis* and some members of the family Criconematidae.

Plant-parasitic nematode dynamics

On average, a total of 1250 plant-parasitic nematodes (100 ml soil)$^{-1}$ were detected in the grass-clover pre-crop immediately before incorporation (Fig. 1). Main effects are shown as no significant interactions were observed ($P > 0.05$). Averaged over both experiments nematode densities increased to 1771 nematodes (100 ml soil)$^{-1}$ in the wheat following grass-clover. The slightly higher densities under non-inversion than conventional tillage were statistically not significant ($F_{1,7} = 0.915$; Fig. 1A). Total densities of plant-parasitic nematodes declined after the subsidiary crops and after the potato crops. The differences between both tillage treatments remained, albeit not statistically significant ($F_{1,7} < 2.085$). However, plant-parasitic nematode densities were similar in both tillage treatments with oilseed radish/black oat subsidiary crops (about 967 and 473 nematodes (100 ml soil)$^{-1}$ after subsidiary crops and potatoes, respectively, data not shown).

The oilseed radish/black oat subsidiary crop mixture (OR) reduced the total density of plant-parasitic nematodes significantly more than the green fallow and the vetch ($F_{2,70} = 3.967$; Fig. 1B). This effect persisted until after potatoes ($F_{2,70} = 5.769$; Fig. 1B). Besides those general trends some more specific differences were observed at the genus level. Populations of *Helicotylenchus* and *Pratylenchus* increased under wheat (Fig. 1) resulting in densities of 500 and 730 nematodes (100 ml soil)$^{-1}$, respectively, compared to initial densities of 408 and 250 individuals (100 ml soil)$^{-1}$, respectively. In the following subsidiary crops and potatoes, densities of both genera decreased to 300 and 170 nematodes (100 ml soil)$^{-1}$, respectively. By contrast, densities of *Tylenchorhynchus* and *Paratylenchus* continuously decreased from an initial density of 148 and 446 nematodes (100 ml soil)$^{-1}$ before wheat to 50 and 150 nematodes (100 ml soil)$^{-1}$ after potatoes, respectively (Fig. 1). Abundance of *Meloidogyne* was low at the beginning of the experiment (<20 individuals (100 ml soil)$^{-1}$), increased under wheat and subsidiary crops reaching a peak of 145 nematodes (100 ml soil)$^{-1}$ in the green fallow, and finally dropped under potato to densities comparable with the initial densities (Fig. 1, 'other').

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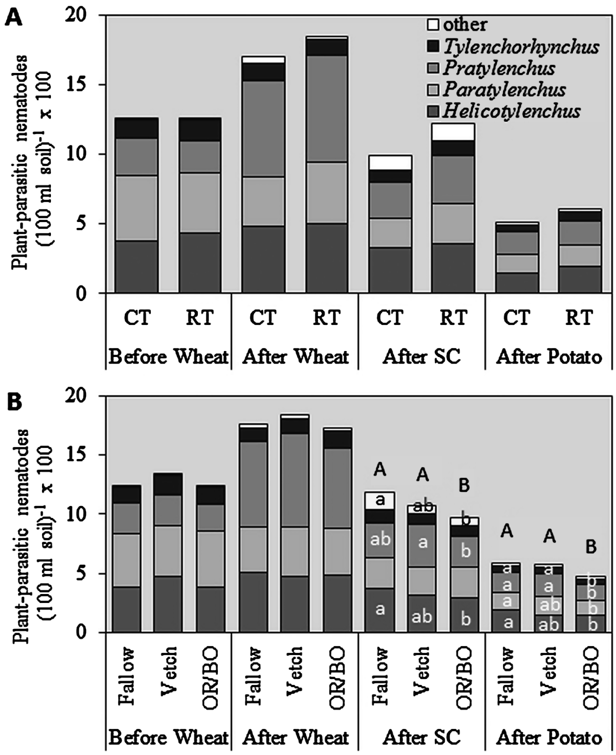

Fig. 1. Nematode dynamics over time (before wheat, after wheat, after subsidiary crops (SC), and after potatoes) for the four most common genera (*Helicotylenchus*, *Paratylenchus*, *Pratylenchus* and *Tylenchorhynchus*) and others (Criconematidae, *Meloidogyne*) affected by (A) conventional (CT) and non-inversion (RT) tillage and (B) spring vetch (Vetch) and oilseed radish/black oat (OR/BO) cover crops sown after wheat compared to a green fallow (Fallow). Data are averaged across both experiments. Different capital and lower letters indicate statistically different treatments for total nematode densities and single nematode genera, respectively, after respective crops ($P < 0.05$, protected LSD-test).

EFFECTS OF TILLAGE AND SUBSIDIARY CROPS

Overall, tillage had no statistically significant effects on single nematode genera. Whilst the four most dominant plant-parasitic nematode genera were uniformly distributed before wheat (Fig. 1), their densities were always slightly higher under non-inversion than inversion tillage after wheat, subsidiary crops and potatoes (Fig. 1A). For example, *Paratylenchus* occurred at 430 individuals (100 ml soil)$^{-1}$ before and after wheat under non-inversion tillage, compared to 465 before to 353 individuals (100 ml soil)$^{-1}$ after wheat under conventional tillage. Subsidiary crops significantly affected *Helicotylenchus*, *Pratylenchus*, and other plant parasitic nematodes, predominantly *Meloidogyne naasi* ($F_{2,70} > 4.32$, Fig. 1B). Accordingly, the highest total densities of plant-parasitic nematodes occurred in the vetch and green fallow treatments again carrying through until after potatoes. Here, the densities of *Helicotylenchus* and *Paratylenchus* were higher in the green fallow than in the oilseed radish/black oat treatment ($F_{2,70} > 3.25$), while the densities of *Pratylenchus* and *Tylenchorhynchus* were significantly higher in the fallow and vetch than in the oilseed radish/black oat treatment ($F_{2,70} = 5.32$).

The models of the redundancy analysis of nematode dynamics and factors for each experiment (Fig. 2) were significant at $P < 0.01$. Constraining (crop, tillage) and conditional (replicates) variables explained 68.7% and 2.5% of the variance in the first experiment, respectively, and 65.7% and 3.8% of the variance in the second experiment, respectively. Furthermore, the first and second RDA axes were significant at $P < 0.01$ in both experiments. The factors tillage and crop (wheat, subsidiary crops and potato) interacted strongly and, therefore, are shown separately (Fig. 2). In Experiment 1 (Fig. 2A), *Helicotylenchus* and *Pratylenchus* were more associated with wheat and *Pratylenchus* was strongly correlated to RT, which is in line with the dynamics shown in Figure 1A. Subsidiary crops were negatively related to the first axis (RDA 1) and, thus, negatively correlated with *Pratylenchus* and Criconematidae. *Meloidogyne* was also negatively correlated with the first axis, indicating positive correlations with subsidiary crops. Potatoes were clustered on the positive site of RDA 1 indicating high correlations with the family of Criconematidae in Experiment 1 (Fig. 2A) but not in Experiment 2 (Fig. 2B). In Experiment 2 (Fig. 2B), the first axis was positively correlated with all plant-parasitic nematode genera and wheat, while it was negatively correlated with subsidiary crops and potatoes, indicating highest densities of all genera after wheat followed by a decline in the subsequent crops.

FREE-LIVING NEMATODES

After potato harvest in Experiment 2, free-living nematodes were significantly lower under conventional tillage (1681 nematodes (100 ml soil)$^{-1}$) compared with non-inversion tillage (3115 nematodes (100 ml soil)$^{-1}$) ($F_{2,30} = 36.5$; Fig. 3). There were no significant effects of subsidiary crops and compost application, although densities of free-living nematodes were lower in

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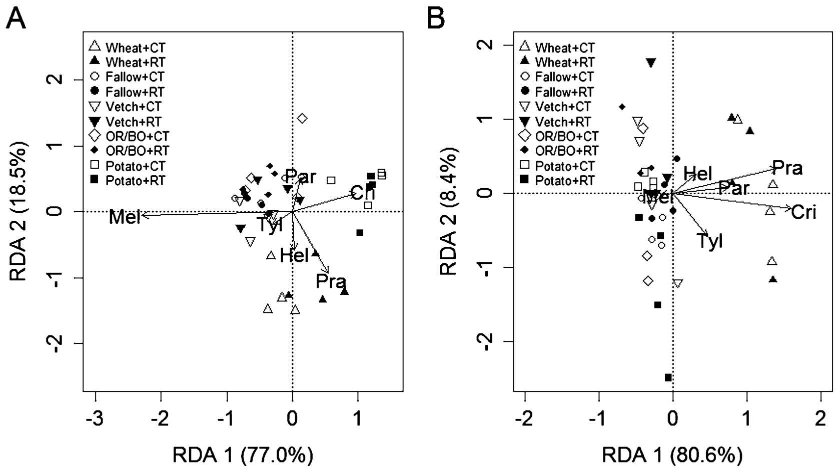

Fig. 2. Redundancy analysis biplots for (A) Experiment 1 and (B) Experiment 2 of plant-parasitic nematode species dynamics ($\ln(P_f + 1) - \ln(P_i + 1)$) averaged across compost and replicates. Responses to the interactions of main crops (wheat, triangles point up; potato, squares) and subsidiary crops (green fallow, circles; vetch, triangles point down; oilseed radish/black oat (OR/BO), diamonds) with tillage (CT, conventional tillage, unfilled symbols; RT, non-inversion tillage, filled symbols) are shown including replicates as co-variables. Axis labels indicate percentage of explained variance. Arrows show directions of increasing nematode species abundance. Abbreviations: Cri = Criconematidae, Hel = *Helicotylenchus*, Mel = *Meloidogyne*, Par = *Paratylenchus*, Pra = *Pratylenchus*, Tyl = *Tylenchorhynchus*.

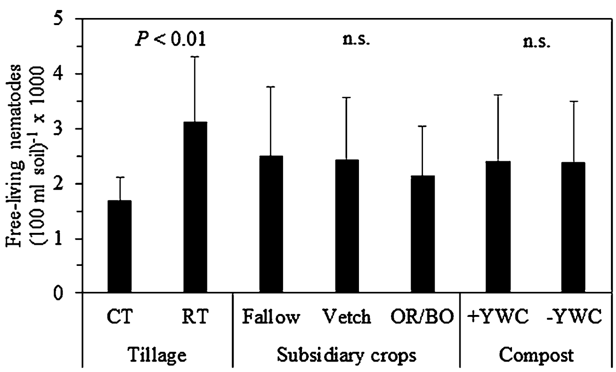

Fig. 3. Densities of free-living nematodes (untransformed means + SD) after harvest of potatoes in the second experiment as affected by conventional (CT) and non-inversion (RT) tillage, subsidiary crops (summer vetch, oilseed radish/ black oat (OR/BO), and green fallow), and yard waste compost (+YWC, with; −YWC, without); P-values and not significant (n.s.) factors are results of the 3-factorial ANOVA with $\ln(x + 1)$-transformed data including replicates as conditional variables; df are 3 and 30 for tillage and subsidiary crops and compost, respectively.

the oilseed radish/black oat mixture (2140 nematodes (100 ml soil)$^{-1}$) than in the green fallow (2500) or vetch (2450). Interactions between main effects were not significant.

Discussion

The most dominant plant-parasitic nematode genera at the experimental site were *Helicotylenchus*, *Paratylenchus*, *Pratylenchus* and *Tylenchorhynchus*. Nematode dynamics were affected by the main crops, types of subsidiary crops *vs* weeds and tillage intensity, but not by compost and mulch application. The highest population densities of *Paratylenchus* and *Tylenchorhynchus* were recorded at the first sampling before grass-clover was incorporated, whilst the highest densities of *Pratylenchus* and *Helicotylenchus* were reached after winter wheat. These plant-parasitic nematodes undergo seasonal fluctuations in soil, which are well detected *via* the centrifugal-flotation method (Barker *et al.*, 1969) as was used in this study for nematode extraction. Quantitative data may therefore differ in other studies, depending on the extraction technique and sampling time.

Effects of crop rotation

The pre-crop grass-clover is a good host for several plant-parasitic nematodes and, thus, explains the high initial densities of *Helicotylenchus*, *Paratylenchus*, *Pratylenchus* and *Tylenchorhynchus* (Sharma, 1971; Wouts & Yeates, 1994; Knight *et al.*, 1997). The subsequently grown winter wheat is a good host for the endoparasitic

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root-lesion nematode, *Pratylenchus*, as well as the semi-endoparasitic spiral nematode, *Helicotylenchus*, as confirmed by Esmenjaud *et al*. (1990), Florini & Loria (1990) and O'Bannon & Inserra (1989). As a result, population densities of *Pratylenchus* and *Helicotylenchus* increased in wheat. By contrast, population densities of *Paratylenchus* and *Tylenchorhynchus* decreased, indicating that wheat is a less preferable host.

Subsidiary crops can, in principle, serve as a food source for plant-parasitic nematodes providing a 'green bridge' between two main crops, *e.g*., between wheat and potato (Gruver *et al*., 2010). Under such conditions, the often reported decline of nematode populations over winter (Hirling, 1977) may be reduced or even turned into an increase. However, in our studies, plant-parasitic nematode densities declined under all subsidiary crops tested. Probable reasons could be a poor host status or weak establishment of those crops and overall low nematode activity over winter. For example, plant biomass for subsidiary crops was ten- to 30-fold lower than the biomass of the previous wheat, thus indicating poor conditions for nematode reproduction.

Among the subsidiary crops, the oilseed radish/black oat mixture tended to reduce plant-parasitic nematodes more than the vetch or the green fallow. Both, oilseed radish and black oat are poor hosts or non-hosts for *Pratylenchus*, the dominating genus after winter wheat (Hirling, 1977; Visser & Molendijk, 2015). By contrast, grass weeds observed in both experiments (*Lolium perenne*, volunteer wheat and *Poa annua*) are a good host for *Helicotylenchus* spp. and *M. naasi* (Wouts & Yeates, 1994; Knight *et al*., 1997; Schmidt *et al*., 2017). Thus, the greater weed biomass in the weedy fallow compared with the oilseed radish/black oat mixture probably fostered the reproduction of both nematode taxa.

The higher biomass of the oilseed radish/black oat mixture compared to vetch or green fallow probably contributed to the greater reduction of *Pratylenchus* in this treatment. The main *Pratylenchus* species in our study were *P. neglectus* and to a lesser extent *P. penetrans*, both known to propagate poorly on oilseed radish. As shown by Hirling (1977), *P. neglectus* was reduced by 45% when using an oilseed radish subsidiary crop after wheat compared with the green fallow control (with weeds and winter wheat volunteers). Likewise, oilseed radish grown as a biofumigation crop resulted in comparable reductions of *P. penetrans* (Korthals *et al*., 2010). In this study, the remarkable effect of the oilseed radish also remained after potatoes confirming earlier results in Germany, where *P. neglectus* was still reduced by 25% in the oilseed radish treatment compared to the green fallow control 1 year after growing the cover crop (Hirling, 1977). Therefore, *P. neglectus* densities declined after oilseed radish followed by a delayed population build-up after subsequent maize and wheat.

Regarding potatoes, plant-parasitic nematodes generally declined from the beginning to the end of the cropping season. It appears that potatoes were poor hosts for those plant-parasitic nematodes occurring in the field experiment. This is somewhat surprising as potato is known to be a good host for *P. penetrans*. Threshold levels of *P. penetrans* for potatoes in loamy soil are reported to be 70-200 individuals (100 ml soil)$^{-1}$ (Hallmann & Kiewnick, 2015); however, in our study even 300 *Pratylenchus* (100 ml soil)$^{-1}$ before potatoes did not cause any yield loss (data not shown). This may in part be explained by the dominance of *P. neglectus* compared with *P. penetrans* and the often uncertain host status of potatoes for *P. neglectus*. According to the breeder (Europlant), nothing is known about the resistance to root-lesion nematodes of 'Marabel' used in our experiments. Whether the damage by *Pratylenchus* spp. was affected by the different environmental conditions in both experimental years can only be speculated.

Effects of tillage and weeds

Non-inversion tillage was accompanied by a continuously higher weed pressure (Table 2) and resulted in consistently, but not significantly, higher plant-parasitic nematode densities throughout the rotation compared to conventional tillage. Under these conditions, *Pratylenchus* benefitted most among the locally observed plant-parasitic nematode community (Figs 1A; 2A). Overall, the effect of non-inversion tillage on plant-parasitic nematodes is discussed controversially. Non-inversion tillage either increased (Thomas, 1978; Okada & Harada, 2007), decreased (Alby *et al*., 1983; Minton, 1986; Govaerts *et al*., 2006) or did not substantially affect (Gallaher *et al*., 1988; McSorley & Gallaher, 1993) nematode densities. Effects of tillage on plant-parasitic nematodes are generally related to crop and weed performance. Furthermore, it has to be considered that most of these studies were conducted under conventional management in long-term trials. Hence, we need to consider that early effects of non-inversion tillage on plant-parasitic nematodes under organic management might be different. During the transition period from conventional to organic conservation agriculture, the overall crop production may be limited

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due to top soil compaction, poorer crop emergence and root establishment, and reduced nitrogen mineralisation. Furthermore, a greater weed pressure is generally foreseen (Peigné *et al.*, 2007). According to FAO (2015), this transition phase ends after 6-7 years, resulting in increased and more stable yields than before altering the management system. Altogether, we hypothesise that crops are more susceptible to plant-parasitic nematodes in fields within this transition phase than in fields that have a long-term conservation agriculture history.

In general, fields under non-inversion tillage are more infested with volunteer crops and grass weeds than conventionally tilled fields (Moyer *et al.*, 1994; Nichols *et al.*, 2015). Monocotyledonous plant species are, in particular, good hosts for *Pratylenchus* and *Paratylenchus* (Wood, 1973; Townshend & Potter, 1976; Sarathchandra *et al.*, 2001; Vanstone & Russ, 2001). Therefore, in the present study perennial grass weeds in non-inversion tilled winter wheat could have fostered reproduction of *Pratylenchus* and *Paratylenchus* resulting in overall higher densities of plant-parasitic nematodes under non-inversion than under conventional tillage.

Furthermore, wheat plants under non-inversion tillage were weaker and produced less biomass, most likely caused by nitrogen deficiency due to lower mineralisation rates in less disturbed soils (Donald *et al.*, 2009). Nutrient-deficient plants are, in general, more susceptible to plant-parasitic nematodes (Melakeberhan *et al.*, 1997) and can result in higher nematode densities as observed here. However, Thompson (1992) and Okada & Harada (2007) observed different effects with higher *Pratylenchus* densities in plants that received nitrogen fertiliser compared to no fertilisation. Nevertheless, regardless of plant available nitrogen in soil, zero tillage with or without high weed infestation resulted in significantly higher *Pratylenchus* densities compared with conventional tillage (Thompson, 1992; Pankaj *et al.*, 2006).

Besides the above-mentioned effects, tillage intensity can also affect the survival strategies of plant-parasitic nematodes in soil. For example, significantly more eggs of the soybean cyst nematode *Heterodera glycines* were obtained from a chisel-ploughed compared to a ploughed soil over a 2-year period (Donald *et al.*, 2009), suggesting higher egg survival rates in chisel-ploughed soils. Furthermore, organic matter generally decays faster under conventional than under non-inversion tillage while the latter generally increases stubble and root fragments near the soil surface (Morris *et al.*, 2010). Likewise, more fragments of stubble and root fragments were noticed under non-inversion than conventional tillage in the present study. These fragments can harbour large densities of plant-parasitic nematodes, such as *Pratylenchus*, which can survive periods of food scarcity and drought in these stubble and root fragments in an anhydrobiotic resting stage (Glazer & Orion, 1983; Talavera & Vanstone, 2001). Altogether, these factors explain the maintenance of higher total plant-parasitic nematode densities under non-inversion than conventional tillage after subsidiary crops and potato in this study.

Free-living nematodes as affected by tillage, subsidiary crops and compost

In our study, non-inversion tillage with mulch application had the strongest positive effect on free-living nematodes, whereas the effect of subsidiary crops and compost was negligible. This appears in contrast to other published results. For example, it is well known that subsidiary crops, such as oilseed radish, can increase bacterivorous nematodes (Gruver *et al.*, 2010; Hallmann & Kiewnick, 2015). Vetch and lupine winter cover crops in a long-term experiment in Brazil resulted in higher microbial biomass than grassy fallow and thus are expected to increase bacterivorous nematodes (Balota *et al.*, 2014). Similarly, densities of free-living nematodes in a wheat-lupine rotation were higher than in a wheat monoculture (Rahman *et al.*, 2007). According to the authors, the higher root dry matter, lower C/N ratio and different canopy structure of the lupine compared to the wheat explained those differences in free-living nematode densities. The overall very low subsidiary crop biomass in our study is probably the main reason for the lack of effects on the free-living nematode abundance. In this study, the application of 12 and 26 t ha^{-1} mulch to plots under non-inversion tillage in Experiment 1 and 2, respectively, might also have concealed any previous soil treatments, such as subsidiary crops and compost application. Overall, free-living nematodes may not be strongly affected by a single application of subsidiary crops, whilst their long-term use may change the abundance of free-living nematodes, such as observed for the microbial biomass in Brazil (Balota *et al.*, 2014).

In contrast to plant-parasitic nematodes, the positive effect of non-inversion tillage on the build-up of free-living nematode populations is desired due to their beneficial effects on the soil food web and nutrient mineralisation (Fu *et al.*, 2000; Pankaj *et al.*, 2006). However, nematode trophic groups may react differently to soil organic matter accumulation in such systems. For example, fast-growing bacterivorous nematodes dominate previously tilled soils

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as a result of stimulated bacterial degradation of organic matter. This also explains why inconsistent or lower densities of bacterivorous nematodes are generally found in long-term systems with reduced tillage compared to systems with intensive soil movement (Hendrix *et al*., 1986; Carter *et al*., 2009). If soil disturbance is reduced and organic compounds are more stable, decomposition will be dominated by fungi and, thus, fungal-feeding nematodes will increase (Freckman & Caswell, 1985; Briar *et al*., 2007; Neher, 2010). Nevertheless, all trophic groups of free-living nematodes are important contributors to the soil food web and suitable indicators for soil health and sustainability of farming systems (Freckman, 1988; Neher, 2010).

Final considerations

Our results suggest that crop diversity in a rotation can be a sustainable option to keep plant-parasitic nematodes below the economic threshold level. Rapid increases of plant-parasitic nematodes, such as observed for *Pratylenchus* under wheat, can be tackled if subsequent crops are poor hosts, non-hosts or even antagonistic. Thus, oilseed radish mixed with black oat used as subsidiary crop can reduce plant-parasitic nematodes, particularly species of the genus *Pratylenchus* and *Helicotylenchus*, and will probably replace fallows if nematode control is desired. By contrast, transition to non-inversion tillage can limit nematode control by non-host crops if weeds are not sufficiently controlled. Although plant-parasitic nematodes did not reduce crop yields under non-inversion tillage in our study, this cannot be generalised for subsequent crops. Cereals potentially harbour high numbers of weeds, particularly in non-inversion tillage systems without adequate weed control, and can contribute to a continuous increase of plant-parasitic nematodes over time. Thus, investigation of all crops in a rotation under non-inversion tillage is needed to evaluate farming systems for their nematode control potential. Free-living nematodes increased under non-inversion tillage in combination with mulch application and therefore may contribute to a higher agricultural sustainability due to their importance for the soil food web.

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