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Présentée par :
Jeremy Detrey

Pratiques agroécologiques en micro-fermes maraîchères : Influence de la culture sur butte et de l'association de cultures sur les performances végétales de la tomate et des nématodes bioindicateurs du fonctionnement du sol

Directeur(s) de Thèse :
Didier Bouchon, Julia Clause

Soutenue le 10 février 2021 devant le jury

Jury :

Président	**Jérôme Cortet**	Professeur, Université Paul Valéry, Montpellier
Rapporteur	**Édith Le Cadre**	Professeure, Agrocampus Ouest, Rennes
Rapporteur	**Joséphine Peigne**	Enseignante-chercheure, ISARA, Lyon
Membre	**Didier Bouchon**	Professeur, EBI, Université de Poitiers
Membre	**Julia Clause**	Maître de conférences, EBI, Université de Poitiers
Membre	**Jean Trap**	Chargé de recherche, Eco&Sols, IRD, Montpellier

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Présentée et soutenue par

Jeremy Detrey

Le 10 Février 2021

Devant la Commission d'Examen

Mme Edith Le Cadre	Professeure, Agrocampus Ouest	Rapportrice
Mme Joséphine Peigné	Enseignante-chercheure (HDR), ISARA Lyon	Rapportrice
M. Jérôme Cortet	Professeur, Université Paul Valery Montpellier III	Examinateur
M. Jean Trap	Chargé de recherche, IRD UMR Eco&Sols	Examinateur
M. Didier Bouchon	Professeur, Université de Poitiers	Directeur de thèse
Mme Julia Clause	Maitresse de conférences, Université de Poitiers	Co-Directrice de thèse

Thèse dirigée par : Julia CLAUSE et Didier BOUCHON, Laboratoire Ecologie et Biologie des Interactions – UMR 7267 CNRS Université de Poitiers, équipe Ecologie, Evolution, Symbiose

Avant-propos

Cette thèse a été menée au sein de l'équipe Ecologie, Evolution, Symbiose du laboratoire Ecologie et Biologie des Interactions – UMR 7267 CNRS Université de Poitiers, dirigé par le Pr. Jean-Marc BERJEAUD. Mon allocation de recherche a été financée par le Ministère de l'Enseignement Supérieur, de la Recherche et de l'Innovation. Ce travail a été partiellement financé par l'Institut Olga Triballat (projets PermaBioSol (2017-2020) et AMASEPT (2018-2021)), la bourse "Ecologie Impliquée - Barbault & Weber" de la Société Française d'Ecologie et d'Evolution (SFE^2), des fonds 'recherche' associés au programme Erasmus Mundus IMAE, et des fonds récurrents du laboratoire. Au cours de ce travail de thèse, j'ai pu encadrer trois stagiaires de Master (Louise Maris, Valentin Cognard et Manon Gauclin) qui m'ont assisté dans la collecte des données et ai bénéficié d'aides ponctuelles du personnel technique de l'équipe Ecologie, Evolution, Symbiose. J'ai également eu l'occasion de travailler en collaboration avec l'équipe SEVE du laboratoire EBI, et avec l'équipe Interactions Plantes-Nématodes de l'Institut Sophia Agrobiotech INRAE.

Le présent manuscrit comprend une introduction générale largement composée d'un travail de revue bibliographique, une présentation des approches expérimentales utilisées, des sites d'études et des plans expérimentaux mis en place au cours de ce travail de thèse, quatre chapitres de résultats et une discussion générale. La première partie de l'introduction, ainsi que les chapitres sont écrits en anglais sous forme d'articles scientifiques en cours de valorisation. Chacun de ces articles est précédé d'une introduction et suivi d'une conclusion, rédigées en français. La discussion générale est rédigée en français.

Résumé

Au cours du siècle dernier, la transition agro-industrielle a profondément modifié le mode de production agricole dans les pays développés, entrainant de nombreux impacts négatifs sur la biodiversité et le fonctionnement des agroécosystèmes. L'agroécologie a récemment émergé comme alternative à ce système de production. A l'interface entre discipline scientifique et pratiques agricoles, l'agroécologie se base sur le support et le maintien de processus écologiques d'intérêts. A travers une analyse bibliographique, nous avons mis en évidence le nombre relativement faible d'études écologiques dans les pratiques agroécologiques. Parmi ces dernières, peu de travaux lient pratiques et biodiversité. Nous avons également montré que les exploitations maraichères étaient sous-représentées, tandis que les micro-fermes étaient quasi inexistantes alors que les pratiques agroécologiques sont fréquentes dans ces deux environnements. C'est dans ce cadre que s'inscrit cette thèse qui vise à comprendre les impacts écologiques de la mise en place I/ de deux associations de cultures et II/ de la culture sur buttes dans un contexte de production de tomates en micro-fermes maraichères. En raison des propriétés biocides des composés soufrés identifiés chez les plantes du genre *Allium* et de la capacité des légumineuses à fixer l'azote atmosphérique dans leur racine à l'aide de bactéries symbiotiques, le poireau et le haricot valorisés en vente directe, ont été sélectionnés pour être associés à la tomate. Une expérimentation *in situ* a été réalisée sur deux sites du Sud-Ouest de la France en 2018 et 2019, pour évaluer les conséquences de la mise en place de ces pratiques sur les performances de la tomate en termes de croissance et de rendement, ainsi que sur les communautés de nématodes, bioindicateurs du fonctionnement du sol. Nos observations ont mis en évidence l'importance de l'historique de culture et de la qualité du sol dans la réponse des plantes et des organismes du sol à la mise en place de ces pratiques. L'analyse des communautés de nématodes nous a permis de mettre en évidence un enrichissement du sol en réponse à l'association haricot-tomate. La culture en association avec le poireau n'a eu que peu d'effets sur les communautés de nématodes, mais est liée à de meilleures performances végétales des tomates. La culture sur buttes n'a pas eu d'effet sur les performances de la tomate, malgré un enrichissement du sol visible à travers les communautés de nématodes, dominées par les bactérivores, et une plus grande abondance d'autres organismes du sol. Une interaction entre culture sur buttes et associations a été observée. Les effets de l'association haricot-tomate étaient d'autant moins marqués que le milieu était enrichi par la culture sur buttes. A l'inverse, l'effet positif de l'association avec le poireau semblait plus marqué avec une culture sur buttes. Une expérimentation en système simplifié a été effectuée pour évaluer le potentiel du poireau à contrôler l'un des ravageurs de la tomate, le nématode à galles *Meloidogyne incognita*. La présence du poireau n'a pas réduit l'infestation des racines de tomates par les nématodes mais a semblé inhiber leur reproduction. La croissance plus importante et la floraison précoce des tomates associées s'expliquent par une compétition entre plantes moins importante qu'en monoculture. Les résultats obtenus lors de cette thèse soutiennent ici l'importance de la prise en compte des organismes bioindicateurs dans l'étude du fonctionnement du sol. Ils apportent également des éléments sur les avantages respectifs de la mise en place des pratiques étudiées, notamment dans le service de biocontrôle, nous ont permis d'émettre l'hypothèse d'un effet de facilitation du poireau sur la croissance des tomates.

Mots clés : Agroécologie, Communautés de nématodes, Culture de tomate, Poireau, Haricot, Biocontrôle, Biofertilization

Abstract

Over the last century, the agro-industrial transition has profoundly changed the mode of agricultural production in developed countries, with many negative impacts on biodiversity and agro-ecosystems functioning. Agroecology has recently emerged as an alternative to this system of production. At the interface between scientific disciplines and agricultural practices, agroecology is based on supporting and maintaining ecological processes of interest. Through a literature review, we highlighted the relatively small number of ecological studies on agroecological practices. Among the latter, few studies linked practices and biodiversity. We also showed that vegetable gardening was underrepresented, while micro-farms were almost absent, although agroecological practices are frequent in those two environments. This thesis aims to understand the ecological impacts of setting up I/ two crop associations and II/ permanent raised beds in a context of tomato production in vegetable small farms. Because of biocidal properties of sulphur compounds identified in plants from the *Allium* genus, and the ability of legumes to fix atmospheric nitrogen in their roots thanks to symbiotic bacteria, the leek and bean cash crops were selected to be associated with tomato. An *in situ* experiment was carried out in 2018 and 2019 in two sites in south-western France to assess consequences of the implementation of these practices on tomato performances in terms of growth and yield, as well as on nematode communities, as bioindicators of soil functioning. Our observations highlighted the importance of the cultivation history and of the soil quality for the response of plants and soil organisms to these practices. The analysis of nematode communities showed a soil enrichment in response to the bean-tomato association. The association with leek had little effect on nematode communities but was linked to improved tomato plant performances. Raised bed cultivation had no effect on tomato plant performances, although a soil enrichment was observed through nematode communities, dominated by bacterivorous, and through a greater abundance of other soil organisms. An interaction between raised bed gardening and associations was observed. The effects of bean-tomato association were less pronounced when the soil was enriched in organic matter in raised beds. Conversely, the positive effect of the leek association seemed to be more pronounced in raised beds. A simplified system experiment was carried out to evaluate the potential of leek to control one of the main parasites of tomato, the root-knot nematode *Meloidogyne incognita*. The presence of leek did not reduce the nematode infestation on tomato roots but appeared to inhibit their reproduction. The higher growth and early flowering of the tomato in association can be explained by a lower competition between plants than in the monoculture. Our work here supports the importance of organisms as bioindicators in studies focusing on soil functioning. It also provides additional information on the advantages of implementing crop association and/or raised bed gardening, particularly with regard to the use of leek as a tool for biocontrol. Our observations also suggest a facilitating effect of leek on tomato growth.

Keywords: Agroecology, Nematode communities, Tomato cultivation, Leeks, Beans, Biocontrol, Biofertilization

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Introduction

L'agroécologie : un contexte d'étude pour l'écologie

Le passage d'une agriculture paysanne à une agriculture industrielle lourdement mécanisée et soutenue par l'industrie pétrochimique dans les pays industrialisés au cours du dernier siècle a induit de profondes modifications du fonctionnement des agroécosystèmes (Matson 1997). De nombreux effets néfastes de cette agriculture industrielle, aussi appelée agriculture conventionnelle, ont d'ailleurs été soulevés concernant l'environnement mais aussi la santé humaine (McLaughlin and Mineau 1995; Poschlod et al. 2005; Willemen et al. 2018). Par exemple, l'utilisation intensive et prolongée d'engrais chimiques assurant la nutrition des plantes cultivées a un effet prononcé sur les propriétés biochimiques du sol dont dépendent les organismes qui y vivent et en particulier les microorganismes (Wei et al. 2017). De même, l'utilisation intensive de pesticides afin de protéger les plantes cultivées des bioagresseurs est toxique pour une grande diversité d'organismes, incluant insectes, oiseaux, mammifères, amphibiens ou poissons (Isenring 2010). Par ailleurs, le labour systématique et profond des cultures affecte négativement les organismes du sol, en induisant par exemple une diminution du nombre de vers de terre et de collemboles, et réduit l'activité des microorganismes (Sheibani and Ahangar 2013).

Or, la biodiversité est une des composantes majeures du fonctionnement des écosystèmes, fournissant et permettant le maintien de nombreux services écosystémiques (Schwartz et al. 2000; Brussaard 2012), définis comme les services et avantages que la nature apporte à la société (Daily 2003; Zhang et al. 2007). Le terme biodiversité d'abord utilisé dans sa version longue 'diversité biologique' (en anglais le terme « biological diversity » a été contracté en « biodiversity ») faisait à l'origine référence à la richesse spécifique (Swingland 2001). Depuis son apparition, la définition de ce terme a évolué de nombreuses fois, pour inclure la variété des organismes vivants et leurs assemblages, les communautés biotiques et même les processus biologiques, qu'ils soient naturels ou anthropisés. Elle peut se mesurer en termes de diversité génétique ou fonctionnelle, d'identité et de nombre d'espèces, à n'importe quelle échelle spatiale, allant des microporosités dans le sol à l'ensemble de la biosphère. La définition la plus simple de la biodiversité, sans spécificité ni contexte, est sans doute celle du nombre d'espèces englobant tous les règnes du vivant. Une définition plus complète est "la variété des organismes vivants, les différences génétiques entre eux, les communautés et les écosystèmes dans lesquels ils se trouvent, et les processus écologiques

et évolutifs qui les font fonctionner, tout en étant en constante évolution et adaptation" (Noss and Cooperrider 1994). Cependant, la biodiversité n'a pas une seule définition bien déterminée et universellement acceptée, mais est souvent redéfinie en fonction du contexte et de l'objectif de l'auteur. Les définitions de la biodiversité vont du "nombre d'espèces différentes présentes dans un endroit donné" à "la diversité et la variabilité de la nature" mais aussi "la variété de la vie et de ses processus" dans sa version la plus complète. De nos jours, la biodiversité, en termes de diversité du vivant et des processus qui y sont associés, est largement prise en compte dans la conception et la réalisation des activités humaines, avec comme question principale : « quels impacts sur la biodiversité ? ». Dans le but de minimiser les impacts de l'agriculture sur la biodiversité et les services écosystémiques associés et d'augmenter la durabilité et la capacité de résilience des agroécosystèmes, c'est-à-dire leur capacité à revenir à leur état initial à la suite d'une perturbation, des méthodes alternatives se développent, parfois innovantes et parfois inspirées de pratiques plus anciennes. C'est dans ce contexte que la notion d'agroécologie apparait en Occident dans les années 1970 (Wezel and Soldat 2009) et se développe afin de devenir une alternative envisagée pour se substituer à l'agriculture conventionnelle. L'agroécologie, à travers un ensemble de pratiques agricoles dites "agroécologiques" basées aujourd'hui sur des connaissances scientifiques du fonctionnement des agroécosystèmes, vise donc à maintenir des taux de rendement élevés, tout en s'appuyant sur des processus écologiques et en les optimisant, plutôt que d'avoir recours à des intrants chimiques ou à des solutions technologiques (Wezel et al. 2014). Ces pratiques sont très diverses et comprennent par exemple l'absence de labour ou un labour réduit comme substitution au labour profond, ou encore les associations de cultures ou couverts végétaux en ce qui concerne l'assolement en substitution d'une monoculture continue (Wezel et al. 2014).

Parmi les études scientifiques portant sur l'agroécologie et dont le nombre a explosé ces 20 dernières années (Wezel and Soldat 2009), peu d'entre elles semblent prendre en compte l'impact des pratiques agroécologiques sur la biodiversité. En me basant sur les données bibliographiques, j'ai donc souhaité évaluer l'importance des recherches sur la biodiversité et l'écologie en agroécologie, et plus particulièrement dans un contexte de maraîchage. J'ai ensuite synthétisé l'impact de six pratiques sur la biodiversité. Les résultats

de cette étude sont présentés sous la forme d'un manuscrit qui vise à être soumis dans la revue *Agronomy for Sustainable Development*.

Agroecological practices and biodiversity in vegetable farming

Jeremy Detrey[a], Didier Bouchon[a] and Julia Clause[a,*]

[1]Université de Poitiers, Laboratoire Écologie & Biologie des Interactions—UMR CNRS 7267, Équipe Écologie Évolution Symbiose, 5, rue Albert Turpain, TSA, 51106,86073, Poitiers Cedex 9, France

*Corresponding author: julia.clause@univ-poitiers.fr

Abstract

As nature-based solutions, agroecological practices are widely appreciated by farmers, and especially small-scale vegetable farmers who want to preserve biodiversity while sustaining farming and food systems. Yet, the actual beneficial or negative impacts of those practices on the biodiversity seem underrepresented compared to agronomic indicators, and particularly in vegetable farming.

Here we attempted i) to clarify the place of studies on ecology within the research in agroecology between 1900-mid-2020, with an emphasis on six agroecological practices in vegetable farming systems and ii) to review the impact of those practices on biodiversity. The practices considered are: intercropping; cover crops; organic amendment; rotation; no-tillage/reduced tillage; permanent raised beds. The analysis was conducted using Web of Science, Scopus and BibCnrs databases and information was extracted from 75 selected papers. The major points are the following: 1) linking practices and ecology in agroecology is recent, as agroecology is mostly associated with socio-economic studies and practices with agronomy, which reveals a gap between the use of terms in social and natural sciences, 2) studies target functional groups of organisms (e.g. pests *vs.* natural enemies) rather than taxonomic diversity, and their occurrence was weakly linked with associated crops and practices, 3) although a generalization of patterns was limited by the short duration of studies, agroecological practices had an overall positive impact on natural enemies and negative impact on herbivores, except in systems with rotation and reduced tillage and, 4) most studies were conducted in Northern America and in Europe, and only 29 % of studies were located within an actual farming context (*i.e.* not experimental site). Raised bed was underrepresented. Some gaps still need to be filled to better understand the impact of agroecological practices on biodiversity and ecological processes in vegetable farming, particularly as it represents an important issue in sustainable farming and food systems.

Keywords: Cover crop; Intercropping; Rotation; Organic amendment; Raised bed; Small-scale farming

1. Introduction

During the past 60 years, industrial agriculture has deeply changed the way food is produced to respond to a growing demand. These changes have consisted in standardizing crops, growing monocultures, increasing field sizes, with the counterpart of intensive use of chemical inputs and water and a high level of mechanization. These practices did increase yields up to the 90s but a stagnation is now observed, and they are associated with significant environmental and sanitary issues (Ramankutty et al. 2002; Huang et al. 2002; Ray et al. 2012). Among them, the intensification of farming systems led to an increasing occurrence of pests and diseases, soil erosion and nutrient loss or water shortage, which were dealt with the use of the petrochemical industry and machines rather than through natural biological and ecological processes (Gomiero et al. 2011; Stehle and Schulz 2015). With more than 33% of the world's land surface and 75% of the freshwater used for crop and livestock production, agriculture has a high negative impact on land degradation, biodiversity and ecosystem functions (Willemen et al. 2018). For instance, removing hedges to increase field size contributed to the homogenization of landscape, to habitat fragmentation and eventually to the loss of many living species and key ecosystem functions such as predator-prey relations, already weakened by the use of chemicals (Haddad et al. 2015). However, ecosystem resilience is strongly associated with biodiversity and natural resources, and any loss of biodiversity can lead to a decrease in the resilience of production systems (Isbell et al. 2015; Oliver et al. 2015; Altieri and Nicholls 2017; Ogilvie et al. 2019; Li et al. 2019).

The concept of 'biodiversity', which includes "all species diversity of plants, animals and micro-organisms existing and interacting within an ecosystem" (Hågvar 1998), has been widely used since the Rio Earth Summit in 1992 and a recent renewed global ecological awareness. More recently, its importance in providing goods and services for human well-being, *i.e.* ecosystem services, has been recognized through the creation of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES). Through sustainable practices, agriculture represents a leverage to maintain, improve or restore ecosystem properties and services and, more generally, to address future issues such as food security and climate change (FAO, 2017). For more than a decade, those sustainable practices have been commonly integrated within the larger concept of 'Agroecology', which includes several major currents of thoughts: a scientific discipline, a social movement, a set of agroecological practices and a broad integration of both farming and food systems (Wezel and Soldat 2009; Gliessman 2013; Wezel et al. 2014). Agroecological practices aim at maintaining high yield rates, while relying on and optimizing ecological processes, rather than on using chemicals and technological solutions (Wezel et al. 2014). Thereby, they aim at favoring nutrient cycling, nitrogen fixation, carbon sequestration, pest regulation or soil and water conservation, depending on the strategic needs of farmers for crop growth.

Some agroecological practices are easier to implement than others. For example, applying organic amendment or reducing tillage are "substitutes" for chemical fertilizer and intensive tillage, while implementing rotations, cover crops, intercropping or raised beds require a deeper "redesign" of the farming system (Wezel et al. 2014). *Organic amendment* seeks to favor nature-based processes of nutrient cycling and nutrient uptake through organic matter decomposition. Several methods are used such as the use of manures, composted waste, or cover crop residues that are left at the soil surface or that are incorporated. *Reduced tillage/no-till* is the use of superficial tillage without soil inversion or the absence of tillage. It aims at reducing soil perturbation and at increasing the activity of soil organisms. It includes rotational tillage, mulch-till, ridge-till, strip-till and no-till. Such practices are often grouped into 'conservation tillage'. *Rotations*, *i.e.* the succession of different crop species or varieties over the same area, aim at optimizing the use of soil resources by plants. *Cover crops* are part of the rotation and aim at increasing the use of resources by the following crop. *Intercropping* consists in growing two crops or more at the same time and place to increase immediate plant complementarity (Brooker et al. 2015). Finally, *raised beds* consist in elevating the ground for cultivation, often by adding a large amount of organic matter combined to no-tillage. It is particularly expected to modify soil physical (*e.g.* moisture, temperature, porosity), and, thereby to modify organic matter decomposition by the soil biota.

Despite a growing interest of farmers to adopt agroecological practices in temperate systems, obstacles remain for the establishment of these practices compared to conventional systems : the lack of knowledge of stakeholders, their consideration for short term benefits, the site-specific constraints or a lack of policies (Altieri 2002; Iles and Marsh 2012; Wezel et al. 2014). The lack of knowledge might be due to a gap between the use of 'biodiversity' within the scientific literature and the demand of stakeholders for clear information. According to Gliessman (2013), agroecological studies largely focused on socio-economics or policies and an gap of information remains on the impact of agroecological practices on biodiversity. Frison et al. (2011)reported a lack of documentation on the use of biodiversity against pest and macro-parasites compared to diseases, while ecosystem services in organic farming were poorly explored (Kremen and Miles 2012). Meanwhile, with the increasing awareness on climate and biodiversity crises, farmers and "neo-rural" farmers experiment on agroecological practices (Sabourin et al. 2005; Wilbur 2013; Orria and Luise 2017). This approach comes from a desire to sustainably produce and trade local goods and is associated with small-scale farming or gardening (Wilbur 2013). Vegetable farming is commonly based on cropping Alliaceae, Apiaceae, Asteraceae, Brassicaceae, Cucurbits, Fabaceae or Solanacae and, as it is more adapted to small-scale farming than cereal cropping, it is a preferred system to experiment agroecological practices. In

addition, small-scale and traditional farming can alleviate poverty compared to large-scale farming if managed efficiently (Altieri 2002; Wiggins et al. 2010).

In this review, we attempt 1) to clarify the place of studies on biodiversity within peer-reviewed agroecological studies for a set of agroecological practices by means of a systematic review, then 2) to synthetize the knowledge regarding the question: "What are the impacts of agroecological practices on 'biodiversity' in a context of vegetable farming?", and 3) to identify gaps of knowledge and avenues to explore, especially in the context of vegetable farming, with regards to small-scale farming.

2. Review methods

In order to limit the scope of this study, it focuses on a set of six biodiversity-based techniques commonly used in small-scale vegetable farming: intercropping, cover crop, living mulch, organic amendment, reduced/no tillage, rotation and raised bed gardening. A systematic review addressed quantitative questions regarding the location of experiments, the type of farming and crops and organisms studied. The narrowed-down results of this quantitative review were then used to qualitatively review the trends and mechanisms of impact.

2.1. Systematic research of the literature

Parallel searches were conducted on three databases: Web of Science Core Collection™ (WOS), Scopus and BibCnrs. WOS Core Collection™ is a global citation database. Scopus combines a comprehensive, curated abstract and citation database with enriched data and linked scholarly content. BibCnrs is a portal that links to associated databases managed by the French National Center for Scientific Research (CNRS). The query used within each database combined five semantic objects that were defined and that included key terms found in the literature (Table 1 and SM1 Table S1 for full query details). The first and second semantic objects set the context (#1; *Agroecology*) and narrowed the field of studies (#2; *Ecology*), the third object focused on the set of six practices (#3; *Practices*), and the fourth and fifth terms targeted vegetable farming (#4; *Vegetable*) and small-scale farming systems (#5; *Microfarms*). Keywords used for 'Ecology' were purposefully generic terms, as they are commonly referred to in policies targeting agroecological practices. Terms within each semantic object were combined by using the logical operator "OR" and were refined in a conservative way after verifying that more complex combinations did not bring additional information (SM1 Table S1). Semantic objects (#1 to #5) were then combined with the logical operator "AND" to address the question "What are the impacts of agroecological practices on 'biodiversity' in a context of vegetable farming?" (Table 1). The inclusion of *Microfarms* (semantic object #5) led to a number of publications record too low (< 10) for the needs of this study, and only articles from the combination of #1, #2, #3 and #4 were further considered.

Table 1. Semantic objects and number of publications found for each semantic object and their combinations from the literature search within three different interrogated databases: Web of Science, Scopus and BibCnrs. The correspondence between combinations and their meaning is indicated. In bold: the final combination of semantic objects to answer the question: "*What are the impacts of agroecological practices on 'biodiversity' in a context of vegetable farming?". The last search was done on 17/08/2020 and the period covered 1900-2020.*

		Database		
Semantic objects	Referred to as	WOS	Scopus	BibCnrs
#1	Agroecology	9,093	55,662	54,735
#2	Ecology	838,987	3,201,423	3,517,929
#3	Practices	55,639	4,402	106,330
#4	Vegetable	145,770	451,633	531,393
#5	Microfarms	16,364	73,099	36,485
Combinations	Corresponds to			
#1 AND #3	Agroecological studies addressing the targeted practices	862	515	3,378
#2 AND #3	Studies addressing ecology and targeted practices	5,485	2,873	18,622
#1 AND #2	Agroecological studies addressing ecology	5,707	46,038	34,340
#3 AND #4	Studies addressing targeted practices within vegetable farming	2,060	1,377	5,214
#1 AND #4	Agroecological studies addressing vegetable farming	446	7,091	2,198
#1 AND #5	Agroecological studies addressing microfarms	748	8,884	1,790
#3 AND #5	Studies addressing targeted practices within microfarms	1,084	396	1,719
#2 AND #3 AND #4	Studies addressing ecology and targeted practices within vegetable farming	213	992	996
#1 AND #2 AND #3 AND #4	**Agroecological studies addressing ecology and targeted practices within vegetable farming**	**44**	**165**	**157**

Our search protocol covered the period 1900 to 20120 and was concluded on 17 August 2020, and only peer-reviewed articles in English were considered. After removing duplicates from the remaining 366 references, results were refined according to Sordello et al. (2017). Publications were manually selected based on their title (88 articles), then on their abstract (62 articles), and finally on their whole content (55 articles). 34 articles that had been selected and found relevant to the study prior to the search protocol were added to the pool of publications. After removing reviews and meta-analyses, the remaining 75 articles were analyzed in greater depth to determine the country where the study took place, the type of study site, the targeted crops and organisms, and were considered for the qualitative analysis (Table SM2 S2). Only one study was found on raised beds. For this reason, this practice will not be included further in the qualitative analysis.

2.2. Co-occurrence map

In order to assess the place of research on 'Biodiversity' and 'Ecology' within the 'Agroecology' field of studies, a co-occurrence map of terms was generated based on text data from publications retrieved with the semantic object 'Agroecology' (#1). A co-occurrence map provides a graphic visualization of the frequency with which terms are used and connected with each other. The co-occurrence map was built with the software VOSviewer 1.6.13 (Van Eck and Waltman 2010), and the 'Full Record and Cited References' was downloaded from the WOS database Core Collection™. The choice of using data from this database was based on the conservative results obtained by comparing results from WOS, Scopus and BibCnrs (Table 1). Retrieving fewer publications decreased the risk of word inflation within the search protocol. Terms that appeared at least 100 times within the publications were extracted from the titles and abstracts through binary counting. The 60% most relevant terms were selected to build the map. Due to the binary counting, many apparitions of a term in a publication was considered as one occurrence for the map construction. The size of circles represents the number or occurrences for each term, lines represent the co-occurrence of two terms, line width represents the frequency of co-occurrence between two terms, and colors automatically segregates clusters of tightly interlinked terms.

2.3. Multiple co-inertia analysis

The main ecosystem services, practices, studied crops and organisms were allocated or retrieved from each of the 75 papers. Ecosystem services were biodiversity (supporting service), biofertilization and biocontrol (regulating) and production (provision). Practices were Organic amendment, Cover crop, Intercropping, Raised Bed, Rotation, Tillage. Crops were considered at the Family level (Amaryllidaceae, Apiacea, Asteraceae, Brassicaceae, Convolvulaceae, Cucurbitaceae, Dioscoreaceae, Euphorbiaceae, Fabaceae, Lamiaceae, Malvaceae, Poaceae, Solanaceae) and organisms at the Domain, Order or Family

level (Archaea, Bacteria, Fungi, Virus, Nematoda, Acari, Collembola, Lumbricidae, Isopoda, Araneae, Opiliones, Myriapoda, Coleoptera (Carabidae, Coccinellidae, Chrysomelidae, Staphylinidae, other), Diptera (Syrphidae, other), Gastropoda, Hemiptera (Aleyrodidae, Anthocoridae, Aphididae, Cicadellidae, other), Dermaptera, Neuroptera, Orthoptera, Hymenoptera (Formicidae, other), Lepidoptera (Noctuidae, other), Mantodea, Odonates, Psocoptera, Thysanoptera), except for the vegetation referred as Weeds. All data were converted into dummy (presence/absence) variables taking a value of 0 or 1, and a multiple co-inertia analysis (mCOA) was performed with the 'ade4' package in R (Team 2020) to highlight similar patterns between two 'context' datasets (practices, crops; SM2 Tables S3 and S4) and one 'organisms' dataset (SM2 Table S5). The multiple co-inertia analysis is an exploratory data analysis that simultaneously ordinates *K*-tables that share the same variable, here the paper identity. It results in a compromise factorial plan that maximizes the co-inertia between these *K* initial matrices, and on which variables are projected. In order to improve the graphical representation, crop Families with less than 4 occurrences and organisms with less than 5 occurrences were removed from the analysis, as well as rows with empty data in the resulting matrices. The final matrices contained 73 lines and 7, 5 and 27 columns for matrices with practices, crops and organisms, respectively. Multiple ecosystem services, practices or crops could be combined for the same article by allowing several variables to take 1 as a value.

3. Results

3.1. Publications in the three databases

The number of publications varied within the three interrogated databases (Table 1). Studies in *Ecology* were more numerous than studies in *Vegetable* in all databases, but numbers differed for the other semantic objects in WOS (*Practices* > *Microfarms* > *Agroecology*), Scopus (*Microfarms* > *Agroecology* > *Practices*) and BibCnrs (*Practices* > *Agroecology* > *Microfarms*). The number of studies in *Agroecology*, *Ecology* and *Vegetable* was at least six, four and three times lower in WOS than in Scopus and BibCnrs. Studies in *Agroecology* were 2 to 10 times fewer than the number of studies in *Practices* in WOS and BibCnrs, while they were 12 times more numerous in Scopus (Table 1).

Combining *Agroecology* with *Practices* (#1 AND #3; Table 1 and Fig. 1) considerably reduced the number of publications found compared to *Agroecology* alone (#1) as well as *Practices* (#3) alone. The combination of *Ecology* with *Agroecology* (#1 AND #2) showed that both these topics seemed to be well considered, as publications linked with *Ecology* (#2) represented 63 % of publications using *Agroecology* (#1) alone (Table 1 and Fig. 1). On the other hand, publications combining *Ecology* and *Practices* (#2 AND #3) represented only 10 % of publications in *Practices* alone.

Studies on vegetable farming within an agroecological context (#1 AND #4) and linked with targeted practices (#3 AND #4) are underrepresented in the literature. They account for only for 5 % and 4 % of publications from *Agroecology* (#1) and *Practices* (#3) respectively (Table 1 and Fig. 1). Similarly, little attention was given to the study of the targeted agroecological practices within a microfarm context (#3 AND #5), which correspond to 2 % of publications from *Practices* (#3) (Table 1 and Fig. 1). Studies in agroecology in a context of microfarm (#1 AND #5) composed 8 % of publications of *Agroecology*. Studies in agroecological that addressed ecological and targeted practices in a context of vegetable farming represented 0.3 to 0.5 % of all publications of *Agroecology*, depending on the database (Table 1).

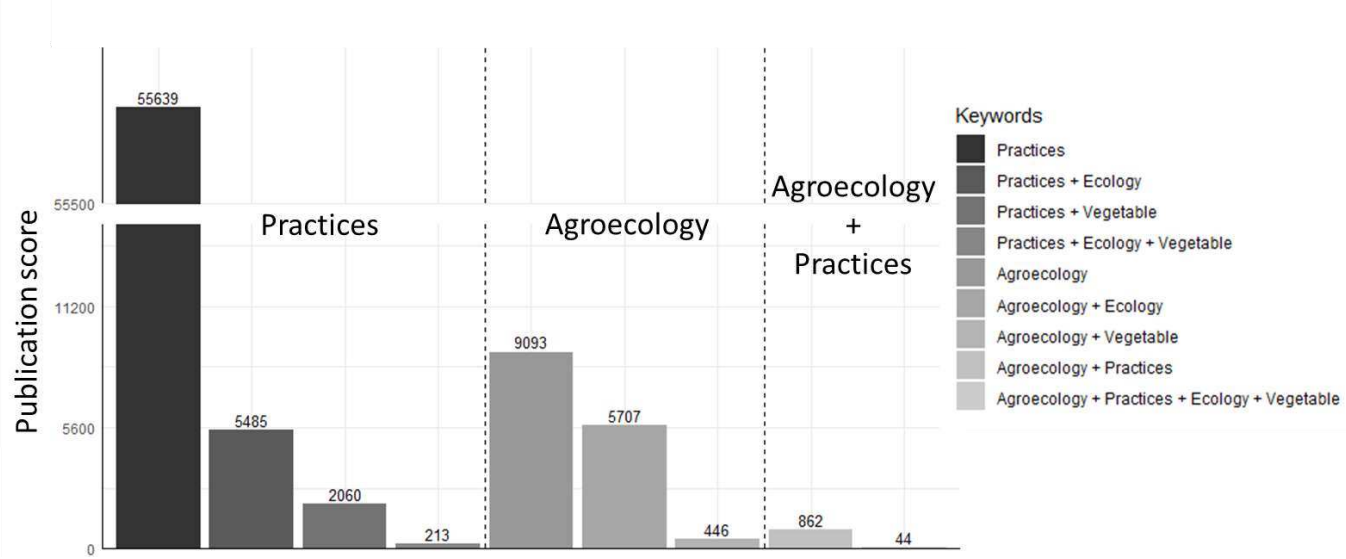


Fig. 1. Number of publications found in the Web of Science (WOS) database with the semantics objects Agroecology (#1), Practices (#3) and their combination (#1 AND #3), and their combination with semantic objects Ecology (#2) and Vegetable (#4).

3.2. Co-occurrence map

The map showing the co-occurrence of terms in publications within *Agroecology* (#1) segregated three main clusters (Fig. 2). These three clusters corresponded to terms associated with 1) biology and science (*e.g.* species, genotype, variation, variability), 2) agronomy and plant science (*e.g.* yield, soil, plant, growth, rate, content), and 3) socio-economy (*e.g.* farmer, development, knowledge, income). The term 'species' occurred the most in the "biology" cluster. 'Soil', 'yield' and 'plant' were the most-occurring terms within the "agronomy" cluster. Although many connections were found between the socio-economy and agronomy cluster, as well as between the agronomy and biology clusters, fewer connections were observed between the socio-economy and biology/science clusters. Additionally,

some terms such as ‘practice’, ‘ecology’ or ‘biodiversity’ were found within the socio-economy cluster and, although connections were observed between ‘species’ and ‘biodiversity and ‘practice’ or between ‘practice’ and ‘yield’ or ‘soil’, only a weak connection was observed between ‘ecology’ and ‘species’ or between ‘biodiversity’ and ‘soil’.

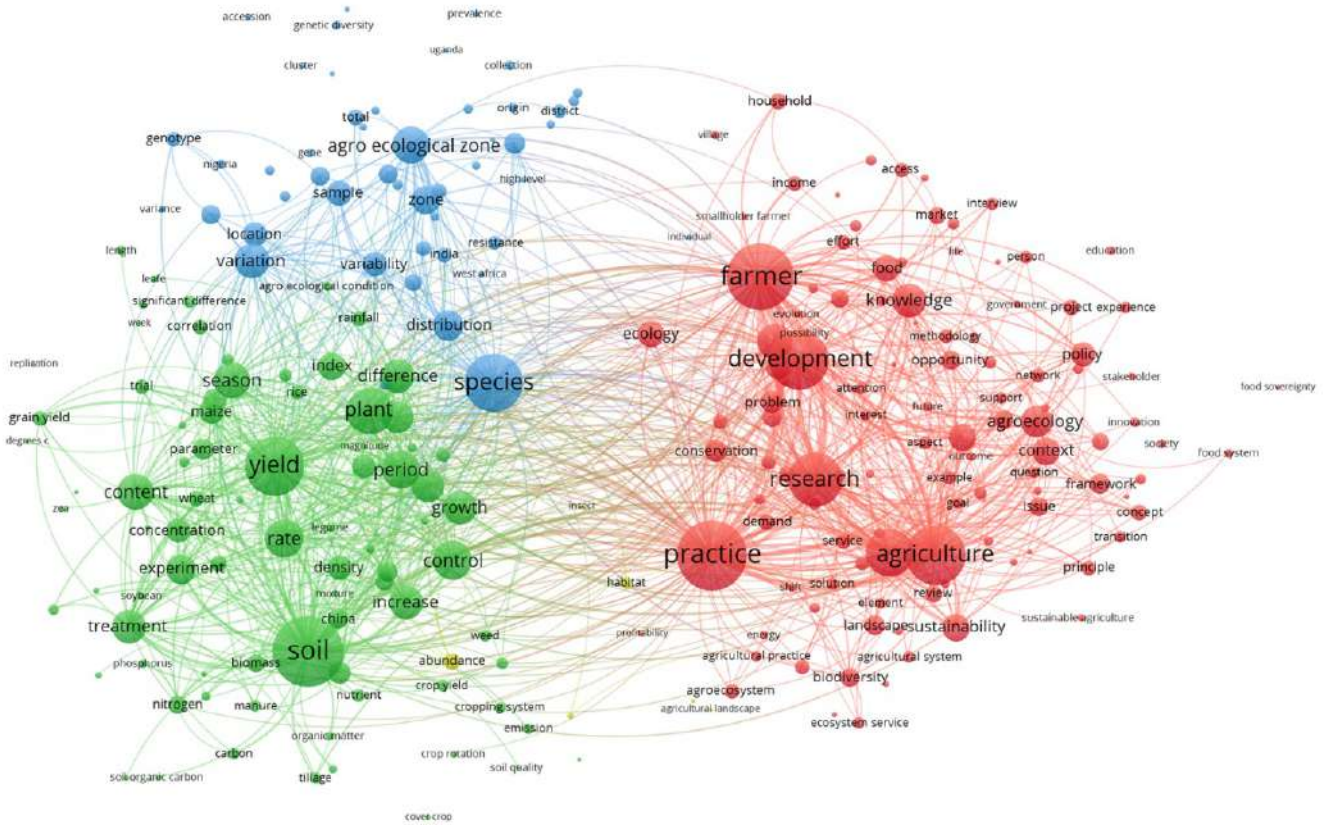


Fig. 1. Map of co-occurrence of terms within publications found in the Web of Sciences database using the semantic object Agroecology (#1). The size of circles represents the number or occurrences for each term, lines represent the co-occurrence of two terms, line width represents the frequency of co-occurrence between two terms, and colors automatically segregates clusters of tightly interlinked terms. Three clusters were automatically segregated and were associated with 1) biology (blue), 2) agronomy (green) and 3) socio-economy (red). Red and blue clusters were less connected than other clusters.

3.3. Countries, study sites, crops and organisms

3.3.1. Countries, study sites, field of studies and ecosystem services

Six regions of the world are represented by the 75 studies (SM2 Table S2). Twenty-eight were carried out in Europe, with 14 in Italy, 6 in other countries of Western Europe (*i.e.* France, United Kingdom), 3 in Eastern Europe (*i.e.* Poland, Estonia, Slovenia) and 6 in several countries. Twenty-six were carried out in North America (*i.e.* the United Stated and Canada), 6 in Eastern and Central Asia (*i.e.* China, Republic of Korea, India), 6 in West Africa (*i.e.* Nigeria, Niger) and 4 in Eastern and South Africa (*i.e.* Kenya, Rwanda, Uganda, Democratic Republic of the Congo) and 4 in Central and South America (*i.e.* Honduras, Brazil). Fifty-three experiments were carried out in research experimental sites, 14 in large vegetable

fields, 4 in microfarms and 4 in multiple types of sites (SM2 Table S2). Twenty-six studies were associated with ecology only, 36 with ecology and agronomy, 8 with ecology and another field of research such as sociology, and 5 did not use ecological concepts (SM2 Table S2). Forty-seven studies were associated with one ecosystem service only and the remaining studies were associated with two at most. Fifty-two studies dealt with biocontrol, 21 with production, 16 with biodiversity and 13 with biofertilization (SM2 Table S2).

3.3.2. Practices, crops and organisms

The most represented practice was intercropping (29 papers), followed by cover cropping as mulch (24), organic amendment (22), tillage (21), rotation (19), cover cropping to be incorporated or live (18 and 16 respectively). Overall, cover crops appeared in 45 papers. Raised bed showed only 1 occurrence. 9 papers dealt with 4 of the detailed practices, 8 with 3 practices, 32 with 2 practices and 26 with only one (SM2 Table S2).

Studies mainly targeted Solanacae, with 31 studies using tomato (19), pepper (7), potato (6) or eggplant (1)(SM2 Table S4). The next main crop families were Brassicaceae (21; cabbage (9), cauliflower (6), kohlrabi (2), turnip (2) and broccoli (2)), followed by Cucurbitaceae (20; zucchini (8), melon (5), cucumber (5), squash (3), pumpkin (1)), Poaceae (20; maize (12), sorghum (2), other cereals (3)) and Fabaceae (19; beans other than soy (11), cow- and chickpeas (4), lupin (1), soybean (1), peanut (1)). Asteraceae (*i.e.* lettuce (9), marigold (3), artichoke (2), safflower (1)) and Apiaceae (*i.e.* carrot, celery, fennel, coriander) concerned 13 and 6 studies respectively, and the least studied families were Amaranthaceae (3; *i.e* Swiss chard), Amaryllidaceae (3; *i.e.* onion, leek), Lamiaceae (2; mint, basil), Malvaceae (2; okra), Convolvulaceae (1; sweet potato), Dioscoreaceae (1; yam), Euphorbiaceae (1; cassava).

The most studied or collected organisms were Coleoptera (25 papers), in particular Carabidae (16) and Staphylinidae (9)(SM2 Table S5). Weeds (21), Hemiptera (21), in particular Aphididae (11), Anthocoridae (9) and Aleyrodidae (8), Aranae (20) and Bacteria (17) followed. Collembola and Fungi were both present in 12 studies and were followed by Thysanoptera and Lepidoptera (10), Nematoda and Diptera (9; dominated by Syrphidae), Hymenoptera (8), Acari and Myriapods (7), Isopoda (6), Opiliones and Dermaptera (5). Neuroptera and Orthoptera (4), Virus (3), Mantidae and Lumbricidae (2), and Archea, Pscocoptera and Odonates (1) were present in less than 5 out of the 75 studies.

The multiple co-inertia analysis (mCOA) revealed a lack of co-structure between the three datasets. Its first three axes explained 20 %, 16 % and 14 % of the covariance, and the pseudo-eigenvalues showed that each dataset was differentially associated with the first three principal components (SM3 Fig S1,

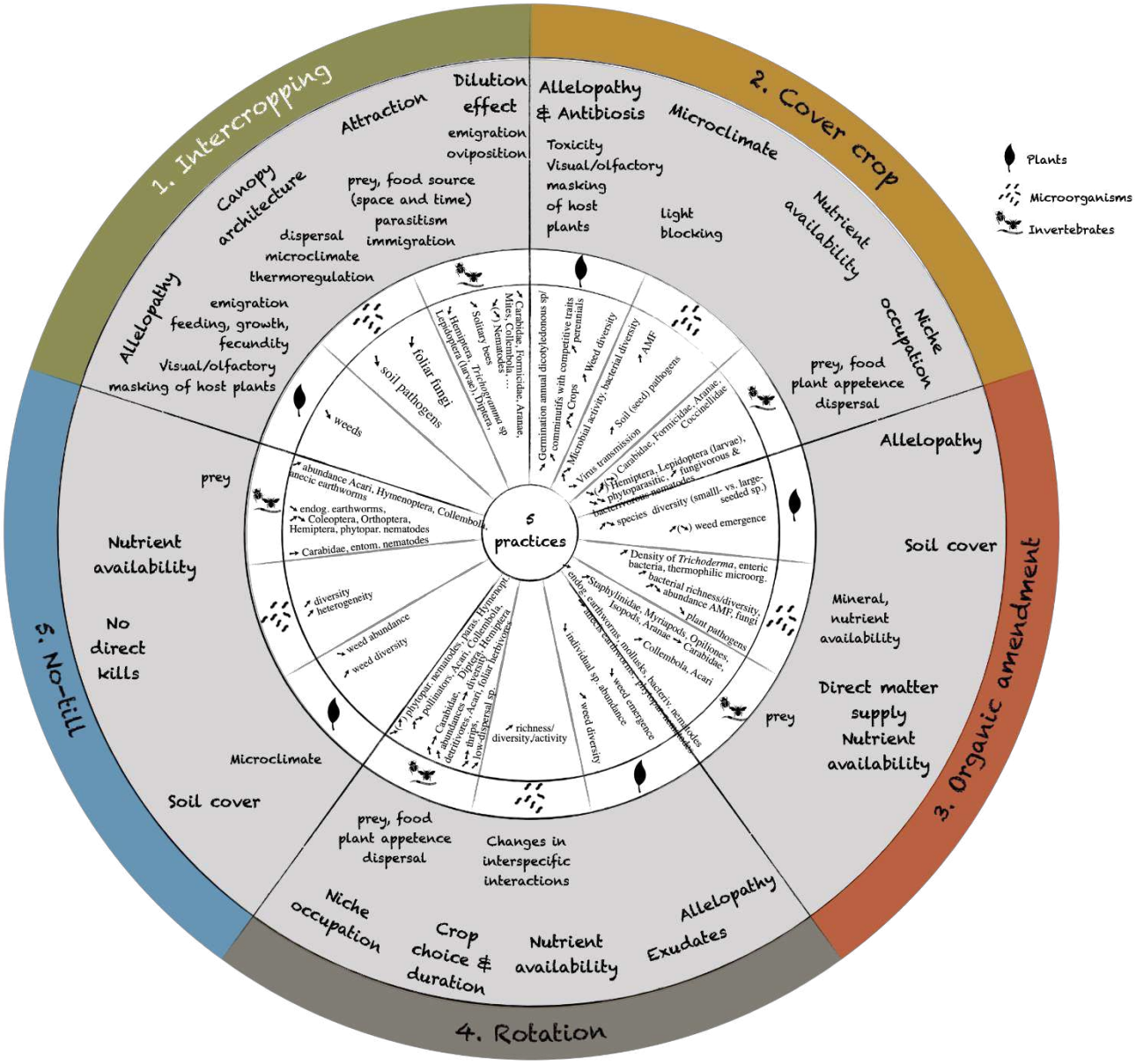
Table S6). The axis 1 was characterized by the occurrence of rotation and cover crops (r = 0.54 and r = 0.46 with axis 1) in presence of Solanaceae and of Cucurbits to a lesser extent (r = 0.64 and r = 0.46, respectively), in opposition to intercropping (r = -0.55) (SM3 Fig. S1B). Organisms showed a weak association with the axis 1, with Coccinellidae and Anthocorids being the most but weakly correlated (r = -0.31). The axis 2 was characterized by the occurrence of organic amendment (r = -0.61) and of rotation (r = -0.50) associated with Brassicaceae and Asteraceae (r = -0.58 and r = -0.57) in opposition to cover crops (r = 0.49). Organisms also showed a weak correlation with the axis 2, with Opiliones, Isopoda and Myriapoda being the most correlated (r = -0.45). The axis 3 was characterized by the co-occurrence of tillage (r = 0.88 with axis 3) and Apiaceae (r = 0.56), and their opposition with cover crops (r = -0.47). The most associated organisms were Nematoda and Cicadellidae (r = 0.49).

3.4. Qualitative analysis

The following sections summarize the impact of the six agroecological practices commonly used in small-scale vegetable farming on biodiversity or ecological processes, based on the selected literature (Fig. 3).

3.4.1. Intercropping

The canopy architecture of intercropped plants offers various conditions at the soil surface favoring protection from predators, microclimate, access to light or wind and rain penetration (Bourassa et al. 2008). For example, while a dense canopy provides moist and shady shelter for the egg deposition of predators such as carabid *Pterostichus melanarius*, an open canopy may favor species that need drier and warmer environments for thermoregulation (Munyuli et al. 2007). The distribution of predators seems to be more influenced, positively or negatively, by the complex intercropped vegetation structure than the distribution of preys (Letourneau et al. 2011). For example, Li et al. (2014) showed that intercropping of peanut (*Arachis hypogaea*) with the medicinal plant *Atractylodes lancea* favored predatory Acari and Collembola densities compared to the peanut monoculture due to the modified vegetal architecture. The presence of several heights or architecture of vegetation reduces the bare ground areas and induces a competition for light that alters the morphology of weeds and inhibits their growth and seed production (Baumann et al., 2001). Additionally, intercrops produce complementary root secretions and exudates that provide energy sources for microorganisms, whose activity is also increased by an increased aggregate macroporosity (Nyawade 2019).



Graphical synthesis of the impacts of the five studied agroecological practices on

Fig. 3. Graphical synthesis of the impacts of the five studied agroecological practices on biodiversity following results of the literature search. ↗, →, ↘ indicate overall positive, neutral or negative impacts on biological diversity, grouped by plants, microorganisms and invertebrate species. Main causes and sub-causes of impact are indicated in the grey area. No study on raised beds resulted from the literature search. Hence, it is not presented.

Within intercropping, the density of each plant species is reduced compared to monocultures. This lower density, added to vegetation architecture, induces a physical barrier and a dilution effect of the host plant that modifies population dynamics of various species, particularly of herbivorous (pest) species in the targeted crop. Thus the establishment and dispersion of species with low mobility such as foliar fungi, caterpillars or aphids is reduced ((Li et al. 2014; Ning et al. 2017). The visual localization

of the plant by pests, but also of natural enemies such as Chrysopidae, is disrupted, which results in a more frequent landing on non-host plants, in a lower oviposition on the host plant, or in an increased emigration of the pest from intercropping (Pitan and Olatunde 2006; Parsons et al. 2007; George et al. 2013).

Crop diversity in intercropping increases the diversity of natural enemies (*i.e.* predators) of herbivorous species, according to the natural enemies' hypothesis, which states that "the low incidence of disease and pests in intercrops is likely due to higher abundance of their predators, antagonists and parasites in diverse cropping systems" (Ehrmann and Ritz 2014). Indeed, the diversification of the intercropped species provides a diverse and less disturbed habitat with preys and alternative non-host food sources, thereby offering better habitat conditions for the development of several species (Munyuli et al. 2007). However, the presence of natural enemies depends on their feeding behavior and preferences, as well as the presence of alternative resources, and their abundance varies with different intercropping treatments and their capacity to find host plants (Razze et al. 2016). Predator-predator competition may occur and reduce specific predator populations, and parasitoids may be disoriented by volatile compounds emitted by intercropped species (Razze et al. 2016). A higher abundance of natural enemies was not necessarily associated with their higher richness (Letourneau et al. 2011).

Shifts in cash crop sowing date and an associated lower development of the cash crop particularly impacted herbivores. For example, the level of infestation by pod-sucking bugs was reduced in a tomato -cowpea intercrop with a shift of 2 to 4 weeks in the sowing date of cowpea (Pitan and Olatunde, 2006), and an early sowing date of cucumber intercropped with maize reduced the density of cucumber and likely reduced the oviposition selection of fruit flies and of herbivorous and predatory Coleoptera (Pitan and Filani 2014).

Intercropping also takes advantage of a chemical plant-plant complementarity. For example, aromatic plants such as marigold or coriander emit aerial olfactive compounds that can attract entomophagous arthropods, thereby increasing their density and diversity (Silveira et al. 2009; Mutisya et al. 2016). In addition, odours emitted by tomato can reduce the feeding, the development or the abundance of herbivores depending on the plant with which it is cropped (Tahvanainen and Root 1972; Facknath 1999; Pitan and Olatunde 2006). Repelling odors could mask the presence of the host plant for the whitefly (Pitan and Olatunde 2006), reduce their consumption, growth and fecundity or increase their emigration (Pitan and Filani 2014). Plants also release chemical compounds in the soil via root exudation that attract or repel organisms, or inhibit their development, through allelopathic effects (Ehrmann and Ritz 2014). For example, the allelopathic effect of *Atractylodes lancea* was shown to reduce soil-borne pathogens (Li et al. 2014). Marigold, mustard and other species act as repellent or

as trap crop, thereby reducing the fitness of phytoparasitic nematodes and lowering their negative impact on cash crops (Bridge 1996). However, species that trigger plant-plant competition can on the contrary lower their resistance and increase the fitness and populations of phytoparasitic nematodes, such as legumes with cucurbit (Powers et al. 1994).

3.4.2. Cover crop: dead and living mulch

Several types of cover crops were found in the literature. Cover crops as mulch are grown as part of the crop rotation and killed before the following crop is sown, whereas a living mulch is grown with the cash crop for at least a short period of time before it is killed. Both practices are commonly used by incorporating residues of the companion crops into the soil or leaving them at the soil surface, for soil fertilization and protection, for weed management or for pest regulation (Hooks et al. 1998; Christoffoleti et al. 2007; Verret et al. 2017). Both cases were treated separately, with the incorporated cover crops treated in the next section on organic amendment.

Plant residues and low vegetation alter light, temperature, or water content at the soil surface, and serve not only as host plants, but also as habitats and/or as food source for competitors, parasites and predators (Magagnoli et al. 2018a). A higher density of fire ants was observed in presence of killed mulch of cahaba white vetch and rye-vetch within spring bell peppers, and this higher density was associated with a higher predation of seeds and of beet armyworm pupae than in conventionally-treated plots (Pullaro et al., 2006). Fire ants were yet also sensitive to the high moisture between the soil and the layer of cover crop (Pullaro et al., 2006). Predatory foliar and epigeic arthropods showed a weak response to mulching, probably due to a lower dispersal within a richer environment (Quinn et al. 2016). Regarding herbivores, the presence of living mulch reduced the density of aphids or whitefly probably due to a lower leaf nitrogen concentration and a lower appetence (Magagnoli et al. 2018b), but also to a disturbed tracking of host plants (Hooks et al. 1998; Depalo et al. 2017) However, it had no effect on the cabbage caterpillar Pieris spp. and increased the percentage of larval parasitism, with effects varying across study sites (Depalo et al. 2017).

Cover cropping also alters soil biodiversity and activity through different soil moistures, carbon (C) and nutrient availabilities. Fungivorous nematodes were more abundant under the cover crop of cowpea than that of non-incorporated sunn hemp which induced drier conditions, whereas the reverse was found for bacterivorous nematodes in turnip and lima bean crops (Wang et al., 2008). Thereby, by favoring some organisms over others, cover crops determine the type of decomposition process (fungal vs. microbial) and communities at high trophic levels (Marinari et al., 2015). Other studies found a low impact on the abundance and composition of soil microbial communities in tomato, bean and bell pepper crops for example (Maul et al. 2014; Brennan and Acosta-Martinez 2017; Kokalis-Burelle et al.

2017). On the other hand, mixing several species as living mulch promoted artichoke root colonization by arbuscular mycorrhizal fungi, improving the phosphorous intake by roots for artichoke (Trinchera et al. 2016). Increasing the amount of surface residues increases soil macro- and mesofauna such as earthworms, arthropods or nematodes, although this increase reaches a plateau and depends on the litter quality (*e.g*. C-to-N ratio) (Ranaivoson et al. 2017; D'Hose et al. 2018). Mulching also modifies extra-guild interactions. For example, retaining maize crop residues directly and indirectly increased the abundance of the detritivorous Collembola *Hypogastrura* sp. via a lower weed biomass (Pereira et al. 2010). This higher abundance led to a cascading effect that resulted in an increasing number of predator ant *Solenopsis* sp. and lower number of herbivorous leafhoppers *E. kraemeri* and *Circulifer* spp.

The physical barrier and the modified soil properties, or the occupation of similar niches by the living mulch and weeds, control the mechanisms of seed dormancy or alter their germination, growth and development (Christoffoleti et al. 2007; Altieri et al. 2011; Ciaccia et al. 2017; Testani et al. 2019). The layer of mulch limits the access to light and increases soil moisture, which prevents seed germination and increases the occurrence of seed pathogens, respectively. Annual dicotyledonous species are particularly sensitive (Wang et al., 2008a), and using dead mulch can increase weed biodiversity as it favors perennial species that are large-seeded, survive crimpling and require lower levels of soil nitrogen to develop (Altieri et al. 2011; Brainard et al. 2016; Bietila et al. 2017; Testani et al. 2019)(Brainard et al. 2016). Weeds under mulched crops also tend to have a later flowering date and a wider flowering span (Ciaccia et al. 2020). Hence, mulching favors weed communities with higher competitive traits.

Cover crops and living mulch also largely rely on allelopathic properties of cover crops to regulate organisms considered as pests. For example, cover crops of Fabaceae (e.g. velvet bean, marigold) or sorghum reduced populations of phytoparasitic nematodes in yam crops or vegetable rotations (Wang et al. 2008a; Claudius-Cole et al. 2016; Djian-Caporalino et al. 2019). These plants are known to release toxic compounds, such as dhurrine for sorghum, which makes them poor hosts for nematodes and, when used as mulch, have stronger or longer effects than used within the crop rotation only (Wang et al. 2008a; Djian-Caporalino et al. 2019). Sturz & Christie (2003) reported an increased competition between microbial communities depending on food substrates, which was supported by allelopathic effects or antibiosis, leading to the down-regulation of root-pathogens. While decomposing, Brassicaceae release glucosinolates that are enzymatically converted into isothiocyanates, which inhibit germination and growth of other exposed plants, including cash crops (Wu et al. 1999; Jabran et al. 2015). A similar pattern was observed with cereals (e.g. barley, rye) in zucchinis and melon when barley was incorporated (Canali et al. 2013; Campanelli et al. 2019).

3.4.3. Organic amendment

Organic fertilization induces changes in the structure of soil invertebrate communities. For example, the addition of bio-organic fertilizer (BOF; mix of components such as rice straw, composted cow manure and ashes, inoculated with endophytic fungi) increased the overall diversity and abundance of Collembola and Acari compared to a chemically-fertilized monoculture of peanut (Li et al. 2014). Incorporated organic soil amendment (e.g. compost, green crop residues and/or cattle manure) also increased propagule densities of *Trichoderma* fungal species, enteric bacteria and thermophilic microorganisms and overall bacterial richness and diversity, whereas the density of plant-pathogenic microorganisms decreased, resulting in a greater suppression of plant diseases (Bulluck et al. 2002; Li et al. 2014; Ali 2019). These results were associated with an increase of minerals (Ca, K, Mg, Mn), nitrogen and organic matter availability in soil. Similar results were found with chicken manure after six years for microbial populations associated with biofertilization (e.g. *Pseudomonas* spp., *Trichoderma* spp., *Aspergillus* spp.; (Mahanta et al. 2017)). Notably, a carbon-rich organic amendment such as compost enhances the production of N-cycles enzymes, probably due to the rapid release of soluble organic carbon as a food source for microbes in soil, compared to manure (Bowles et al. 2014). However, Lee et al. (2013) also showed that the community of Actinomycetes and AMF was reduced compared to chemical fertilizers.

Larger soil communities were also impacted by the addition of organic amendment. For example, the addition and incorporation of an intermittent sorghum cover crop within a legume-vegetable rotation system inhibited the development of bacterivorous, fungivorous and herbivorous nematodes, while it stimulated predators and omnivorous nematodes (Sánchez-Moreno et al. 2006). Myriapods, Staphylinidae, Aranae and Isopods were more abundant in kohlrabi fields in which the green manure and compost had been incorporated than in fields in which cover crops were left dead at the soil surface, while Collembola showed an inverted pattern and Carabids and Opiliones were little or unevenly impacted respectively (Madzaric et al. 2017, 2018; Ciaccia et al. 2019). Adding chicken or pig slurry favored endogeic earthworms, saprophagous macroarthropods and mollusks and bacterivorous nematodes, contrary to anecic earthworms, epigeic springtails and phytoparasitic nematodes, for which no significant effect was observed (Ponge et al. 2013).

Compared to mulching, the increased fertilization resulting from incorporated residues reduces weed diversity since opportunistic nitrophilous species occupy the ecological niche, and tillage associated with organic matter incorporation favors small- vs. large-seeded species (Testani et al. 2019). The organic input increased the growth of clover, thistles and ray-grass but decreased that of *Rumex* sp. and mustard compared to inorganic fertilizer, suggesting a species-specific impact on weeds (Eyre et al.

2011). Allelopathic effects are the same as those described in the 'Cover crop: dead and living mulch' section, and composted chicken manure inoculated with a plant-beneficial fungus (*Trichoderma virens*) suppressed weed emergence more than a chemical herbicide due to its production of antibiotic compounds within tomato crops (Héraux et al. 2005).

3.4.4. Rotation

Preceding crops that are poor hosts or antagonist trap crops reduce populations of organisms by reducing their feeding opportunities and, thereby, their fitness and establishment, or by exporting the infested plants. For example, populations of phytoparasitic nematodes are reduced in fields by the use of preceding poor hosts such as maize, rice, sorghum, bell pepper and other non-leguminous crops, and their development is altered by crops such as Crotalaria, mustard or marigold that release nematicidal compounds (Bridge 1996; Navarrete et al. 2016; Schmidt et al. 2017; Djian-Caporalino et al. 2019). However, genera with a wide range of hosts are likely to be little impacted (Djian-Caporalino et al. 2019). Compounds released by the preceding crop can also increase the diversity and activity of microorganisms, and reduce or suppress plant emergence in the following crop (Sturz and Christie 2003).

Preceding crops can provide poor or rich habitats in terms of microclimate or food provision. In a potato-wheat-bean rotation, the composition of Carabidae was likely influenced by the different canopy densities between bean and wheat (Bourassa et al. 2008). Similarly, corn favored soil arthropods dominated by Acari and Collembola while soybean favored foliar arthropods dominated by Diptera and Hemiptera within a conventional long rotation (Adams et al. 2017). Corn as preceding crop reduced adult thrip populations in an onion crop, either due to an indirect effect of nitrogen depletion in the soil on the tissue and attractivity of onions, or due to a less favorable overwintering site (Buckland et al. 2013). Organisms with a weak dispersion capacity and that overwinter near the crop field are more impacted by rotating crops than those with a large dispersion capacity due to the disturbance of their habitat and to the lower number of sites to overwinter (Zehnder et al. 2007).

Beside the choice of crop species or variety, patterns of rotation also impact arthropod diversity (Adams et al. 2017). Higher arthropod abundances of soil detritivores, foliar herbivores and fungivores, as well as Carabid beetles, were found in long rotations compared to shorter conventional rotations, but pollinators showed an opposite pattern (Burgio et al. 2015; Adams et al. 2017). In addition, crop rotations including a meadow contained more anecic earthworms, more macroarthropods, more phytoparasitic nematodes and a higher microbial biomass than rotations without meadows, probably due to the reduced soil disturbance associated with crop management (Ponge et al. 2013). On the other hand, (Hummel et al. 2002a) reported no difference between a continuous tomato crop system

and a yearly rotation of sweet corn, cucumber and tomato on damage by thrips and shield bugs. Regarding wild plants, different crop types in a rotation promote the development of more diverse weed communities but with fewer individuals per species, which may be partly due to differential cropping operations that disrupt plant life cycles, also favoring quickly maturing species (Mohler et al. 2018). Eyre et al. (2011) also showed that the crop identity of the preceding years affected weed species and cover, as well as the time of planting.

3.4.5. Reduced tillage

Soil disturbance alters individuals both directly (through direct kills) and indirectly (by making the habitat less favorable in terms of nutrients, preys, temperature or moisture) (Adams et al. 2017). In a vegetable farming context, the lowest disturbed treatments show a higher activity of carabids (*e.g. Amara* spp.), with no effect on the other epigeal arthropods (*e.g.* spiders) (Hummel et al. 2002b; Bourassa et al. 2008) On the contrary, a higher carabid activity (mostly *Harpalus sp.*) was also found in full-tilled compared to strip-tilled zucchini cropping systems, which showed a resilience of carabid to soil disturbance (Quinn et al. 2016). Within conservation agriculture - which implies no-till farming - and without the use of pesticides, Brainard et al. (2016) reported a net dis-service in the regulation of pest compared to conventional tillage in snap bean production.

Bal et al. (2014; 2017) found no effect of tillage on the dispersion of entomopathogenic nematode *H. bacteriophora* in a vegetable production of carrots, maybe due to its high mobility and its ability to move deeper into the soil. However, the authors reported previous study, in which reduced tillage favored populations of entomopathogenic nematodes linked with higher soil moisture and/or the presence of suitable hosts (Bal et al. 2014). No or little effect was also found on plant-parasitic nematodes, with genera *Helicotylenchus* and *Pratylenchus* occurring in higher densities under no-till than conventional tillage, probably associated with a higher weed density that acts as host plants (Schmidt et al. 2017). Sanchez-Moreno (2006), on the other hand, found a strong influence of tillage on nematode communities in a tomato-sorghum-garbanzo cropping system, depending on their trophic roles and on their position along the colonizer to persister gradient. Bacterial- and fungal-feeders were “mildly stimulated by tillage”, while herbivores, predators and omnivores were “mildly inhibited by tillage” within the continuous cropping system (Sanchez-Moreno et al., 2006). The trophic network was less diverse in the upper soil, in which opportunistic and resistant species were favored. These were directly associated with nematode sensitivity to soil disturbance, but also indirectly through the incorporation of residues, the stimulation of microorganisms and bottom-up interactions. Reduced-tillage and no-till enhance soil microbial diversity as well as the heterogeneity of their populations, due to heterogeneously improved soil conditions, of which the volume of pores and food

availability at this microsite level (Welbaum et al. 2004; D'Hose et al. 2018). Overall, the abundance of earthworms was higher in no-till (D'Hose et al. 2018).

The impact of no-till or reduced tillage on wild plants is mainly driven by the impact of crop residues left at the soil surface, in other words mulching (see section 'Cover crop: dead and living mulch').

4. Discussion

4.1. Practices and biodiversity within agroecological studies

Search results on our targeted practices within the Agroecology field of studies represented only 9 % of its studies. This result suggests a possible bias in the literature created by not referencing publications with keywords 'practices' and 'agroecology' or 'agroecological'. However, the co-occurrence map showed that the word 'practice' still appeared as central in the search results and was related to Humanities (*e.g.* development, knowledge, policy) and Agronomy, as well as Biology through with the word 'species'. Agroecology was defined as the triptych Movement / Science / Sets of Practices ten years ago (Wezel et al. 2009), and weaker yet existing links with the words 'ecology', 'biodiversity', 'agroecosystem', 'habitat' or 'agroecosystem services' reveal an increasing interest in connecting practices and environmental sciences, in addition to the long-lasting connection between practices and agronomy. The recent field of study also explains the low number of references on targeted practices *and* ecology compared to the semantic objects *Practices* and *Ecology* alone (10 % and 1 % respectively). Other terms such as 'organic' or 'sustainable' might also be preferred by authors. 27 % of the papers indeed selected in our qualitative review were associated with either of those concepts as opposed to conventional agriculture. Using the word 'agroecology' may also be voluntarily avoided in studies that are agronomy-oriented. Vegetable and small-scale farming were underrepresented within the literature in agroecology, which may be due to the larger diversity of practices within vegetable farming than within cereal farming. Vegetables are grown from the garden scale (m^2) to a much larger scale (hectares), which implies a diversity of systems to adapt practices to various landscapes, climates and much more heterogenous and complex biological interactions.

The overall place of biodiversity/ecology appeared to be well represented in agroecological studies. However, terms usually related to ecological concepts were surprisingly connected to the socio-economic cluster (*e.g.* ecology, biodiversity) or the agronomy cluster (*e.g.* species) on the co-occurrence map. Moreover, there were only few connections between these two clusters. This pattern can be explained by the fact that social scientists address biodiversity and ecology as an integrated concept to target an audience of non-specialists of natural sciences, whereas ecologists, biologists and agronomists target an audience of specialists of their field. Research in natural science is technically

constrained by the measurements of a limited number of parameters at the local scale, and using terms such as 'biodiversity' and 'ecology' to address specific issues would be perceived as too broad and not suitable. This divergence in the use of those terms likely contributes to a gap between social and natural scientists, who do not study agroecosystems at the same scale.

Based on the selected pool of 75 papers, the disparities between studies undertaken in Northern and Southern countries (72 % *vs.* 28 % respectively) is not surprising and is commonly found in bibliometric articles and meta-analyses (Ferguson and Lovell 2014). It can be explained by a lack of funding for such studies, by the access to experimental sites, but can also be explained by the attention paid by scientists to agroecological practices across the world. Wezel et al. (2009) highlighted that agroecology as a science or a set of practices was driven by European and northern American countries, whereas agroecology as a movement was held by a Southern American perception, integrated to subsistence agriculture. In Europe, half of studies were undertaken in Italy and authors were obvious collaborators, who likely used the same referencing methods when publishing.

4.2. Impact of practices on biodiversity in vegetable farming

With this review, we hoped to synthesize the impact of six agroecological practices commonly used in vegetable farming on biodiversity. Distinguishing clear patterns was a challenge, as illustrated in Fig. 3. For example, organic amendment could have a positive or a negative impact on ecological indices of fungi or weed species, or the rotation positively or negatively impacted populations of Diptera and Hemiptera. Different studies or different experiments on the same sites showed opposite effects on ecosystems or ecological processes, often due to inter-annual variations and climatic conditions(Parsons et al. 2007). Most studies were conducted over one to three cropping seasons and did not allow the generalization of results. Taken together, this underlines the need to run long-term studies in order to overcome such temporal variation. Moreover, most experiments integrated more than one practice (49 out of 75), making it more difficult to reach conclusions on the impact of a single practice. This was particularly the case of no-till/reduced tillage and mulching that are two of the main components of conservation agriculture, which relies on soil cover and reduced soil disturbance (Ranaivoson et al. 2017). For example, no-till reduces the abundance of wild plant species (*i.e*. weeds), but also and probably because of the effects of surface crop residues such as rye that block light or release allelopathic compounds, thereby reducing their germination (Fig. 3). The main mechanisms of impact were common across all practices, such as an allelopathic effect of crops grown as companion crop or in the rotation, a modification of the microclimate at the canopy level, at the soil surface or in the soil, and the resulting availability of food resources throughout the trophic chains (Fig. 3). However,

the dilution effect on arthropods appeared only in the intercropping, and the reduced direct kills appeared only in the reduced-till systems.

A large part of the selected articles focused on groups of organisms such as pests/herbivores, natural enemies or weeds to target organisms involved in biological control. Hence, aphids and whiteflies (Hemiptera), weeds, Carabidae and Araneae were the most studied. Their occurrence was yet weakly to not associated with a particular practice or crop. Only natural enemies Coccinellidae and Anthocoridae were noticeably associated with intercropping, Opilionids, Isopoda and Myriapods with organic amendment, and Nematoda and Cicadellidae with tillage. Overall, organisms formed three to five clusters that are explained by the method of sampling (SM3 Fig. S2). Foliar arthropods are sampled through visual inspection or sweep netting (e.g. Pitan and Filani 2014; Brainard et al. 2016; Adams et al. 2017), soil crawling organisms are sampled with pitfall traps (e.g. Pullaro et al. 2006; Madzaric et al. 2018), belowground organisms through digging of soil cores (e.g. Sanchez-Moreno et al., 2006; Ponge et al., 2013), and weeds through visual inspection and estimation of soil coverage (Ciaccia et al., 2020). Each of those method alone allows the estimation of populations of several species within similar habitats with a limited additional processing time of samples, which explains the co-occurrence of soil arthropods. The abundance and diversity of predators (Carabidae, Formicidae, Araneae; Fig. 3) are favored through intercropping but not through cover crops. On the other hand, both intercropping and cover crops reduce the abundance and activity of herbivores (Fig. 3). A multiple co-inertia analysis with an additional matrix with ecosystem services revealed that practices and ecosystem matrices were associated (data not shown). The study of rotation was associated with an interest in biodiversity but was opposed to biocontrol, whereas the study of cover crops was associated with biofertilization, but surprisingly negatively with biocontrol and biodiversity. Organic amendment was also not associated with biofertilization. This is likely due to the method of data extraction from the literature. Organic amendment was counted as present even when it was not a target practice, nor were soil organisms the targeted organisms.

Few of the selected studies focused on organisms or ecological processes linked with biofertilization (17 %) and pollination services (0 %). Detritivores were variably represented, with bacteria, fungi and Collembola being the most cited. Earthworms were surprisingly almost absent from the selected studies, despite their know significant impact in agroecosystems (Blouin et al. 2013). Soil organisms play a key role in ecosystem functioning and are known to respond to soil-plant direct and indirect interactions and to soil disturbances (Brussaard et al. 2007). Hence, their role should also be studied in a context of vegetable farming. Pollinators were also quasi-absent from the extracted organisms. Syrphidae and Lepidoptera were mostly associated with biocontrol, and only one study associated Lepidoptera with biodiversity (SM3 Table S3 and S5). This is due to the fact that ecosystem services

such as pollination was not explicitly mentioned in the semantic formula. It also highlights the fact that a diversity of pollinators such as bees or Lepidoptera is not well represented in the literature. The practice of raised bed gardening was also surprisingly little explored in the literature. This can be linked with the underrepresentation studies in small-scale farms. Most of the selected studies were performed in research experimental sites or large-scale farms (71 % and 20 % respectively), in which raised bed is harder to implement because of logistics constraints.

5. Conclusion

Through a systematic review, our study showed that studies on the impact of agroecological practices on biodiversity in vegetable farming are underrepresented, as well as in small-scale farming. It is likely due to the recent field of agroecology and, within that field, to the recent interest in combining the study of practices and ecology. A quantitative analysis on selected papers showed that the most represented organisms were wild plants (*i.e.* weeds), Hemiptera, Carabidae, Aranae and Bacteria, but that soil organisms and pollinators were underrepresented. Also, also one study dealt with raised bed gardening, highlighting the lack of knowledge on such practice. Overall, the occurrence of those organisms in the literature was weakly to not linked with the vegetable crops and practices. A qualitative analysis on the selected papers highlighted that intercropping, cover crops, organic amendment, rotation and reduced tillage overall increased the abundance and richness of taxa, in particular of predators and detritivores such as Collembola. Populations of herbivores were reduced in intercropping and cover crops but not in rotations and reduced tillage systems. All impacts varied across year and site, and with the availability of food resources, which altered the selection for competitive traits. Common mechanisms were found across practices, which could reveal some redundancy or antagonist effects when several practices are used together. Overall, more effort should be made to study the diversity of biological organisms and associated on-site ecological functioning under multiple practices in vegetable small-scale farms to optimize research-action and the adoption of agroecological practices in a context of growing food demand.

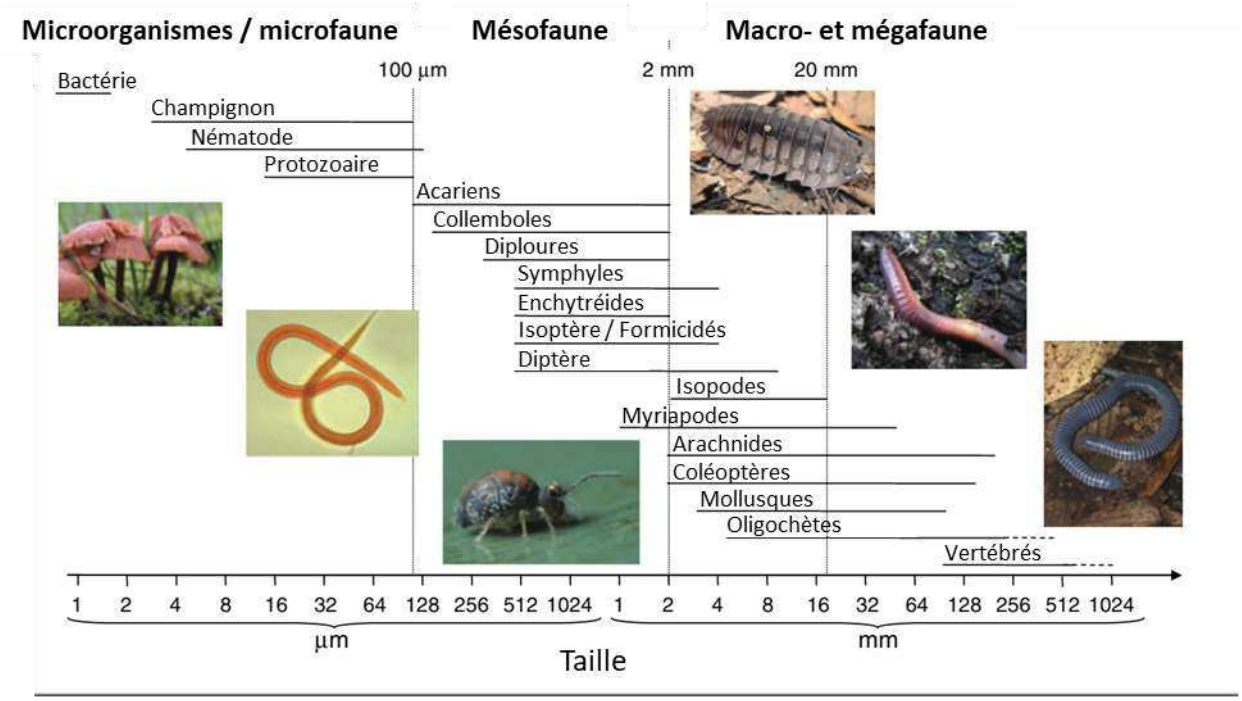


Figure 1. Représentation des principaux groupes taxonomiques d'organismes du sol classé suivant leur taille (Extrait et traduit et adapté de Decaëns, (2010), d'après (Swift et al. 1979)).

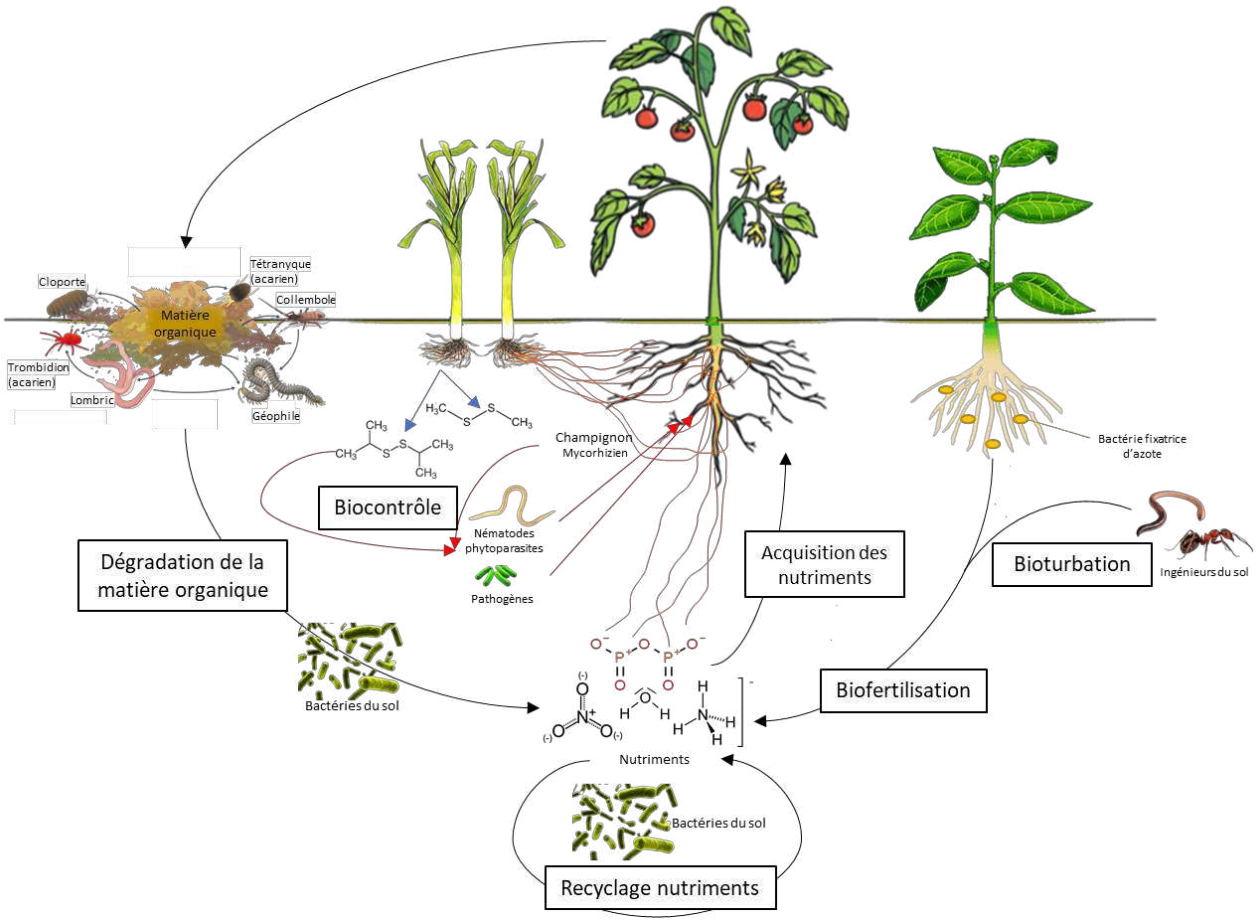


Figure 2. Schéma synthétique des principaux processus écologiques résultant des interactions entre les plantes, le sol et les organismes du sol.

Importance des interactions plantes-sol-organismes

Le sol représente un habitat pour une grande diversité d'organismes, du macroscopique au microscopique (Figure 1), qui interagissent avec le sol et les plantes ainsi qu'entre eux au sein de réseaux trophiques complexes. Ces réseaux font intervenir diverses interactions telles que la prédation, la compétition, la coopération, la symbiose ou le parasitisme. De ces interactions découlent des processus écologiques (Kibblewhite et al. 2008) tels que la décomposition de la matière organique, le recyclage des nutriments, le maintien de la structure du sol, la régulation biologique des populations de bioagresseurs ou encore la protection des plantes contre les agents pathogènes du sol (Figure 2).

Les plantes interagissent avec le sol en puisant dans les ressources en eau et en minéraux nécessaires à leur croissance. La structure de leur système racinaire, fortement variable d'une plante à l'autre, agit directement sur la structure du sol (Angers and Caron 1998), et l'architecture du couvert végétal modifie l'accès à la lumière et les conditions microclimatiques à la surface du sol (Bourassa et al., 2008; Hurej & Twardowski 2006). Par exemple, alors qu'un couvert dense offre un abri humide et ombragé pour la ponte de certains prédateurs (Munyuli et al., 2007; Tréfas & Van Leter 2008), une canopée ouverte peut favoriser les espèces qui ont besoin d'un environnement plus sec et plus chaud pour leur thermorégulation (Bourassa et al., 2008 ; Tréfas & Van Leter 2008). De manière générale, la répartition des insectes prédateurs semble être davantage influencée par une structure plus complexe de la végétation que par la répartition des proies (Letourneau et al. 2011). Les plantes sont aussi capables d'interagir de manière directe ou indirecte avec les organismes présents dans le sol et à sa surface. Par exemple, elles peuvent établir des relations symbiotiques avec des microorganismes tels que les champignons mycorhiziens qui facilitent leur acquisition d'eau et de nutriments (Gerdemann 1968; Mosse 1973) et les protège potentiellement contre les pathogènes du sol (Azcón-Aguilar and Barea 1997). De nombreuses plantes produisent également des molécules qu'elles relâchent dans le milieu *via* des exsudats racinaires, et dont certains sont impliqués dans les interactions avec les microorganismes, pathogènes ou non (Doornbos et al. 2012; Baetz and Martinoia 2014; el Zahar Haichar et al. 2014). Par exemple, les plantes de la famille des Alliacées sont connues pour produire des composés soufrés dans leurs tissus qu'elles peuvent émettre sous forme de molécules volatiles (Arnault et al. 2009). Ces composés ont des propriétés répulsives voire biocides et

dont leur utilisation s'est avérée efficace pour contrôler des populations de bioagresseurs (Arnault et al. 2005, 2013). Les plantes de la famille des Fabacées sont quant à elles capables de fixer l'azote atmosphérique au niveau de leurs racines grâce à des bactéries symbiotiques du genre *Rhizobium*. Elles sont notamment utilisées en culture de couverture, en rotation ou associées avec d'autre plantes comme fertilisant organique, via un enrichissement en azote minéral stocké et relâché au niveau des racines (Warman 1990; Shennan 1992; Fustec et al. 2010; Wang et al. 2020). Les modifications des disponibilités en nutriments dans le sol ont des conséquences directes sur la croissance des autres plantes ainsi que sur les organismes du sol (Knelman et al. 2014).

Les organismes du sol interagissent aussi avec leur environnement, modifiant ses propriétés physico-chimiques. Les microorganismes sont par exemple considérés comme faisant partie des principaux acteurs du recyclage des nutriments dans le sol, essentiel pour la nutrition des plantes (Alexander 1977; Coleman et al. 1983; Kibblewhite et al. 2008). Les organismes considérés comme ingénieurs du sol, comme par exemple les fourmis, les termites ou encore les vers de terre, contribuent quant à eux à l'aération et au maintien de la structure du sol en creusant des galeries et en brassant les particules minérales et la matière organique à travers le sol (Lavelle 1997; Holt and Lepage 2000; Cammeraat and Risch 2008; Blouin et al. 2013; Bottinelli et al. 2015). D'autre part, les interactions entre organismes sont complexes et peuvent se répercuter sur les processus écologiques associés aux organismes avec lesquels ils interagissent. Par exemple, certain décomposeur comme les cloportes broutent des bactéries présentent sur des biofilms et le redispersent dans le milieu via les fèces, participant ainsi à la dynamique des communautés de microorganismes dans le sol (Zimmer and Topp 1999; Zimmer et al. 2005). Il a aussi été montré que des enzymes secrétées dans le tube digestif des vers de terre peuvent stimuler ou inhiber le développement et l'activité de microorganismes présents dans le sol ingéré, et ainsi indirectement affecter les cycles de nutriments dans lesquels ces microorganismes sont impliqués (Parkin and Berry 1999; Bernard et al. 2012). D'autre part, dans certains cas, la présence de nématodes bactérivores stimule la croissance ainsi que l'activité des communautés bactérienne dans le sol, et favorise ainsi les processus de décomposition de la matière organique et de recyclage des nutriments (Djigal et al. 2004; Trap et al. 2016).

Bien qu'ils soient capables de modifier les propriétés du sol *via* leurs interactions entre eux ou avec le sol, les organismes du sol sont aussi connus pour répondre temporellement aux perturbations (Doran and Zeiss 2000; Brussaard 2012), qui leur sont souvent néfastes (Roger-Estrade et al. 2010; van Capelle et al. 2012; Mandal et al. 2020). Or, les perturbations physicochimiques du sol sont plus fréquentes en contexte agricole qu'en système naturel en raison de nombreuses stratégies de gestion (régimes de labours, fertilisations chimiques/organiques, couvert végétaux, incorporation de matière organique, inoculation d'organismes, ...). Le labour par exemple a des effets complexes sur l'environnement physique et chimique du sol, affectant la température, l'aération et la teneur en eau du sol, ainsi que le degré de contact entre les matières organiques et les particules minérales du sol (Kladivko 2001). Ainsi, bien que les pratiques agroécologiques aient pour but de réduire ces perturbations, elles impactent tout de même l'écologie du sol. Par exemple, l'utilisation de fertilisant organique ou de matière compostée apporte un surplus de matière organique dans le sol et est souvent associée à une plus grande disponibilité des nutriments, en particulier d'azote (Eghball et al. 2004 ; Adugna 2016). Cette modification induit des changements dans la structure des communautés de microorganismes et d'invertébrés tels que nématodes, collemboles et acariens, ou encore myriapodes, staphylins ou araignées (Nahar et al. 2006; Li et al. 2014; Madzaric et al. 2018). L'utilisation de fertilisant organique peut aussi avoir des conséquences directes sur l'activité des microorganismes du sol entrainant une augmentation de l'activité enzymatique du sol (Liu et al. 2017). Cependant, les organismes ne réagissent pas tous de la même manière à une même perturbation. Certaines espèces dites sensibles sont généralement plus impactées que d'autres espèces dites opportunistes, et ainsi la réponse du sol à une perturbation dépend fortement de l'identité des espèces dans les communautés d'organismes. (Allen-Morley and Coleman 1989; Kibblewhite et al. 2008). Par exemple la plupart des espèces de nématodes bactérivores sont catégorisés comme pionnières et répondent généralement de manière favorable à une perturbation tels qu'un enrichissement du sol, tandis que les espèces de nématodes prédateur vont être généralement impactés plus négativement, réduisant ainsi leur occurrence à court terme dans un sol (Bongers and Ferris 1999).

Pour une gestion appropriée des agroécosystèmes, l'état de santé des sols passe par l'analyse de multiples paramètres abiotiques (conditions physico-chimiques), mais aussi de plus en plus fréquemment par la prise en compte de paramètres biotiques en utilisant divers organismes du sol comme indicateurs (Doran and Zeiss 2000; Neher 2001). Outre la diversité de ces organismes, la présence et l'identité de certains organismes ou groupes d'organismes apportent d'importantes informations sur le déroulement de certains processus écologiques. Par exemple la présence et l'abondance de prédateurs témoigne de la présence de proies potentielles et donc de la complexité des chaines trophiques dans un sol (Ferris 2010a; Birkhofer et al. 2015). De même, la proportion de bactérivores et de fongivores dans le sol renseigne sur la nature des voies de décomposition de la matière organique (fongique ou bactérienne) (Ruess 2003; Ruess and Ferris 2004). À partir de ces différents constats, diverses méthodes d'analyses de l'état de santé des sols ont été développées qui se basent sur la présence, l'abondance et la diversité de certains groupes d'organismes spécifiques, tels que les microarthropodes (par ex. collemboles et acariens) ou encore les nématodes (Bongers and Ferris 1999; Ponge et al. 2003; Ferris 2010a).

Le cas des micro-fermes maraichères

Comme mis en avant dans la revue bibliographique, les micro-fermes sont peu représentées dans les recherches sur les pratiques agroécologiques. De plus, les études sur les micro-fermes se concentrent encore majoritairement sur des aspects agronomiques ou socio-économiques, tels que notamment les études réalisées sur la ferme du Bec Hellouin (Morel et al. 2015; Hervé-Gruyer 2019), tandis que peu de suivis de la biodiversité sont réalisés dans ce type de production agricole. Or, dans une optique de développement d'une agriculture durable et plus respectueuse de l'environnement, se pose la question de l'impact de ces micro-fermes sur la biodiversité associée, notamment à travers l'étude de l'impact des pratiques qui y sont mises en place.

Aujourd'hui, face au constat des impacts environnementaux et sanitaires négatifs d'un modèle de production agricole intensive, les consommateurs des pays occidentaux sont de plus en plus sensibles aux conditions de productions alimentaires. Ils revendiquent une alimentation de qualité, c'est-à-dire sans résidus de pesticides, nutritive, et surtout locale et respectueuse de l'environnement (Deverre and Lamine 2010; Holt Giménez and Shattuck

2011; Fernandez et al. 2013). En réaction aux monocultures intensives sur grandes surfaces, les agriculteurs et néo-ruraux en reconversion se tournent vers la production agricole diversifiée sur petite surface. Ainsi, les micro-fermes maraichères sont caractérisées par leur taille généralement inférieure aux tailles standards pour le statut d'exploitation agricole, c'est-à-dire 12,5 ha selon la Loi d'avenir pour l'agriculture, l'alimentation et la forêt (loi 2014-1170 du 13 octobre 2014). Les acteurs de ces exploitations agricoles cherchent à contribuer à un bon état de santé des écosystèmes comme à un bien-être social, tout en encourageant l'agriculture biologique et s'inspirant de pratiques et de philosophies alternatives comme par exemple la micro-exploitation (Fortier and Bilodeau 2014), la permaculture (Mollison and Holmgren 1981; Mollison et al. 1991; Holmgren 2002; Whitefield 2004; Mollison 2010; Ferguson and Lovell 2014) ou encore l'agriculture naturelle (Fukuoka 1985). Elles s'inspirent de pratiques innovantes et diversifiées en se basant sur la dimension écologique du système, impliquant une grande diversité de plantes cultivées et un faible niveau de motorisation et d'investissement, et avec une prise en compte des interactions sol-plantes et de la dimension paysagère comme une source de biens dont les services de régulation (Wezel et al. 2014). Par ailleurs, les micro-fermes favorisent aussi la vente directe et de proximité avec les consommateurs (Morel and Léger 2016).

La tomate (*Solanum lycopersicum*) est l'une des cultures à haut rendement les plus importantes au monde sur le plan économique (FAO, 2014). Elle est un produit-phare en maraichage et particulièrement dans un contexte de micro-fermes et de vente directe due à son haut rendement et à la durée de sa culture relativement courte. Toutefois, la tomate est une culture particulièrement sensible à divers agents pathogènes et parasites de plantes tel que le mildiou ou encore les nématodes à galles (ex: *Meloidogyne* sp.), posant de sérieuses contraintes de culture pour le maintien de son rendement (Djian-Caporalino et al. 2009). Cette plante représente donc un modèle végétal intéressant dans un contexte d'étude des pratiques agroécologiques en micro-fermes.

Objectifs de la thèse

En me basant sur six pratiques agroécologiques répandues en petit maraîchage, j'ai évalué l'importance des termes « biodiversité » et « écologie » parmi les études portant sur l'agroécologie, à travers une analyse de la littérature. Les résultats de cette analyse ont permis de mettre en évidence un intérêt croissant pour la recherche sur l'agroécologie et les pratiques agroécologiques. Cependant, un nombre relativement faible d'études liant pratiques agroécologique et biodiversité a été observé. Par ailleurs, les exploitations maraichères étaient largement sous-représentées dans les études sur les pratiques agroécologiques tandis que les micro-fermes étaient quasi inexistantes dans les résultats de notre recherche. Cette analyse bibliographique a permis de mettre en évidence une faible quantité d'informations sur le rôle écologique de la mise en place de pratiques agroécologiques, notamment dans un contexte de micro-fermes maraichères, en particulier sur les buttes de culture, et avec une faible représentativité de la faune du sol. C'est dans ce cadre que s'inscrit cette thèse qui vise à comprendre les impacts écologiques de deux pratiques agroécologiques sur des organismes bioindicateurs du sol et les interactions sol-plantes, dans un contexte de production de tomates en micro-fermes maraichères. Ce travail de thèse a été organisé autour de deux objectifs principaux.

1. Evaluer les impacts écologiques de deux pratiques agroécologiques à travers l'étude de plusieurs composantes de l'écosystème (expérimentation de terrain)

Lors de ce travail de thèse, je me suis particulièrement intéressé à deux pratiques agroécologiques : l'association de cultures et la culture sur buttes, dans un contexte de micro-fermes maraichères dans le Sud-Ouest de la France, en partenariat avec deux maraîchers. L'objectif de ce projet était de relier les réponses d'une culture cible, la tomate, les paramètres physico-chimiques du sol et la diversité biologique du sol à ces pratiques. J'ai donc effectué un suivi *in situ* de deux ans en 2018 et 2019 sur un ensemble de paramètres biotiques et abiotiques du système plantes-sol-organismes dans l'optique d'obtenir une description la plus complète et précise possible de ce système à différentes échelles spatiales et en tenant compte de différents contextes d'étude : biologique, agronomique et écologique. Ce

deuxième objectif se décline en deux sous-objectifs, correspondant chacun à un chapitre présenté dans la partie résultats en fonction des organismes ciblés.

1.1. Evaluer l'impact de l'association de cultures et de la culture sur butte sur les performances végétales de la tomate

Le but de cette expérience était de mesurer les performances végétales de la tomate en réponse à l'association de cultures et à la culture sur buttes, à travers la croissance végétale et le rendement. Ce chapitre s'inscrit dans un contexte biologique *via* l'étude de la croissance des plants de tomate, mais aussi agronomique en ce qui concerne le rendement de tomates récoltées et les propriétés physico-chimiques du sol.

Trois questions principales ont été abordées :

- *Les associations de cultures étudiées ont-elles un effet mesurable sur les performances des plants de tomates comparées à la monoculture ?*
- *Les buttes de culture ont-elles un effet mesurable sur les performances végétales des plants de tomates en comparaison des plants cultivés sur sol plat ?*
- *Un effet de l'interaction entre l'association de culture et la culture sur butte est-il observé sur les performances des plants de tomate ?*

1.2. Utiliser les communautés de nématodes pour évaluer l'impact de l'association de culture et de la culture sur butte sur le sol

Le but de cette étude a été d'utiliser les communautés de nématodes libres de la rhizosphère des plants de tomate comme indicateurs d'état de santé et de fonctionnement du sol.

Trois questions principales ont été abordées :

- *Quel est l'état global du sol évalué par l'analyses des communautés de nématodes ?*
- *Les assemblages de nématodes sont-ils impactés par les associations de cultures et la culture sur buttes ?*
- *Quelles implications les éventuels changements dans les communautés de nématodes ont-elles sur le fonctionnement du sol ?*

2. Evaluer le potentiel du poireau, d'un champignon mycorhizien et d'un ver de terre comme outils de biocontrôle du nématode à galles *Meloidogyne incognita* dans un contexte d'association de cultures (expérimentation en laboratoire)

En complément de l'expérimentation de terrain, une expérimentation en laboratoire a été mise en place à l'Université de Poitiers. L'objectif de cette expérimentation était de tester l'effet potentiel du poireau, d'une espèce de vers de terre et d'un champignon mycorhizien, seuls ou en interaction, sur le contrôle d'un des parasites les plus importants de la tomate, le nématode à galles du genre *Meloidogyne.*

Trois questions principales ont été abordées :

- *La présence du poireau permet-elle de contrôler l'infestation des racines de tomates par les nématodes à galles ?*
- *La présence du poireau permet-elle de minimiser les effets néfastes des nématodes à galles sur les performances végétales de la tomate lors de son développement ?*
- *La présence du poireau et celle d'autres organismes du sol interagissent-elles sur le contrôle des nématodes à galles chez la tomate et sur les performances végétales de la tomate ?*

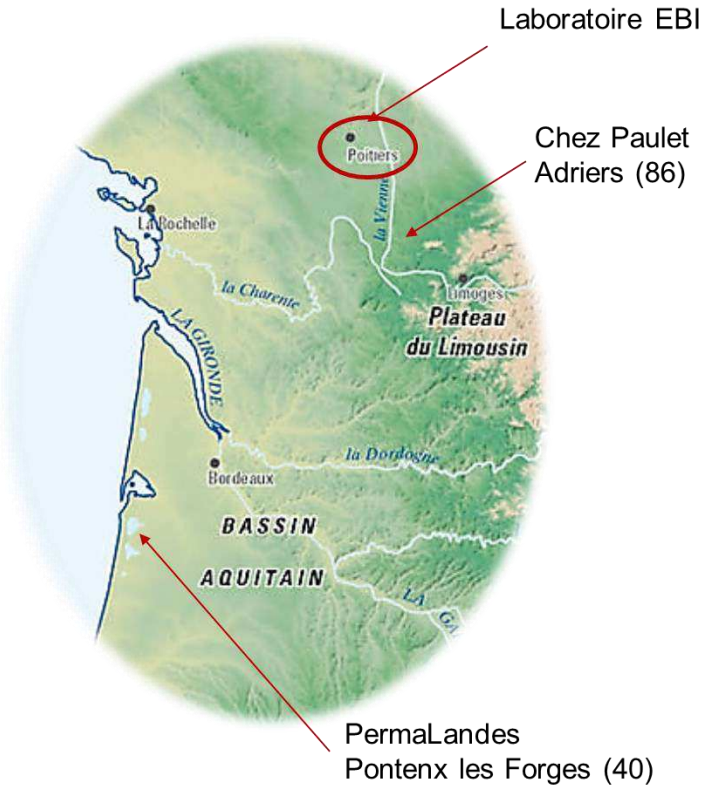


Figure 3. Localisation géographique des sites d'étude et du laboratoire d'accueil.

Approches expérimentales et sites d'études

Dans cette partie nous aborderons les différentes approches expérimentales utilisées au cours de ce travail, ainsi que les différents sites d'études, les plans expérimentaux et les modèles biologiques étudiés. Les analyses statistiques sont présentées et détaillées dans la partie Matériels et Méthodes de chaque chapitre. Au cours de ce travail de thèse, deux types d'approches expérimentales ont été utilisées et sont présentées ci-dessous.

1. Expérience *in situ*

Cette expérimentation de terrain a été mise en place afin de répondre à l'objectif 2 de ce travail de thèse concernant les impacts agronomiques biologiques et écologiques de deux associations de cultures avec la tomate, et de la culture sur buttes organiques. En 2018 et 2019, deux campagnes d'échantillonnage ont été réalisées, dans deux micro-fermes maraichères du sud-ouest de la France. Ces suivis ont été réalisées sous serres-tunnels en plastique.

1.1. Sites d'étude

Le premier site d'étude 'chez Paulet' (exploitation Jean Charry) à Adriers (Figure 3) dans le département de la Vienne (86) et est soumis à un climat océanique de transition sur un sol limon-sableux. J. Charry mène son exploitation maraichère en agriculture biologique depuis 2009 et est en partenariat avec une AMAP à Poitiers depuis 2010 (AMAP du Chaudron d'Or). Sur ce site, seul l'impact de l'association de cultures a été étudié car la mise en place de buttes ne correspondait pas à l'historique de culture de l'agriculteur.

Le second site d'étude a été mis en place en collaboration avec Jonathan Fournier, Président de l'Association La Graine des Forges, à Pontenx-les-Forges (Figure 3) dans le département des Landes (40). Le site est soumis à un climat océanique sur un sol sableux. Depuis Janvier 2017, J. Fournier est porteur d'un projet de maraichage (PermaLandes) sur une ancienne friche d'acacias, sur une surface totale cultivée de 800 m2. Un de ses objectifs principaux est de réaliser une production agricole basée sur la permaculture tout en évaluant l'impact de ses pratiques sur la biodiversité fonctionnelle et la qualité du sol. Il a souhaité tester les deux facteurs : l'association de cultures et la culture sur buttes.

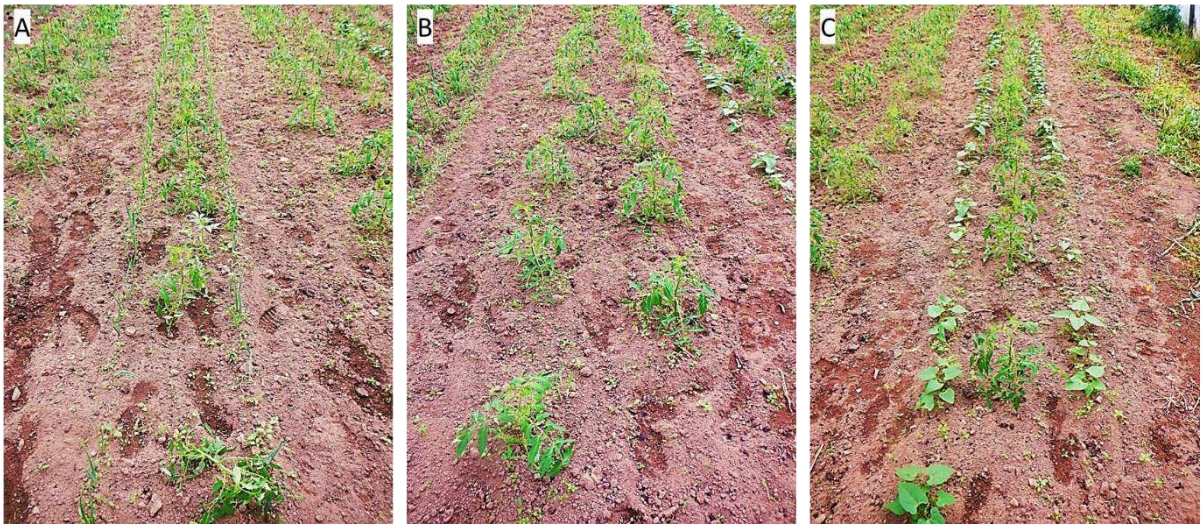


Figure 4. Photo des associations de cultures A. Poireau-Tomate, B. Monoculture de tomate et C. Haricot-Tomate lors de leur mise en place sur le site d'Adriers.

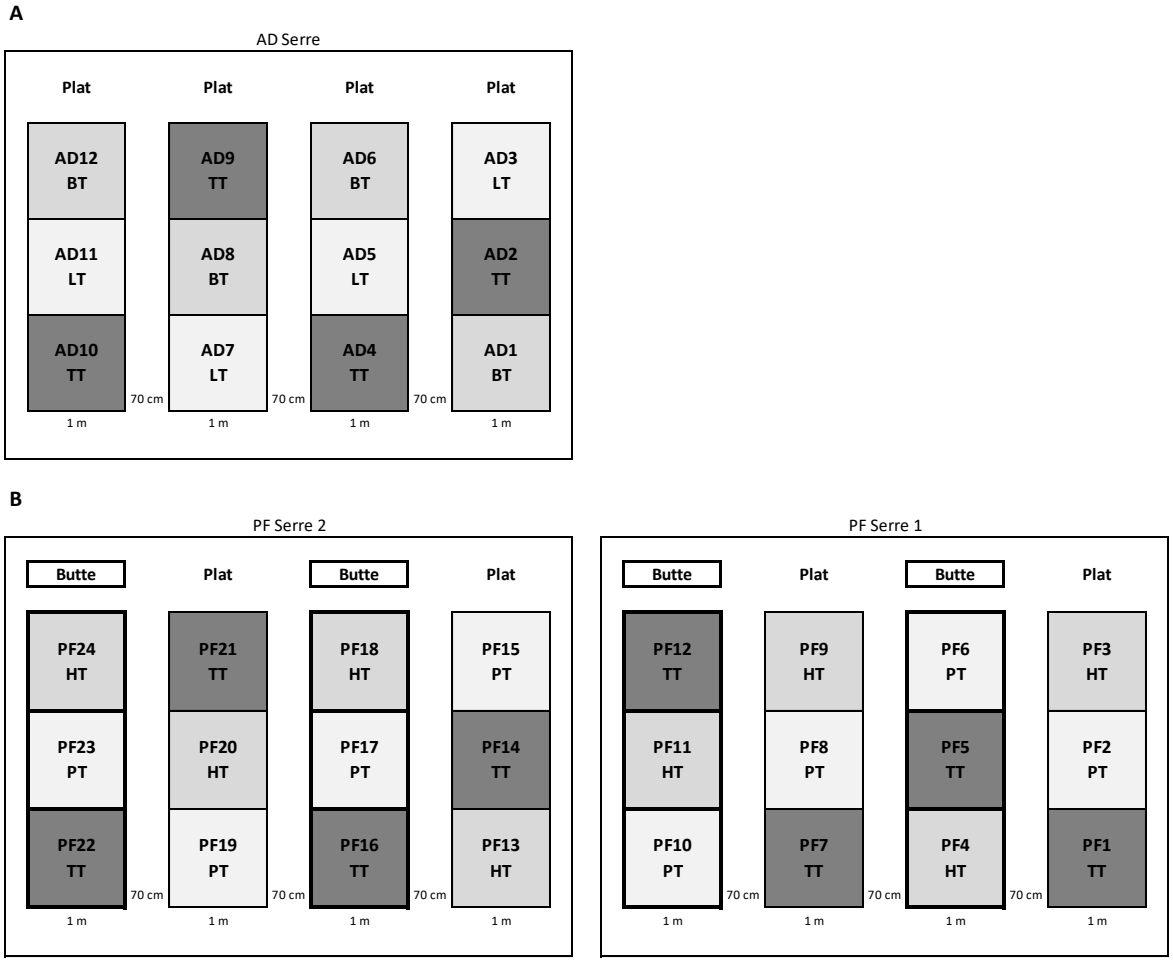


Figure 5. Plan expérimental dans les deux sites d'études : A. Adriers (AD) et B. Pontenx-les-Forges (PF). Pour chaque association de cultures, quatres réplicats ont été établis en bloc randomisés. Gris foncé : Monoculture de tomate (TT), gris : association Haricot-Tomato (HT) et gris clair: association Poireau-Tomato (PT).

1.2. Plantes cultivées et cultivars

Le cultivar de tomate (*Solanum lycopersicum* cv. "Coeur de boeuf rouge" ; AGROSEMENS, France) a été sélectionné pour son potentiel économique car il est couramment trouvé sur les marchés et apprécié par les consommateurs. Les cultivars de poireau (*Allium porum* cv. 'Lancia' ; AGROSEMENS, France) et de haricot (*Phaseolus vulgaris* cv. 'nanus' HAR19 ; AGROSEMENS, France) ont été sélectionnés par les agriculteurs pour leur intérêt agronomique et pour leur période de croissance estivale. Toutes les semences ont été produites biologiquement.

1.3. Plan expérimental

Sur le site d'Adriers (AD), les performances végétales des plants de tomate ont été mesurées dans le cadre de deux associations de cultures (Haricot-Tomate et Poireau-Tomate) en comparaison avec une monoculture de tomates (Figure 4). Quatre réplicats ont été mis en place pour chacun des trois traitements, répartis sur quatre bandes de culture, résultant en 12 parcelles d'échantillonnage (Figure 5A, Figure 6). Chaque planche de culture consistait en une bande de 21 m2 divisée en trois parcelles de 7 m x 1 m, de manière à avoir chacun des trois traitements dans chaque bande de culture. Une randomisation de l'emplacement des trois traitements a été réalisée au sein de chaque planche de culture (randomisation en bloc). Les planches de culture étaient séparées de 70 cm les unes des autres. Pour chaque traitement, l'espacement entre les plantes a été établi selon les recommandations de la compagnie de semences (AGROSEMENS). Du fumier organique de bovins composté (20 t/ha) a été enfoui dans le sol (15-20 cm) avec un motoculteur une semaine avant la plantation (Figure annexe 1). Les cultures ont été irriguées par un système d'irrigation goutte à goutte (2 heures, par semaine) en 2018 pour réduire le risque de moisissure, et par un arroseur en 2019. Ce changement avait pour but d'améliorer les performances des poireaux. Les parcelles expérimentales ont été désherbées à la main quatre fois pendant la saison de croissance.



Figure 6. Photo de la serre tunnel sous laquelle ont été réalisées les expérimentations sur le site d'Adriers.



Figure 7. Photo des serres tunnel sous lesquelles ont été réalisées les expérimentations sur le site de Pontenx-les-Forges.



Figure 8. Photo de la mise en place des buttes de culture par superposition de foin de fumiers et de bois composté, sur le site de Pontenx-les-Forges.

Sur le site de Pontenx-les-Forges (PF), la mise en place des deux associations (Haricot-Tomate et Poireau-Tomate) et de la monoculture de tomate a suivi le même plan expérimental qu'à Adriers. Cependant, cette configuration a été doublée pour tester l'interaction avec les différents modes de gestion des sols : culture sur buttes organiques permanentes en comparaison à la culture sur sol plat, résultant en 24 points d'échantillonnage repartis sous deux serres-tunnels en plastique (Figure 5B, Figure 7). Pour ce site, l'agriculteur était intéressé par l'utilisation de buttes organiques comme moyen de compenser la texture sableuse du sol, initialement pauvre en matière organique. Les buttes organiques permanentes ont été préparées en superposant du foin, de l'amendement, et du bois broyé composté (Figure 8). Pour les planches de culture sur sol plat, l'amendement organique a été incorporé dans le sol (15-20 cm) une semaine avant la plantation. Les cultures ont été irriguées avec un système d'irrigation goutte à goutte (2 heures hebdomadaires en 2018) pour réduire le risque de mildiou, avec une utilisation occasionnelle d'un arroseur en cas de sécheresse (2 m^3 tous les deux jours), et avec un arroseur en 2019. Aucune culture d'hiver n'a été effectuée entre 2018 et 2019.

Sur les deux sites, tous les plants de tomates ont été semés un mois avant le début de l'expérience, transplantés une fois et conservés en pots dans une pépinière sur le site PF (Figure annexe 2). Les poireaux ont été semés dans un terreau professionnel dans une serre non chauffée sur le site AD quatre mois avant le début de l'expérimentation (Figure annexe 3). Lors de la plantation, les poireaux les plus développés ont été utilisés pour les associations avec la tomate. Les racines et feuilles des poireaux ont été habillés, c'est-à-dire coupés à ras lors du repiquage de manière favoriser la reprise du développement de la plante (Figure annexe 4). Les graines de haricots ont été semées directement sur les parcelles correspondantes au début de l'expérimentation, en même temps que la transplantation des plants de tomate et des poireaux sous les serres de culture.



Figure 9. Photo de l'échantillonnage des nématodes. A. à Adriers et B. à Pontenx-les-Forges en juin 2018, lors de la première session d'échantillonnage.

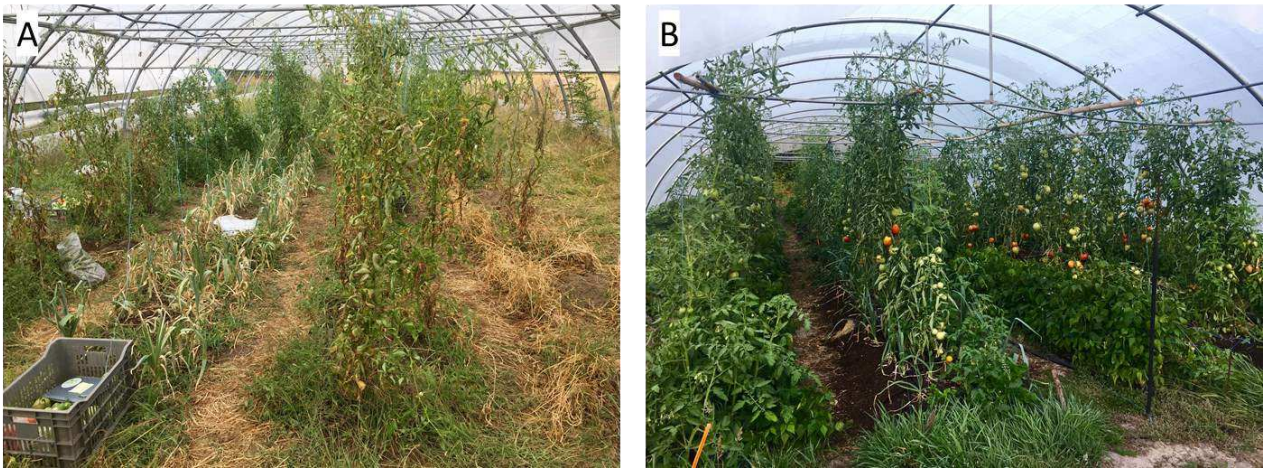


Figure 10. Photo de l'état de la végétation dans les serres en septembre 2018 lors de la seconde session d'échantillonnage ; A. à Adriers et B. à Pontenx-les-Forges.

1.4. Echantillonnage

Deux sessions annuelles d'échantillonnage ont eu lieu sur chaque site dans les 12 parcelles à AD et les 24 parcelles à PF. La première session d'échantillonnage a eu lieu en Juin, un mois après la mise en place des associations de culture (Figure 9), c'est-à-dire lors de la transplantation des tomates et des poireaux et des semis de haricots effectués en Mai. Une deuxième session d'échantillonnage a été réalisée en Septembre, en fin de récolte des tomates (Figure 10) d'après le calendrier des maraichers. Un ensemble de paramètres biotiques et abiotiques présentés ci-dessous (Tableau 1) a été mesuré à chaque session d'échantillonnage. Le détail des méthodes d'échantillonnage, des mesures de chaque paramètre est précisé dans la partie Matériels et Méthodes des chapitres correspondant aux objectifs donnés dans le tableau 1

Tableau 1 : Liste des paramètres mesurés lors des sessions d'échantillonnage en fonction des objectifs de la thèse

	Paramètres mesurés	*Objectifs*
Paramètres biotiques		
Plants de tomates	Hauteur de plantes Biomasse sèche (aérienne et racinaire)	II-1
Adventices (2019)	Biomasse sèche	II-1
Nématodes libres du sol	Abondance Diversité Indices (Bongers 1999) Empreintes métaboliques (Ferris 2010b)	II-3
Paramètres abiotiques		
Propriétés physiques du sol	Température Humidité	II-1/2/3
Propriétés chimiques du sol	pH, P (Olsen), CEC, K^+, Ca^{2+}, Mg^{2+}, Na^+ $C_{organique}$, N_{total}, Matière Organique NH_4^+ et NO_3^-	II-1/2/3

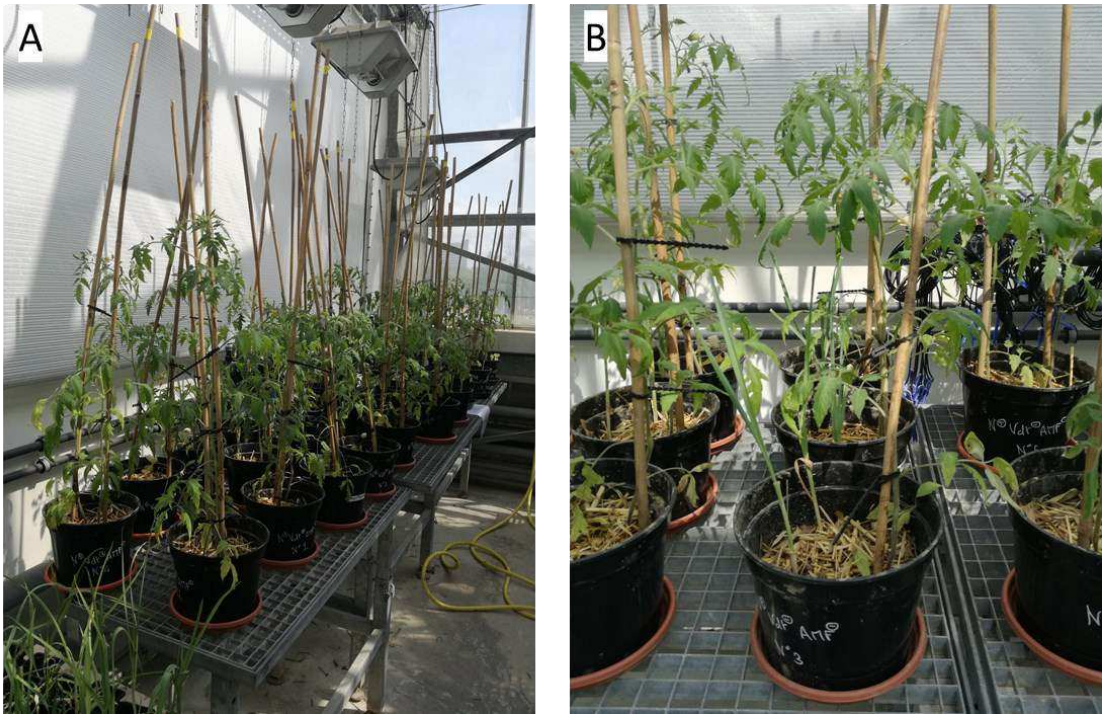


Figure 11. Photo de plants de tomate cultivés en pots sous serre expérimentale au laboratoire EBI, A. en monoculture et B. en association avec les poireaux.

Tableau 2 : Détail des différents facteurs et niveaux de facteur utilisés pour la mise en place des traitements de l'expérimentation en laboratoire

Facteur	*Niveau de facteur*	*Abréviation*
Association	Monoculture de tomates	**TT**
	Association Poireau-tomate	**LT**
Organismes du sol	Sans organisme du sol	**Control**
	Nématodes *M. incognita* seul	**RKN**
	Nématodes *M. incognita* Champignon mycorhizien à arbuscules *R. irregularis*	**RKN/AMF**
	Nématodes *M. incognita* Ver de terre épigé *E. andrei*	**RKN/EW**
	Nématodes *M. incognita* Champignons mycorhiziens à arbuscules *R. irregularis* Vers de terre épigé *E. andrei*	**RKN/AMF/EW**

2. Expérience en laboratoire

Pour répondre à l'objectif 3, et en complément de l'expérimentation de terrain, une expérience *ex situ* a été réalisée au laboratoire EBI sous serre expérimentale de Mai à Juillet 2019 (Figure 11). Cette étude a pour but d'évaluer le potentiel du poireau, seul ou en interaction avec des organismes du sol, sur le contrôle du nématode à galles *Meloidogyne incognita* (Root-Knot Nematode RKN) dans la culture de tomates sur sol préalablement stérilisé et en milieu contrôlé. Dans cette expérience, des tomates ont été cultivées en pot, en monoculture (Tomato-Tomato TT) ou associées avec des poireaux (Leek-Tomato LT), dans un sol contaminé par des œufs de nématodes à galles en présence de poireaux, de champignons mycorhiziens (Arbuscular Mycorrhizal Fungi AMF ; *Rhizophagus irregularis*) et/ou de vers de terre épigés (Earthworm EW ; *Eisenia andrei*). Cette partie présente brièvement le plan expérimental, la préparation des plantes et les différentes mesures effectuées lors de cette expérience.

2.1. Plan expérimental

Un plan expérimental randomisé à deux facteurs a été mis en place. Les deux facteurs étaient le type d'association (avec 2 niveaux : Monoculture de tomate (TT) et association poireau-Tomate (LT)), et le type d'organismes du sol (avec 5 niveaux). Le détail des différents niveaux de facteur et indiqué dans le Tableau 2.

La combinaison de ces deux facteurs a donné lieu à 10 traitements, comprenant chacun 5 réplicats biologiques (n=5), soit un total de 50 pots (Figure 12). Afin d'être le plus représentatif possible des conditions de terrain, où la densité de culture d'une monoculture peut être deux fois plus élevée que celle d'une association de cultures, deux pieds de tomates ont été placés dans un pot en monoculture de tomates, et un seul dans l'association poireau-tomate. La même quantité d'inoculum d'œuf de nématodes *M. incognita* a été appliquée aux pots en monoculture et en association, sans tenir compte de la densité des plants de tomates. Des spores de champignons en solution ont été versés sur les radicules des graines germées, 7 semaines avant la transplantation des tomates concernées, pour assurer une colonisation des racines de tomates par les hyphes mycorhiziens. Le sol utilisé pour cette expérience provient du site d'étude d'Adriers, tamisé à 2 mm et autoclavé 2 mois avant la transplantation

des tomates et l'inoculation des organismes. Cette stérilisation préliminaire a été effectuée afin d'éviter toute présence d'autres organismes pouvant interférer dans l'expérimentation.

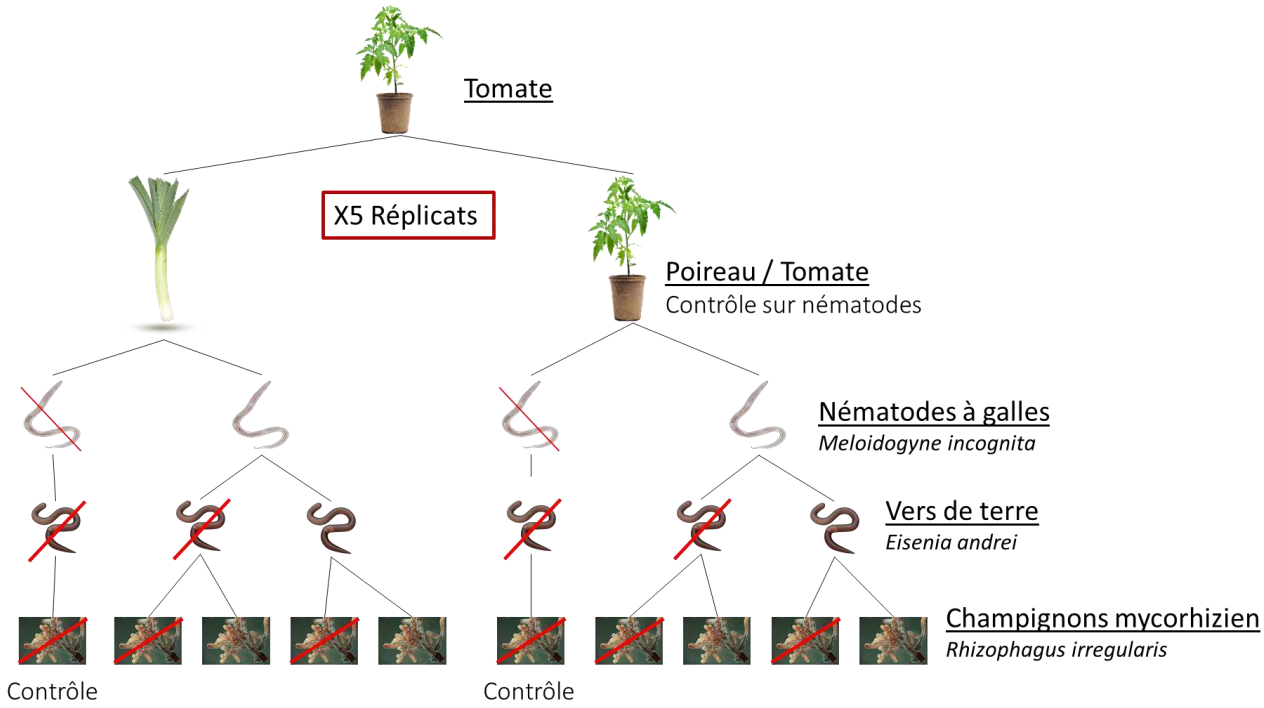


Figure 12. Plan expérimental présentant les différents organismes utilisés lors de l'expérimentation en laboratoire ainsi que leur combinaison dans les pots.

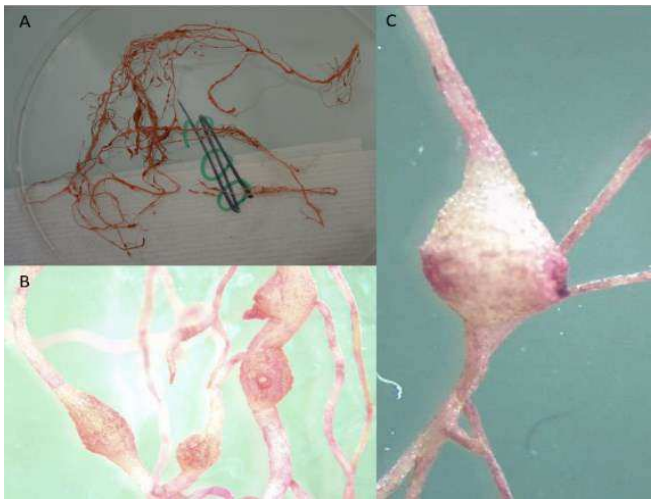


Figure 13. A. Galles induites par le nématode *M. incognita* sur racine de tomate, B. Marques résiduelles de ponte de *M. incognita* sur galles, et C. Galle avec plusieurs pontes, observées à l'œil (A) et sous loupe binoculaire (B et C).

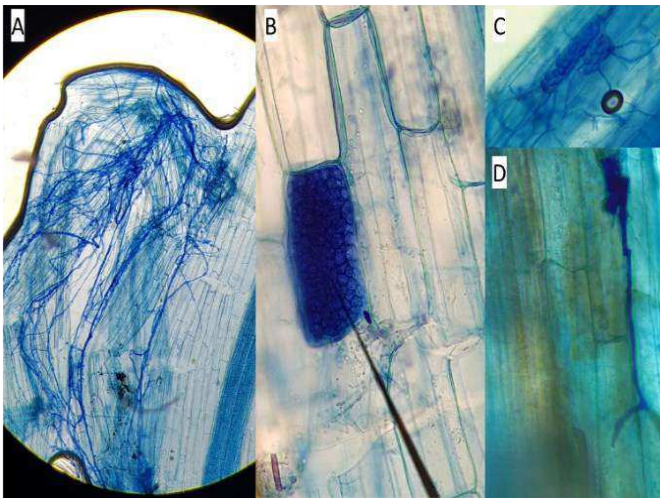


Figure 14. A. Hyphes mycorhiziens sur fragment de racine de tomate, B. Arbuscules mycorhiziens dans une cellule de racine de tomate, et C. et D. Hyphes mycorhiziens sur fragment de reines de tomate ayant pénétrés une cellule pour y former un arbuscule. Observations au microscope après colorations des racines de tomate à l'encre de chine.

2.1. Echantillonnage

L'ensemble des mesures sur les plants de tomates, l'infestation des nématodes, les paramètres du sol, la survie des vers de terre et la colonisation des champignons mycorhiziens a été effectué après 7 semaines (t7) de croissance. Dans les pots en monoculture, un des deux pieds de tomate avait été préalablement aléatoirement marqué au début de l'expérience pour effectuer un suivi hebdomadaire de la croissance. C'est sur ce pied qu'ont également été récoltées les mesures finales. Les paramètres échantillonnés lors de cette expérience sont présentés ci-dessous (Tableau 3). Les détails des différentes méthodes d'échantillonnage pour chaque paramètre, ainsi que les détails des mesures, des comptages, et des analyses sont précisés dans la partie Matériels et Méthodes du chapitre 4.

Tableau 3 : Détail des différents paramètres mesurés lors de l'échantillonnage

Echantillons	*Paramètres mesurés*
Plants de tomates	Hauteur de plantes (hebdomadaire)
	Biomasse sèche (aérienne et racinaire)
	Nombre de fleurs
Nématodes	Nombre de galles (Figure 13A)
	Nombre de pontes (Figure 13B)
	Nombre de galles avec plusieurs pontes (Figure 13C)
Colonisation mycorhizienne des racines de tomates	Fréquence de colonisation [F%] (Figure 14)
	Intensité de colonisation [M%]
	Intensité de la colonisation dans les fragments de racines colonisés [m%]
Vers de terre	Nombre de vers restant dans les pots
Propriétés physicochimiques du sol	pH, P (Olsen), CEC, K^+, Ca^{2+}, Mg^{2+}, Na^+
	$C_{organique}$, N_{total}, Matière Organique
	NH_4^+ et NO_3^-

Résultats et discussion

Chapitre 1. Etude des performances végétales de la tomate en réponse à l'association de cultures et la culture sur buttes

Cette première partie traite des effets de l'association de cultures et de la culture sur buttes sur les performances végétales de la tomate en 2018 et 2019, dans un contexte de micro-fermes maraichères. Les performances végétales mesurées ici correspondent à la croissance et au rendement des pieds de tomates, auxquels a été ajoutée la biomasse des adventices en 2019.

Les travaux présentés sont le résultat d'une première analyse. Les performances végétales sont comparées entre traitements et mises en relation avec les propriétés physico-chimiques du sol, et les avantages et inconvénients des pratiques pour les agriculteurs sont discutés. Ainsi, cette étude s'inscrit dans le cadre d'études biologiques et agronomiques, focalisées sur la plante-cible cultivée, la tomate.

Les travaux préliminaires de cette expérience sont ici présentés et discutés sous la forme d'un article scientifique.

1

Impact of intercropping and raised beds on tomato yield and growth in vegetable farming

Jeremy Detrey[a], Didier Bouchon[a], Julia Clause[a,*]

[a] University of Poitiers, Laboratory of Ecology & Biology of Interactions - UMR CNRS 7267, TEAM EES – Ecology Evolution Symbiosis, 5 rue Albert Turpain, TSA, 51106, 86073, Poitiers Cedex 9, France.

1. Introduction

Agroecological practices are defined as agricultural practices that aim to maintain high yield rates, while relying on and optimizing ecological processes rather than on using chemicals and biotechnological solutions (Wezel et al. 2014). Thereby, ecological processes and ecosystem services such as nutrient cycling, biological N fixation, natural regulation of pests, soil and water conservation, biodiversity conservation and carbon sequestration are directly integrated as necessary elements in farming to ensure the sustainability of the production. Ecosystem services include benefits that humans receive from ecosystems and that directly or indirectly support their survival and quality of life (Leemans and De Groot 2003). In agroecosystems, the belowground biological activity of plants and the soil microorganisms and fauna have an impact on ecosystem services such as soil structuration, water availability, fertilization and pest regulation (Bender et al. 2016).

Among agroecological practices, intercropping and raised bed cultivation techniques are both used in small-scale organic farming, where nature-based low-technology practices are common. Intercropping optimizes several ecosystem services such as soil fertilization or pest regulation and has been shown to improve the yield and crop quality in cereal-legume intercropping (Bedoussac et al. 2015) as well as in vegetable farming (Malézieux et al. 2009). This practice is based on plant-plant interaction and consists in cropping at least two plants coexisting for a period of time (Brooker et al. 2015). Plants physically and chemically interact with their environment through roots exudates, which can lead to facilitation, protection or competition between plants. For example, plants from the *Allium* genera produce sulphur compounds in their tissues that they can emit as volatile molecules (Arnault et al. 2009). These compounds have repellent or even biocidal properties and have already been proven to control pest populations (Arnault et al. 2005, 2013). On the other hand, plants of the Fabaceae

family fix atmospheric nitrogen in their roots thanks to symbiotic bacteria of the *Rhizobium* genus. The atmospheric nitrogen is captured, transformed and released at the root level which makes of Fabaceae useful crops for soil fertilization, as cover crops, in rotation or in association with other plants (Warman 1990; Shennan 1992; Fustec et al. 2010; Wang et al. 2020). Raised-bed farming of gardening aims to improve soil conditions by adding a large amount of organic matter at the soil surface to increase soil fertility and to indirectly favor the diversity of organisms, their associated ecological processes and, *in fine*, crop health and yield (Govaerts et al. 2007; Naresh et al. 2012).

The aim of this study was to assess the impact of intercropping and raised bed cultivation on the plant performances of an economically important crop in a context of vegetable farming. Tomato (*Solanum lycopersicum*) was chosen as the target species and the potential of two other cash crops to benefit tomato growth was tested: leek (*Allium porrum*) and bean (*Phaseolus vulgaris*).

2. Materials and methods

2.1. Study sites

A two-year field experiment (2018-2019) was performed under plastic tunnel greenhouses in two organic vegetable small-scale farms in south-western France. The first site was located in Adriers (AD), France (46° 25’ 20.53” N, 0° 75’ 70.95” E; mean annual temperature/rainfall: 12.4°C/0.92 mm) on a sandy loam soil that has been organically cultivated for the last 10 years. The second site was located in Pontenx-les-Forges (PF), France (44° 22’ 84.79” N, -1.088596 E; mean annual temperature/rainfall: 15.0°C/1.59 mm) on a sandy soil in a reconverted acacia wasteland.

2.2. Experimental design

2.2.1. Site I: Adriers

At the AD site, the tomato plant performances were measured in two crop associations (Bean-Tomato (BT) and Leek-Tomato (LT)) in comparison with a tomato monoculture (Tomato-Tomato (TT)). Four replicates were set up in a total randomized block design for each of the three treatments (TT, BT and LT), spread over four crop strips, resulting in 12 sample plots (Fig.

1A). Each strip consisted in a 21 m^2 strip divided into three plots of 7 m x 1 m. All three treatments were represented within each strip. The crop strips were 70 cm apart from each other. For each treatment, plant spacing was established according to the recommendations of the seed company (AGROSEMENS; Fig. S1). Composted organic cattle manure (20 t/ha) was incorporated into the soil (15-20 cm) with a tiller one week before planting. The crops were irrigated with a drip irrigation system (2 hours per week) in 2018 to reduce the risk of mildew, and with a sprinkler in 2019. This change was intended to improve the performance of leeks. The experimental plots were hand-weeded four times during the growing season. Cruciferous crops were grown during winter between both years of experiment.

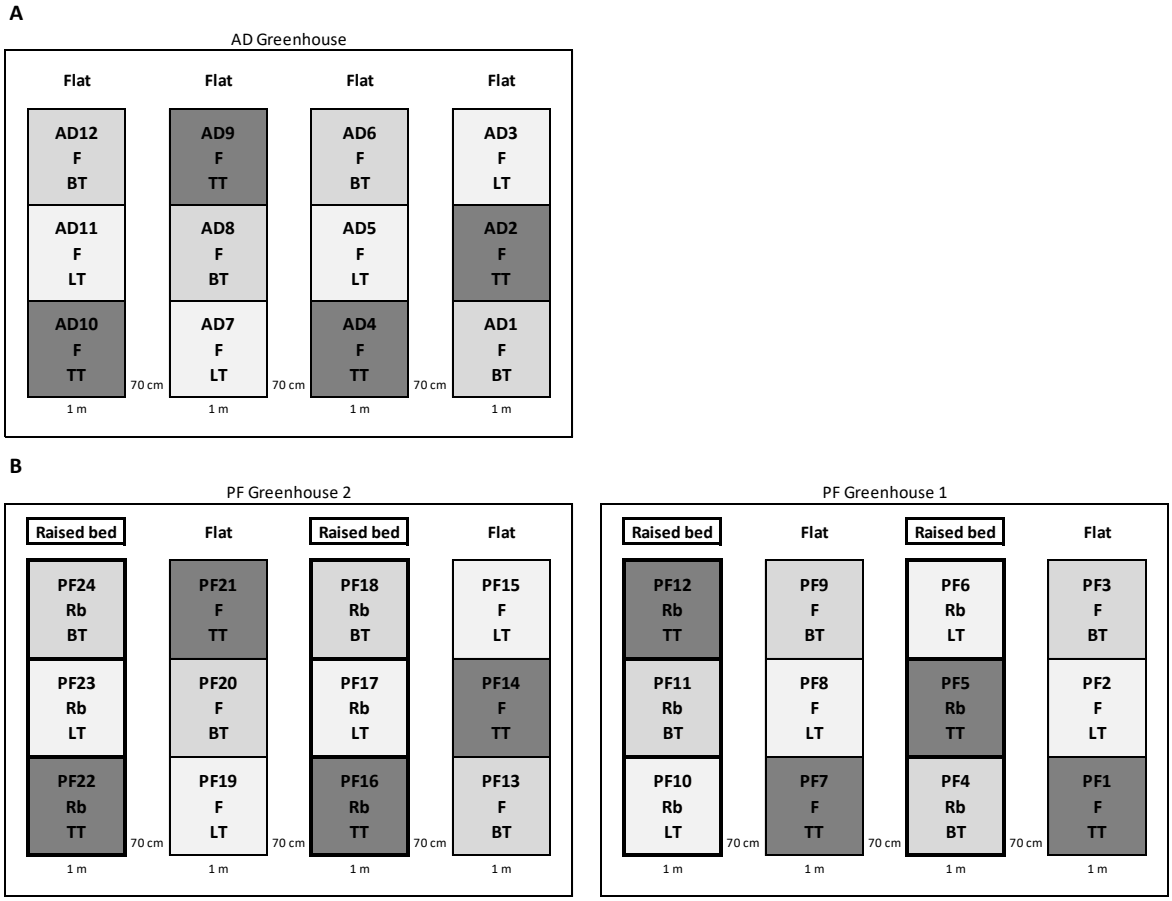


Fig. 1. Experimental design at both study sites: A. Adriers (AD) and B. Pontenx-les-Forges (PF). Three replicates for each crop association were established in a total randomized block design on Flat grounds (F) and Raised beds (Rb). Dark grey: Tomato monoculture (TT), medium grey: Bean-Tomato (BT) and light grey: Leek-Tomato (LT) associations.

2.2.2. Site II: Pontenx-les-Forges

At the PF site, the setup of the two associations (Bean-Tomato (BT) and Leek-Tomato (LT)) and the tomato monoculture (TT) followed the same protocole as in AD. However, this configuration was doubled to test the interaction with different soil management methods: cultivation on permanent organic raised bed (Rb) vs. cultivation on flat soil (F), resulting in 24 sampling points, under two plastic tunnel greenhouses (Fig. 1B). For this site, the farmer was interested in using organic raised bed as a means of compensating for the sandy texture of the soil, which was initially low in organic matter. The permanent organic mounds were prepared by superimposing hay, amendment (horse manure (20 t/ha) in 2018 or a mixture of horse manure with an organic amendment (Vegethumus; FRAYSSINET, France; 20 t/ha) in 2019), and composted wood chips. For the flat soil beds, these amendments were incorporated into the soil (15-20 cm) one week before planting. The crops were irrigated with a drip irrigation system (2 hours, weekly in 2018) to reduce the risk of mildew, with occasional use of a sprinkler in case of drought (2 m^3 every two days), and with a sprinkler in 2019. No winter crop was grown between 2018 and 2019.

2.3. Crop preparation and cultivars

The tomato cultivar (*Solanum lycopersicum* cv. "Coeur de boeuf rouge"; AGROSEMENS, France) was selected for its economic potential as it is commonly found on markets and appreciated by consumers. The leek cultivar (*Allium porum* cv. 'Lancia'; AGROSEMENS, France) and the bean cultivar (*Phaseolus vulgaris* cv. 'nanus' HAR19; AGROSEMENS, France) were selected for their summer growing period. All seeds were produced organically. All tomato plants were sown one month before the start of the experiment, transplanted once and stored in pots in a nursery at the PF site. The leeks were sown in a professional potting soil in an unheated greenhouse at the AD site four months before the start of the experiment. The most developed leeks were used upon intercropping with tomato. The roots and leaves of the leeks were cut short at the time of transplanting to stimulate their development.

2.4. Plant performances

Tomato plants and soil were sampled at harvest in September 2018 and 2019, at both sites. Tomatoes were harvested, counted, and weighed by farmers in each sampling plot throughout the growing season. At the sampling date, red and green tomatoes were harvested, counted, and weighed separately. The number of tomato plants was counted in each sampling plot to standardize the yield per tomato plant. The total number of fruits corresponded to the addition of green and red tomatoes at the end of the experiment. The global maturation of tomatoes was indicated by the ratio “number of red tomatoes/total number of fruits”.

In each sampling plot, three plants had been randomly tagged one month after the crops were planted. Shoots of the monitored plants were cut at the ground level and plant height was measured from the stem base to the apical meristem. Tomato root systems were carefully extracted from the soil and washed, and tomato shoot and root were oven-dried (70°C, 3 days) and weighed. It must be noted that all tomato plants were mistakenly cut at 2.5 m aboveground by the farmer in July 2018 at PF. Weed biomass was sampled in 2019 only. At both sites, a 1 m x 1 m area was delimited in each sampling plot, in which no weeding occurred throughout the season. At the sampling date, weeds were collected, dried (70°C, 3 days) and weighed.

2.5. Soil properties

Two soil cores (diam. 4.8 cm; depth 20 cm) were taken at random and pooled in each plot, one month after the tomato planting (T1 and T3 in 2018 and 2019 respectively), and at harvest (T2 and T4 in 2018 and 2019 respectively). All chemical soil analyses were carried out by a certified laboratory (Laboratoire d'Analyses de la Chambre d'Agriculture du Loiret, France). NH_4^+ and NO_3^- were extracted with a KCl solution and measured by colorimetry (540 nm and 660 nm). Organic matter (OM) was measured by dry combustion (ISO NF 14235). The pH was measured with water (ratio 1:5; NF ISO 10390). Total C and N (C_{orga} and N_{tot}) concentrations were measured with a CHN pyrolysis microanalyser (NF ISO 10694 and NF ISO 13878). Available Phosphorus (P) was measured by spectrophotometry according to the Olsen method (NF ISO 11263). The cation exchange capacity (CEC) was measured by the Metson method (NF X 31-130) and the exchangeable cations (K^+, Ca^{2+}, Mg^{2+}, Na^+) were measured by flame atomic emission from ammonium acetate extracts (NF X 31-108). Soil moisture was measured at

three random points with a FieldScout TDR 100 probe (12 cm deep; Spectrum Technologies, IL, USA) and the values were averaged per plot. Stabilised soil temperature was measured at a random point in the middle of each plot (11 cm deep: HANNA Instruments, France).

Nutrient dynamics in the soil was calculated as the ratio of the difference between the nutrient contents one month after planting in greenhouses (T1, T3) and at harvest (T2, T4) over the nutrient contents one month after planting (T1): ΔNutrient = T2-T1.

2.6. Statistical analyses

All statistical analyses were carried out using the R software (R Core Team 2020). When the data met the assumptions of normality and homogeneity of the variance, one-way and two-way ANOVAs were performed to compare the different associations alone (AD) and in interaction with soil management (PF). When the interaction was not significant, an additive model was used for the two-way ANOVA. Tukey post-hoc tests were carried out to compare the means. When possible, logarithmic transformations were applied to the data in order to reach assumptions of normality and homogeneity. If not, non-parametric bi-directional Scheirer-Ray-Hare (SHR) tests were carried out. The years were not included in models, as the addition of this parameter would have reduced the statistical power of the tests and increased the errors of type 2.

Table 1. Tomato plant performances and weed dry biomass (Mean % ± se) in the three crop associations (Tomato monoculture (TT), Bean-Tomato (BT) and Leek-Tomato (LT) associations), at Adriers (AD) for the two years of experimentation.

	2018			**2019**		
	Flat			**Flat**		
	Tomato-Tomato	**Bean-Tomato**	**Leek-Tomato**	**Tomato-Tomato**	**Bean-Tomato**	**Leek-Tomato**
Growth						
Tomato shoot dry biomass (g)	156.26 ± 3.64	105.44 ± 3.04	188.10 ± 6.71	138.61 ± 1.08	175.46 ± 4.44	125.56 ± 2.60
Tomato root dry biomass (g)	8.84 ± 0.18	7.86 ± 0.23	9.68 ± 0.15	9.17 ± 0.19	10.41 ± 0.26	8.20 ± 0.17
Tomato plant height (cm)	243.17 ± 3.14	199.08 ± 2.84	245.42 ± 3.34	275.75 ± 3.34	261.58 ± 3.08	253.50 ± 2.63
Tomato production						
Tomato yield per plant						
Yield of red tomatoes per plant (g)	2961.97 ± 46.70	2184.40 ± 102.54	3407.09 ± 214.21	4750.73 ± 82.38	4414.54 ± 255.23	4186.80 ± 172.75
Yield of green tomatoes per plant (g)	1025.15 ± 65.45	938.13 ± 102.09	1337.82 ± 92.78	976.23 ± 52.71	859.06 ± 141.21	974.51 ± 72.37
Yield of fruits per plant (g)	3987.11 ± 60.81	3122.52 ± 125.18	4744.91 ± 283.25	5726.95 ± 88.38	5273.60 ± 372.63	5161.31 ± 244.49
Number of tomatoes per plant						
Number of red tomatoes per plant	12.36 ± 0.35	10.94 ± 0.31	13.63 ± 0.55	15.37 ± 0.64	15.05 ± 0.66	14.14 ± 0.25
Number of green tomatoes per plant	10.24 ± 0.43	9.69 ± 1.04	15.27 ± 0.71	9.49 ± 0.49	8.63 ± 0.61	8.44 ± 0.64
Number of fruits per plant	22.59 ± 0.21	20.63 ± 0.87	28.90 ± 0.84	24.86 ± 0.59	23.68 ± 0.95	22.58 ± 0.88
Characteristics of tomatoes						
Mean mass of red tomato (g)	242.01 ± 7.61	199.21 ± 6.93	248.16 ± 10.19	313.14 ± 8.18	296.52 ± 14.91	294.66 ± 7.61
Maturation of tomatoes	0.55 ± 0.02	0.54 ± 0.03	0.47 ± 0.02	0.62 ± 0.02	0.64 ± 0.02	0.63 ± 0.01
Total tomato yield						
Total yield of red tomatoes (g)	52461.50 ± 915.35	15813.00 ± 895.50	24678.50 ± 1526.97	83958.25 ± 287.05	31754.00 ± 1842.41	30409.00 ± 1430.60
Total yield of green tomatoes (g)	18413.50 ± 1513.31	6917.00 ± 873.27	9796.00 ± 814.31	17359.00 ± 1018.71	6327.50 ± 1104.97	7092.50 ± 556.32
Total yield of fruits (g)	70875.00 ± 2161.96	22730.00 ± 1375.42	34474.50 ± 2182.41	101317.25 ± 1071.65	38081.50 ± 2871.07	37501.50 ± 1981.12
Total number of tomatoes						
Total number of red tomatoes	218.25 ± 4.40	79.00 ± 2.70	98.50 ± 3.47	270.50 ± 7.74	108.00 ± 4.38	102.50 ± 2.35
Total number of green tomatoes	182.25 ± 9.35	71.50 ± 9.12	111.50 ± 6.87	168.25 ± 8.82	62.50 ± 4.90	61.25 ± 4.69
Total number of fruits	400.50 ± 6.92	150.50 ± 9.73	210.00 ± 8.13	438.75 ± 3.98	170.50 ± 7.31	163.75 ± 6.89
Weeds						
Weed dry biomass (g)	-	-	-	187.83 ± 31.49	87.08 ± 19.37	224.54 ± 13.65

3. Results

3.1. Plant performances

3.1.1. Site I: Adriers

A positive effect of the crop association was found on the tomato plant height in 2018 (ANOVA, $F_{(2,33)} = 6.81$, $p = 0.003$) but not in 2019. Plants in the bean-tomato association (BT) had a significant lower height than plants in the monoculture (TT) and in the leek-tomato association (LT) (Fig. 2A). Crop association also affected shoot dry biomass, both years of experiment. In 2018, tomato had a significantly lower shoot dry biomass in BT (ANOVA, $F_{(2,33)} = 7.13$, $p = 0.002$), while the pattern was inverted in 2019 (ANOVA, $F_{(2,29)} = 5.49$, $p = 0.009$; Fig. 2B). The crop association had no significant effect on the root dry biomass, although the same trends as the shoot biomass were observed (Table 1).

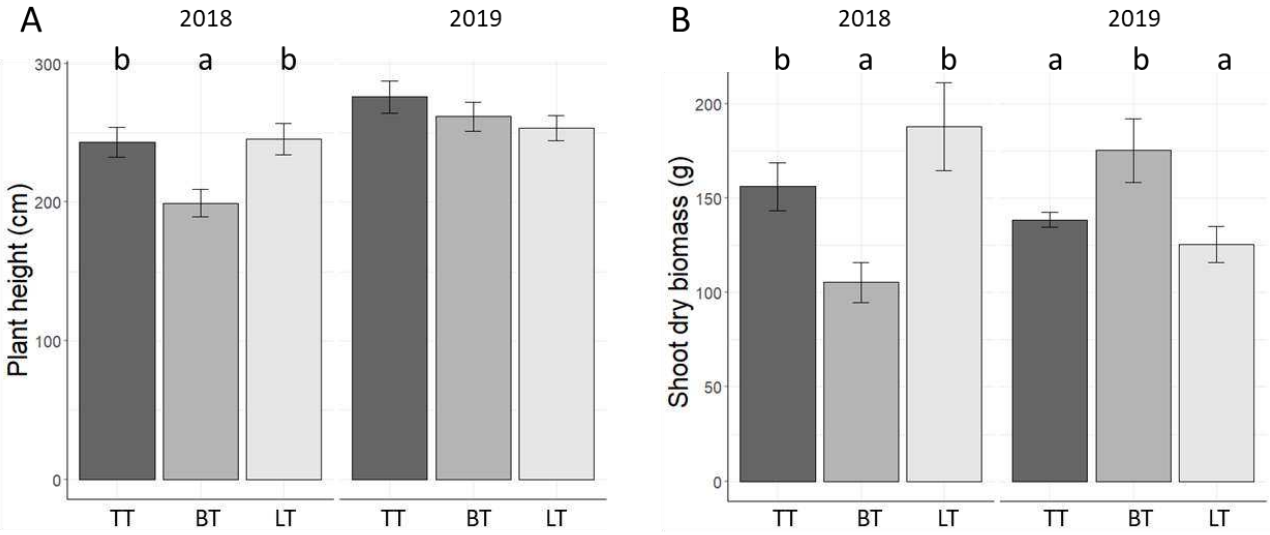


Fig. 2 A. Tomato plant height (Mean ± se); and B. Tomato shoot dry biomass (Mean ± se) for each crop association and for the two years of experimentation at Adriers (AD). Dark grey: Tomato monoculture (TT), medium grey: Bean-Tomato (BT) and light grey: Leek-Tomato (LT). Different letters indicate significant differences within each year ($p < 0.05$).

Crop association significantly impacted the yield of red tomatoes per plant in 2018 (ANOVA, $F_{(2,9)} = 4.90$, $p = 0.036$). It was the highest in LT and the lowest in BT (Fig. 3A), and so was the number of fruits per plant (red and green tomatoes) (ANOVA, $F_{(2,9)} = 9.29$, $p = 0.006$; Fig. 3B). This difference was mainly due to the higher number of green tomatoes in LT (ANOVA, $F_{(2,9)} = 4.03$, $p = 0.056$; Table 1), and no difference was found for red tomatoes (Table 1). The crop association did not affect the yield or number of tomatoes in 2019 nor the mean mass of red tomatoes and the proportion of red tomatoes (*i.e.* their overall maturation) both in 2018 and 2019 (Table 1). Weed dry biomass was lower in BT, although results were not significant (ANOVA, $F_{(2,9)} = 2.44$, $p = 0.141$; Table 1).

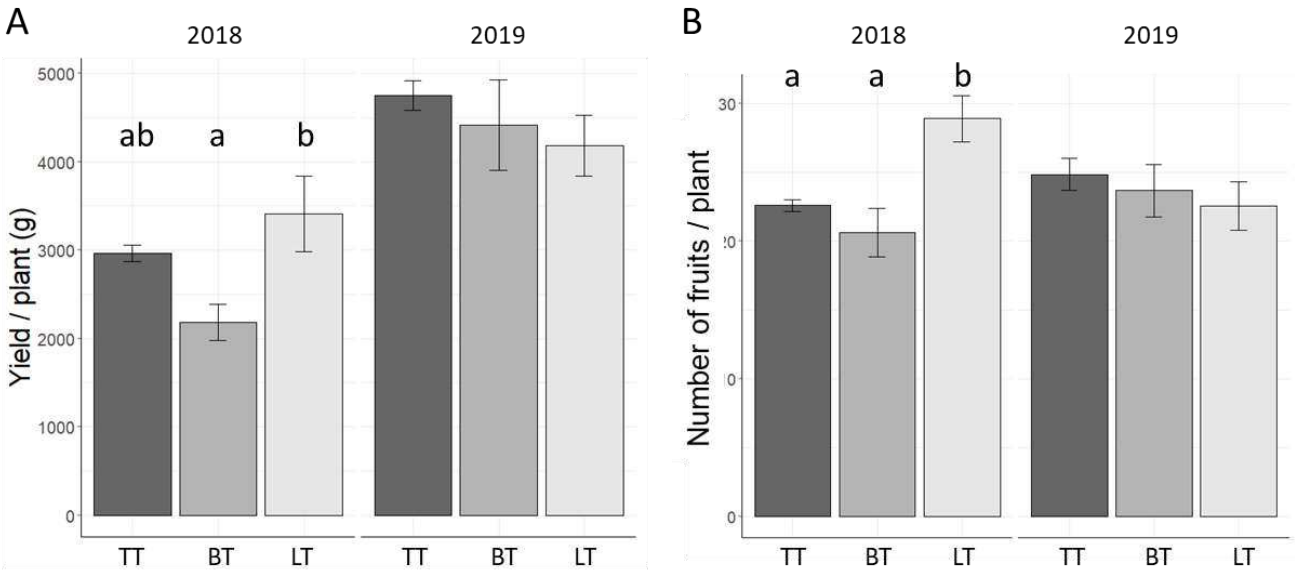


Fig. 3 A. Yield of red tomatoes per plant (Mean ± se); and B. Number of fruits per plant (Mean ± se) for each crop association and for the two years of experimentation at Adriers (AD). Dark grey: Tomato monoculture (TT), medium grey: Bean-Tomato (BT) and light grey: Leek-Tomato (LT). Different letters indicate significant differences within each year ($p < 0.05$).

3.1.2. Site II : Pontenx-les-Forges

In PF, we found no impact of the interaction between the crop association and raised bed cultivation for any of the measured parameters. The crop association positively affected the tomato plant height, in 2019 only (ANOVA, $F_{(2,68)}$ = 4.58, p = 0.013). It was the highest in LT and the lowest in TT (Fig. 4A). A significant crop association effect was also found on the tomato shoot dry biomass in 2018 and 2019. It was significantly higher in LT than in BT (Fig. 4B; ANOVA, $F_{(2,68)}$ = 3.48, p = 0.036) in 2018 and significantly higher in LT than in TT (Fig. 4B; SRH, $H_{(2,64)}$ = 8.74, p = 0.012) in 2019. Both years, the crop association had no effect on the tomato root dry biomass and the raised bed cultivation had no effect on the tomato plant height, shoot and root biomasses (Table 2).

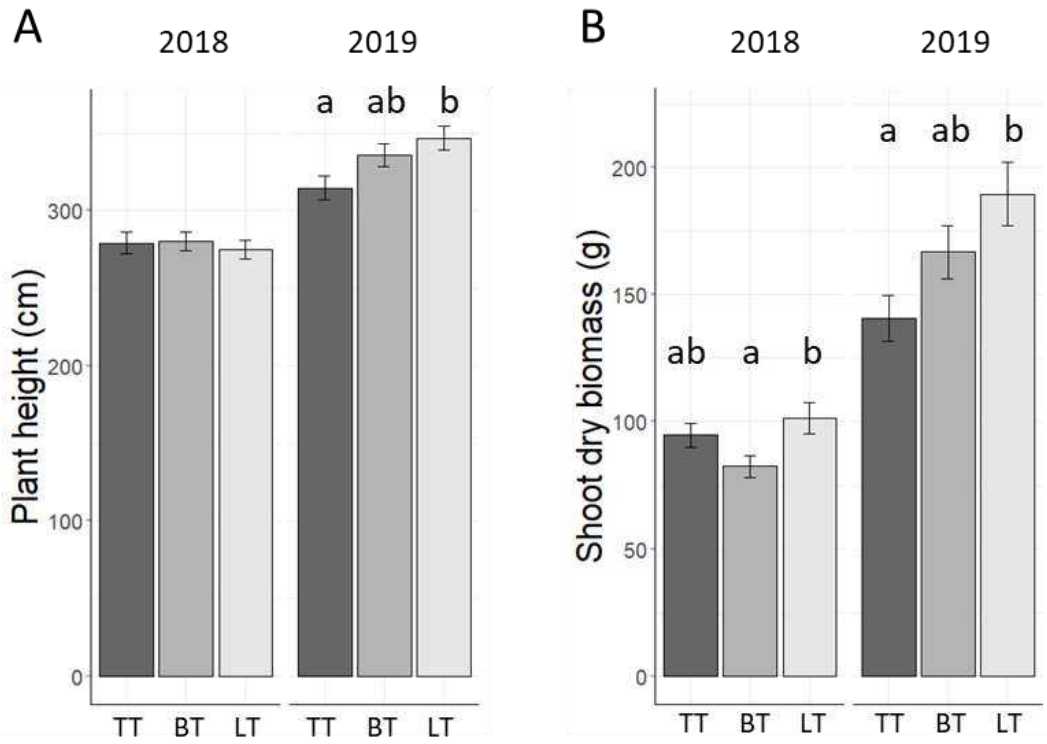


Fig. 4 A. Tomato plant height (Mean ± se); and B. Tomato shoot dry biomass (Mean ± se) for each crop association and for the two years of experimentation at Pontenx-les-Forges (PF). Dark grey: Tomato monoculture (TT), medium grey: Bean-Tomato (BT) and light grey: Leek-Tomato (LT). Different letters indicate significant differences within each year ($p < 0.05$).

Table 2. Tomato plant performances and weed dry biomass (Mean % ± se) in the three associations (Tomato monoculture (TT), Bean-Tomato (BT) and Leek-Tomato (LT)) and the two soil managements (Flat ground *vs*. Raised bed), at Pontenx-les-Forges (PF) for the two years of experimentation.

	2018					
	Flat			**Raised bed**		
	TT	**BT**	**LT**	**TT**	**BT**	**LT**
Growth						
Tomato shoot dry biomass (g)	93.34 ± 1.98	76.02 ± 1.85	103.88 ± 1.70	95.98 ± 1.95	88.82 ± 1.47	98.75 ± 3.21
Tomato root dry biomass (g)	5.15 ± 0.11	4.62 ± 0.12	4.93 ± 0.15	5.42 ± 0.15	4.88 ± 0.14	5.51 ± 0.12
Tomato plant height (cm)	272.92 ± 3.34	278.67 ± 2.40	273.58 ± 1.32	285.50 ± 2.25	282.17 ± 2.69	276.58 ± 3.25
Tomato production						
Tomato yield per plant						
Yield of red tomatoes per plant (g)	3616.16 ± 280.47	3734.11 ± 396.55	3895.53 ± 152.96	3841.36 ± 133.21	3222.47 ± 129.13	4501.91 ± 295.75
Yield of green tomatoes per plant (g)	1745.44 ± 104.00	2079.46 ± 165.17	2332.05 ± 119.15	2031.58 ± 199.16	2955.30 ± 259.89	2605.07 ± 230.85
Yield of fruits per plant (g)	5361.61 ± 335.90	5813.57 ± 397.42	6227.59 ± 248.77	5872.94 ± 214.06	6177.77 ± 188.92	7106.98 ± 486.67
Number of tomatoes per plant						
Number of red tomatoes per plant	10.30 ± 0.64	11.08 ± 0.92	11.72 ± 0.27	10.97 ± 0.39	8.77 ± 0.60	10.99 ± 0.54
Number of green tomatoes per plant	9.68 ± 0.99	10.16 ± 0.17	13.71 ± 0.86	10.41 ± 0.65	14.37 ± 0.51	16.34 ± 1.27
Number of fruits per plant	19.98 ± 1.33	21.24 ± 0.85	25.43 ± 1.05	21.39 ± 0.86	23.14 ± 0.51	27.34 ± 1.75
Characteristics of tomatoes						
Mean mass of red tomato (g)	345.04 ± 8.20	329.56 ± 9.68	323.72 ± 7.22	348.68 ± 4.76	371.71 ± 16.50	399.05 ± 8.07
Maturation of tomatoes	0.51 ± 0.02	0.47 ± 0.02	0.43 ± 0.01	0.51 ± 0.01	0.34 ± 0.02	0.36 ± 0.01
Total tomato yield						
Total yield of red tomatoes (g)	40494.00 ± 2833.91	15987.50 ± 1611.35	17485.00 ± 778.14	43537.50 ± 1557.39	12917.50 ± 421.46	18792.50 ± 1126.97
Total yield of green tomatoes (g)	20882.50 ± 941.66	10847.50 ± 770.76	12745.00 ± 546.73	24015.00 ± 2208.92	14435.00 ± 1240.39	13960.00 ± 1130.66
Total yield of fruits (g)	61376.50 ± 3305.86	26835.00 ± 1777.97	30230.00 ± 1225.60	67552.50 ± 2431.60	27352.50 ± 1072.55	32752.50 ± 2225.92
Yield per plant						
Total number of red tomatoes	116.00 ± 5.40	47.75 ± 3.72	53.75 ± 1.55	125.00 ± 4.35	36.25 ± 2.94	47.00 ± 2.64
Total number of green tomatoes	112.00 ± 6.89	53.50 ± 1.38	71.00 ± 2.98	122.00 ± 7.12	70.25 ± 3.22	83.00 ± 5.94
Total number of fruits	228.00 ± 8.02	101.25 ± 4.36	124.75 ± 4.22	247.00 ± 9.52	106.50 ± 4.32	130.00 ± 8.37
Weeds						
Weed dry biomass (g)	-	-	-	-	-	-

Table 2. (*continued*)

	2019					
	Flat			Raised bed		
	Tomato-Tomato	Bean-Tomato	Leek-Tomato	Tomato-Tomato	Bean-Tomato	Leek-Tomato
Growth						
Tomato shoot dry biomass (g)	160.55 ± 4.00	166.21 ± 4.20	197.20 ± 5.93	122.24 ± 2.57	167.13 ± 4.31	181.70 ± 4.40
Tomato root dry biomass (g)	9.62 ± 0.16	10.08 ± 0.21	11.24 ± 0.29	8.98 ± 0.22	9.78 ± 0.25	10.61 ± 0.29
Tomato plant height (cm)	316.67 ± 2.40	337.83 ± 2.79	358.83 ± 3.11	312.50 ± 3.79	333.83 ± 3.46	334.67 ± 3.09
Tomato production						
Tomato yield per plant						
Yield of red tomatoes per plant (g)	5185.63 ± 347.47	5716.96 ± 273.31	4730.98 ± 166.94	5702.51 ± 426.76	5283.17 ± 116.07	6208.12 ± 279.53
Yield of green tomatoes per plant (g)	705.10 ± 112.62	1074.46 ± 121.09	1004.31 ± 114.39	1016.91 ± 221.52	1322.79 ± 85.37	1838.38 ± 287.21
Yield of fruits per plant (g)	5890.73 ± 359.75	6791.43 ± 238.14	5735.28 ± 279.54	6719.42 ± 457.34	6605.96 ± 200.03	8046.50 ± 437.71
Number of tomatoes per plant						
Number of red tomatoes per plant	17.37 ± 0.96	19.38 ± 0.62	16.14 ± 0.52	18.07 ± 2.27	15.28 ± 0.46	20.30 ± 1.80
Number of green tomatoes per plant	4.93 ± 0.82	9.04 ± 1.30	8.20 ± 1.02	5.78 ± 1.04	10.56 ± 1.26	14.71 ± 1.75
Number of fruits per plant	22.30 ± 0.68	28.42 ± 1.25	24.34 ± 1.30	23.84 ± 2.11	25.84 ± 1.31	35.01 ± 0.77
Characteristics of tomatoes						
Mean mass of red tomato (g)	309.78 ± 17.56	305.50 ± 6.17	302.48 ± 8.94	341.62 ± 12.10	350.80 ± 9.53	351.74 ± 20.67
Maturation of tomatoes	0.79 ± 0.03	0.70 ± 0.02	0.66 ± 0.02	0.75 ± 0.03	0.59 ± 0.03	0.63 ± 0.02
Total tomato yield						
Total yield of red tomatoes (g)	51118.00 ± 2414.63	21895.00 ± 2324.09	20052.50 ± 838.72	48690.00 ± 1221.03	17412.50 ± 313.89	25352.50 ± 993.61
Total yield of green tomatoes (g)	6262.50 ± 725.52	4045.00 ± 415.29	4095.00 ± 140.10	8510.00 ± 1556.93	4742.50 ± 191.17	4910.00 ± 370.44
Total yield of fruits (g)	57380.50 ± 2370.90	25940.00 ± 2651.63	24147.50 ± 761.38	57200.00 ± 2178.99	22155.00 ± 336.67	30262.50 ± 1172.59
Yield per plant						
Total number of red tomatoes	170.25 ± 11.82	73.00 ± 8.98	67.75 ± 4.81	144.75 ± 6.26	50.25 ± 2.05	76.25 ± 6.37
Total number of green tomatoes	44.25 ± 5.30	29.75 ± 2.06	33.25 ± 1.39	50.25 ± 7.61	36.00 ± 2.79	43.00 ± 1.46
Total number of fruits	214.50 ± 11.05	102.75 ± 9.83	101.00 ± 3.97	195.00 ± 5.96	86.25 ± 1.16	119.25 ± 6.99
Weeds						
Weed dry biomass (g)	138.95 ± 39.59	99.98 ± 17.92	213.93 ± 65.03	1.74 ± 0.74	8.04 ± 2.80	38.82 ± 9.85

The yield of red tomatoes per plant was neither affected by the type of association nor by the raised bed cultivation in 2018 and in 2019, although it tended to be higher on raised beds in LT and TT, both years of the experiment (n.s.; Fig. A.1, Fig. A.2). The trend was inverted in BT in 2019 (Table 2). The number of fruits per plant (red and green tomatoes) was significantly higher in LT than in TT in 2018 (ANOVA, $F_{(2,20)} = 3.79$, $p = 0.039$), and a similar pattern was found in 2019 (ANOVA, $F_{(2,20)} = 2.59$, $p = 0.099$; Fig. 5A). Like at the AD site, this difference was due to the difference in the number of green tomatoes in 2018 (ANOVA, $F_{(2,20)} = 5.71$, $p = 0.011$; Fig 5B) and in 2019 (ANOVA, $F_{(2,20)} = 3.35$, $p = 0.055$; Fig. 5B) but not in the number of red tomatoes per plant (Table 2). The number of fruits or the number of red tomatoes per plant was not impacted by the raised bed cultivation in 2018 and in 2019. However, although not significant, the number of green tomatoes per plant tended to be higher on raised beds than on flat grounds in 2018 (ANOVA, $F_{(1,20)} = 4.16$, $p = 0.054$; Fig. 5B).

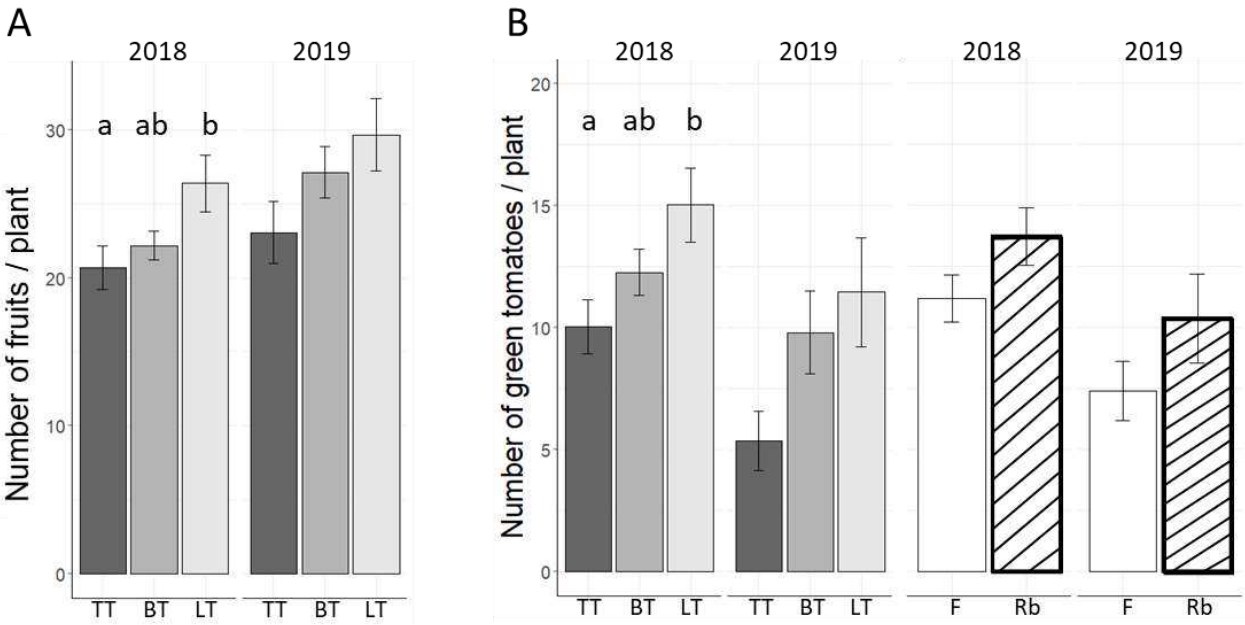


Fig. 5 A. Number of fruits per plant (Mean ± se); and B. Number of green tomatoes per plant (Mean ± se) for each crop association and soil management at Pontenx-les-Forges (PF). Dark grey: Tomato monoculture (TT), medium grey: Bean-Tomato (BT) and light grey: Leek-Tomato (LT), white: Flat cultivation (F) and hatched: raised beds (Rb). Different letters indicate significant differences within each year ($p < 0.05$).

Overall, the proportion of red tomatoes harvested in LT and BT was lower than in TT in 2018 and 2019 (Fig. 6), and on raised beds in 2018, which suggests a delayed maturation of tomatoes compared to the monoculture and the flat grounds.

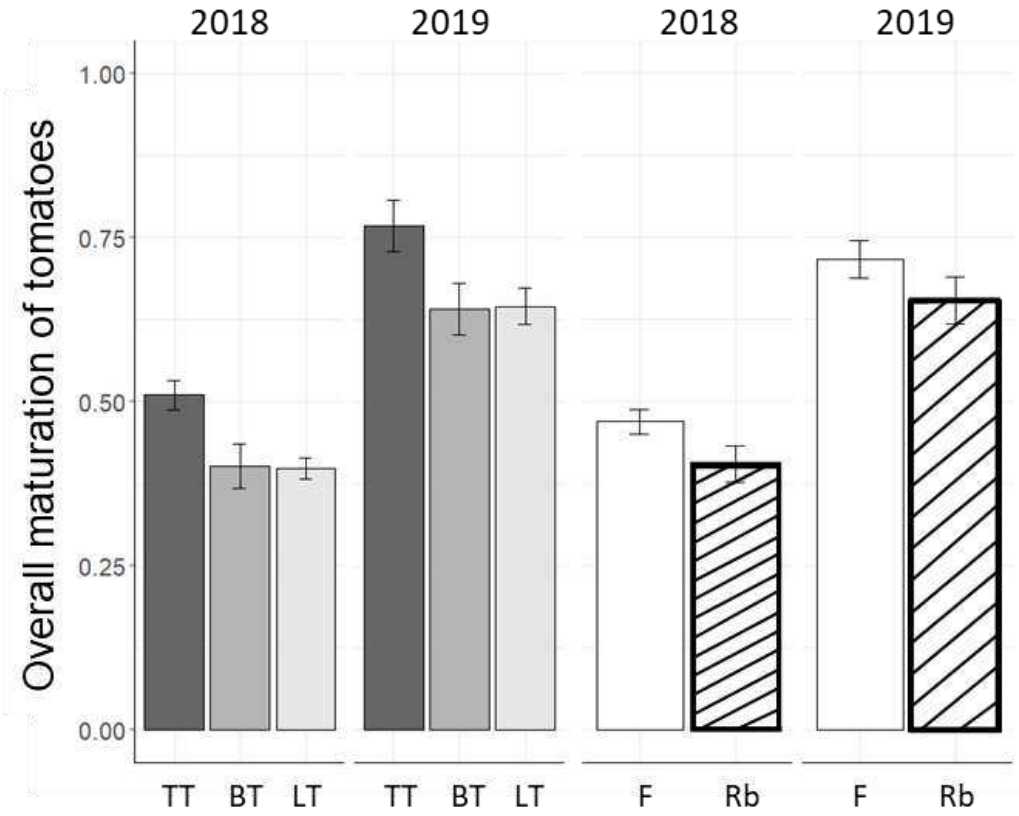


Fig. 6. Overall maturation of tomatoes (proportion of red/green tomatoes) (Mean ± se) for each crop association and for the two years of experimentation at Pontenx-les-Forges (PF). Dark grey: Tomato monoculture (TT), medium grey: Bean-Tomato (BT) and light grey: Leek-Tomato (LT); and for each soil management. White: Flat cultivation (F) and hatched: raised beds (Rb). Different letters indicate significant differences within each year ($p < 0.05$).

The mean mass of red tomatoes was not modified by the crop association, while it was significantly higher on raised beds than on flat grounds in 2018 (ANOVA, $F_{(1,20)} = 5.99$, $p = 0.023$; Fig. 7). The same trend was found in 2019 (ANOVA, $F_{(1,20)} = 4.04$, $p = 0.058$; Fig. 7). The weed dry biomass was significantly lower on raised beds than on flat grounds (ANOVA, $F_{(2,17)} = 19.52$, $p < 0.001$; Fig. 8) but was not impacted by the crop association.

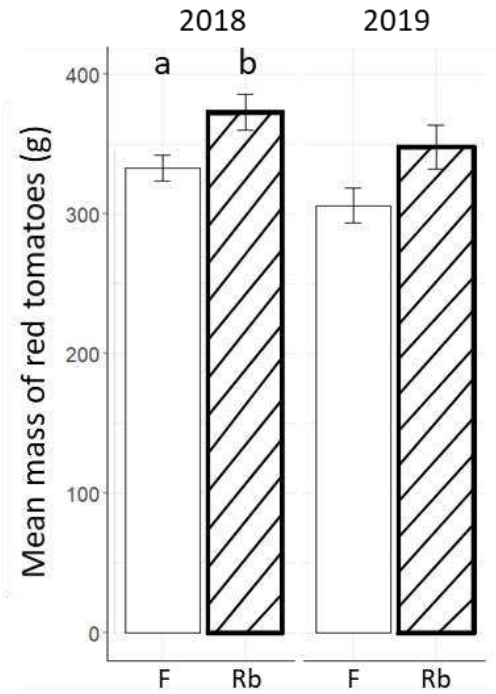


Fig. 7. Mean mass of red tomatoes (Mean ± se) for each soil management. White: Flat cultivation (F) and hatched: raised beds (Rb) for the two years of experimentation at Pontenx-les-Forges (PF). Different letters indicate significant differences within each year ($p < 0.05$).

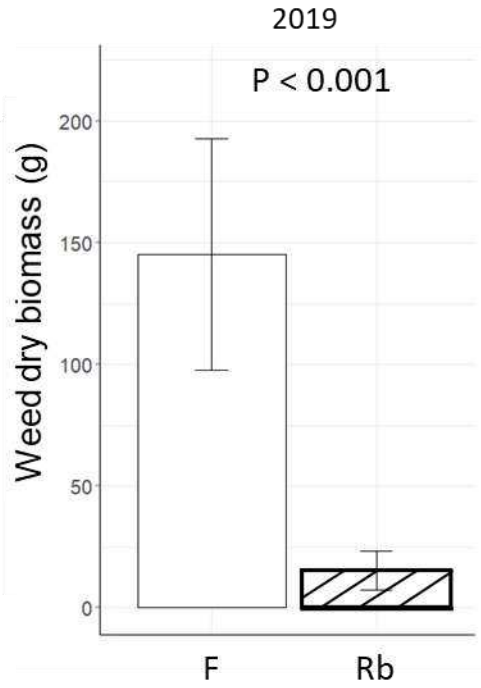


Fig. 8. Weed dry biomass (Mean ± se) for each soil management. White: Flat cultivation (F) and hatched: raised beds (Rb) at Pontenx-les-Forges (PF). Different letters indicate significant differences ($p < 0.05$).

3.1. Soil properties

All soil parameters for each treatment at both sites are summarized in the Table 3. Regardless of the site or the crop association, there was no significant variation in total nitrogen in soil during the growing season (Table 3).

At the AD site, a significant loss of available phosphorus was found in the soil at harvest in BT (Kruskal-Wallis, df = 2, $\chi^2 = 6.5$, $p = 0.038$; Fig. 9A) in 2018, while a gain of available phosphorus was observed in TT and LT. However, no significant difference of phosphorus dynamics was found between crop associations at harvest in 2019. Furthermore, a loss of magnesium and calcium was also found in BT in 2018 during the cultivation, while it increased in TT and LT (ANOVA, $F_{(2,9)} = 3.10$, $p = 0.094$; Kruskal-Wallis, df = 2, $\chi^2 = 5.65$, $p = 0.056$, respectively; Appendix 3). At the PF site, a significant higher loss of available phosphorus in soil was found in TT (SHR, $H_{(1,18)} = 6.62$, $p = 0.036$, Fig. 9B) in 2019. A significant higher content of available Phosphorus, Potassium, Magnesium, Calcium, Sodium, Total Nitrogen, and Organic Carbon

was found on raised bed, both years (Fig. 10, Table 4). Finally, a significantly higher soil temperature was found at harvest on raised bed in 2018 (ANOVA, $F_{(1,20)} = 4.75$, p = 0. 0.041), while soil humidity only tended to be higher. No significant difference of soil temperature and humidity was found at harvest between raised beds and flat ground in 2019 (Table 4).

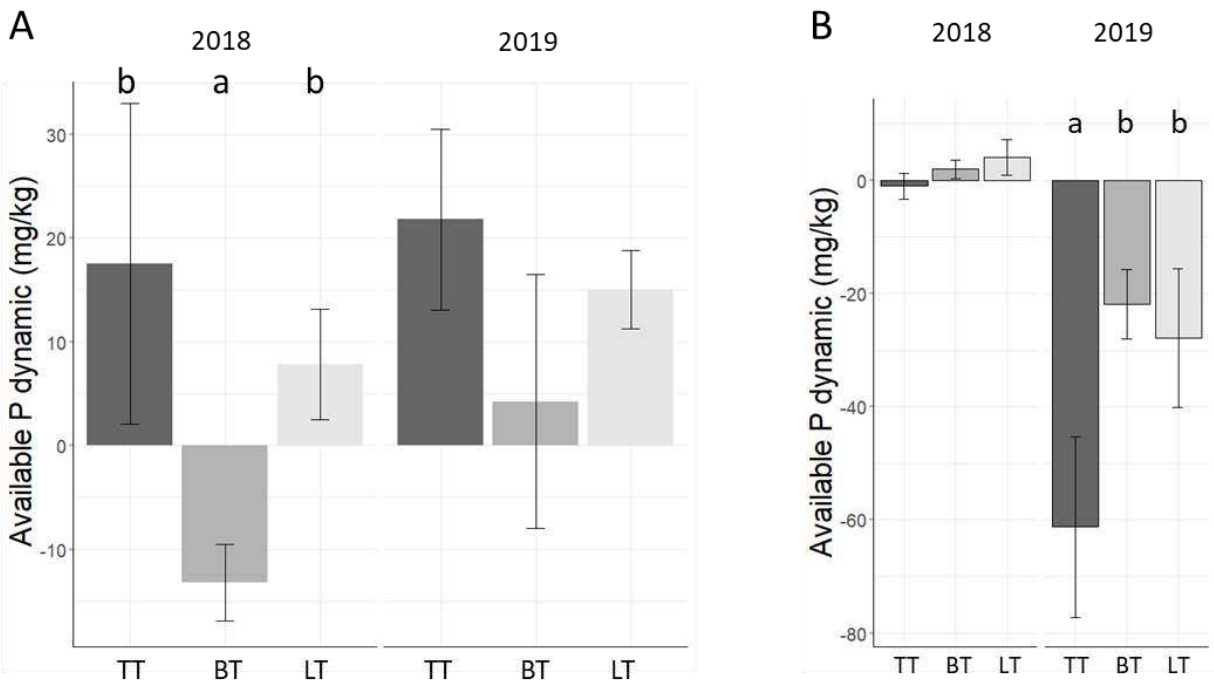


Fig. 9. Dynamics of available phosphorus in the soil (ΔNutrient; Mean ± se) for each crop association and for the two years of experimentation A. at Adriers (AD) and B. at Pontenx-les-Forges (PF). Dark grey: Tomato monoculture (TT), medium grey: Bean-Tomato (BT) and light grey: Leek-Tomato (LT). Different letters indicate significant differences within each year ($p < 0.05$)

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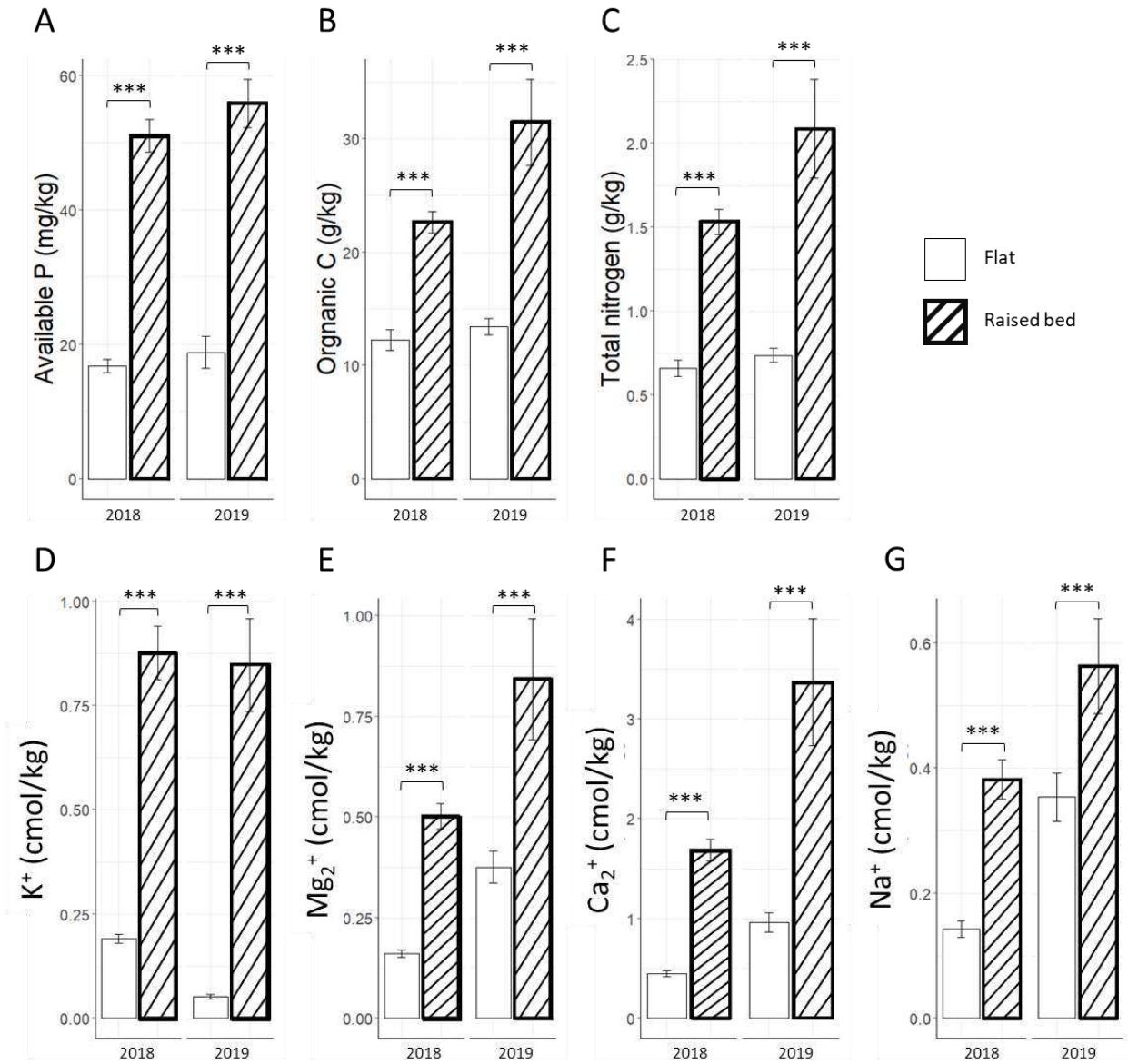

Fig. 10. Soil chemical properties (Mean ± se) for each soil management and within each year of experimentation at Pontenx-les-Forges (PF). A. Available phosphorus, B. Organic carbon, C. Total nitrogen, D. Potassium, E. Magnesium, F. Calcium and G. Sodium. White: Flat cultivation (F) and hatched: raised beds (Rb). Significant differences are indicated with asterisks (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$).

Table 3. Physicochemical soil properties (Mean % ± se) in the three crop associations (Tomato monoculture (TT), Bean-Tomato (BT) and Leek-Tomato (LT) associations) and the two soil managements (Flat ground (F) and Raised bed (Rb)), at Adriers (AD) and Pontenx-les-Forges (PF) for the two years of experimentation.

	AD					
	2018			**2019**		
	F			**F**		
	TT	**BT**	**LT**	**TT**	**BT**	**LT**
Temperature (°C)	22.82 ± 0.14	23.23 ± 0.14	22.90 ± 0.13	17.48 ± 0.52	18.70 ± 0.08	18.90 ± 0.21
HUmidity (%)	9.32 ± 0.24	9.30 ± 0.23	8.97 ± 0.16	6.55 ± 0.13	6.75 ± 0.31	5.58 ± 0.05
pH_{water}	8.05 ± 0.05	8.13 ± 0.05	7.99 ± 0.05	8.23 ± 0.06	8.29 ± 0.03	8.31 ± 0.04
Total N (g/kg)	1.84 ± 0.15	1.36 ± 0.05	1.66 ± 0.06	1.76 ± 0.08	1.65 ± 0.02	1.64 ± 0.08
Organic C (g/kg)	21.98 ± 1.59	15.72 ± 0.68	19.82 ± 0.89	20.25 ± 0.84	18.75 ± 0.27	19.80 ± 1.34
P Olsen (mg/kg)	111.94 ± 17.59	69.54 ± 2.61	86.76 ± 8.92	114.45 ± 6.71	98.64 ± 2.14	105.95 ± 4.85
CEC (mmol/kg)	10.86 ± 0.73	7.98 ± 0.27	10.29 ± 0.48	9.31 ± 0.37	9.21 ± 0.11	9.29 ± 0.28
K^+ (mmol/kg)	2.42 ± 0.28	1.73 ± 0.14	2.20 ± 0.24	1.77 ± 0.06	2.05 ± 0.17	2.16 ± 0.08
Ca^{2+} (mmol/kg)	51.45 ± 3.83	38.97 ± 1.47	48.16 ± 2.32	44.86 ± 1.18	43.02 ± 1.39	47.52 ± 1.24
Mg^{2+} (mmol/kg)	22.24 ± 1.61	17.77 ± 0.58	21.38 ± 1.27	19.96 ± 0.43	20.02 ± 0.71	21.33 ± 0.48
Na^+ (mmol/kg)	1.83 ± 0.11	1.53 ± 0.03	1.54 ± 0.10	0.88 ± 0.10	0.58 ± 0.06	0.94 ± 0.09
CaCO3 (mg/kg)	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	2.00 ± 1.00	0.50 ± 0.25
NH_4^+ (mg/kg)	-	-	-	2.30 ± 0.12	2.40 ± 0.12	1.75 ± 0.08
NO_3^- (mg/kg)	-	-	-	6.05 ± 0.08	6.40 ± 0.26	5.42 ± 0.68

Table 3. (*continued*)

	PF					
	2018					
	F			Rb		
	TT	BT	LT	TT	BT	LT
Temperature (°C)	21.62 ± 0.10	21.27 ± 0.16	21.77 ± 0.21	22.50 ± 0.12	21.77 ± 0.07	21.80 ± 0.03
HUmidity (%)	7.70 ± 0.70	8.95 ± 0.73	7.58 ± 0.24	6.70 ± 0.38	11.78 ± 0.53	11.05 ± 0.29
pH_{water}	5.37 ± 0.05	5.50 ± 0.07	5.29 ± 0.01	5.93 ± 0.05	6.17 ± 0.07	6.09 ± 0.07
Total N (g/kg)	0.61 ± 0.05	0.79 ± 0.04	0.58 ± 0.01	1.38 ± 0.08	1.52 ± 0.07	1.70 ± 0.03
Organic C (g/kg)	11.47 ± 1.02	14.70 ± 0.66	10.57 ± 0.25	20.18 ± 0.96	23.58 ± 0.74	24.23 ± 0.40
P Olsen (mg/kg)	16.24 ± 0.86	17.33 ± 0.97	16.79 ± 1.02	49.49 ± 2.63	51.34 ± 2.67	52.21 ± 1.31
CEC (mmol/kg)	2.80 ± 0.22	2.64 ± 0.12	2.63 ± 0.02	4.87 ± 0.19	5.86 ± 0.11	5.62 ± 0.15
K^+ (mmol/kg)	2.04 ± 0.05	1.96 ± 0.07	1.73 ± 0.14	8.55 ± 0.67	10.13 ± 0.23	7.61 ± 0.61
Ca^{2+} (mmol/kg)	4.21 ± 0.08	4.95 ± 0.33	4.26 ± 0.29	15.16 ± 1.00	17.71 ± 1.01	17.70 ± 0.92
Mg^{2+} (mmol/kg)	1.52 ± 0.05	1.75 ± 0.11	1.52 ± 0.08	4.49 ± 0.33	5.61 ± 0.20	4.96 ± 0.24
Na^+ (mmol/kg)	1.20 ± 0.04	1.85 ± 0.10	1.22 ± 0.11	3.28 ± 0.17	4.93 ± 0.21	3.23 ± 0.21
CaCO3 (mg/kg)	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
NH_4^+ (mg/kg)	-	-	-	-	-	-
NO_3^- (mg/kg)	-	-	-	-	-	-

Table 3. (*continued*)

	PF					
	2019					
	F			Rb		
	TT	BT	LT	TT	BT	LT
Temperature (°C)	20.50 ± 0.30	20.27 ± 0.20	20.58 ± 0.23	20.60 ± 0.13	20.30 ± 0.24	20.08 ± 0.10
HUmidity (%)	5.70 ± 1.13	8.97 ± 0.86	6.68 ± 0.51	4.35 ± 0.44	5.68 ± 0.99	5.20 ± 0.75
pH_{water}	6.65 ± 0.08	6.25 ± 0.14	6.21 ± 0.19	6.41 ± 0.15	6.48 ± 0.08	6.26 ± 0.04
Total N (g/kg)	0.69 ± 0.05	0.73 ± 0.01	0.79 ± 0.04	2.31 ± 0.43	2.13 ± 0.18	1.82 ± 0.10
Organic C (g/kg)	12.55 ± 0.83	13.18 ± 0.35	14.57 ± 0.62	34.27 ± 5.51	31.92 ± 2.40	28.20 ± 1.40
P Olsen (mg/kg)	13.30 ± 1.16	18.20 ± 1.81	24.85 ± 2.30	52.21 ± 3.92	58.10 ± 4.07	57.23 ± 1.32
CEC (mmol/kg)	3.28 ± 0.26	3.38 ± 0.06	3.50 ± 0.26	8.23 ± 1.21	8.19 ± 0.21	6.99 ± 0.31
K^+ (mmol/kg)	0.44 ± 0.03	0.50 ± 0.07	0.60 ± 0.02	8.27 ± 1.25	10.25 ± 0.86	6.90 ± 0.80
Ca^{2+} (mmol/kg)	9.45 ± 0.91	9.67 ± 0.62	9.75 ± 1.14	43.00 ± 9.85	31.67 ± 1.27	26.40 ± 1.35
Mg^{2+} (mmol/kg)	3.99 ± 0.36	3.45 ± 0.20	3.81 ± 0.51	10.18 ± 2.32	8.35 ± 0.32	6.77 ± 0.51
Na^+ (mmol/kg)	3.58 ± 0.39	3.45 ± 0.20	3.58 ± 0.46	6.32 ± 1.03	6.18 ± 0.31	4.40 ± 0.48
CaCO3 (mg/kg)	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.50 ± 0.25	0.00 ± 0.00	0.00 ± 0.00
NH_4^+ (mg/kg)	5.90 ± 0.89	6.45 ± 1.24	4.90 ± 0.99	9.50 ± 2.13	33.75 ± 10.01	7.30 ± 0.78
NO_3^- (mg/kg)	3.02 ± 0.46	1.98 ± 0.16	2.10 ± 0.29	2.22 ± 0.11	1.77 ± 0.16	2.65 ± 0.33

Table 4. Physicochemical soil properties (Mean % ± se) in the two soil managements: Flat ground (F) and Raised bed (Rb), at Pontenx-les-Forges (PF) for the two years of experimentation.

	PF			
	2018		**2019**	
	F	**Rb**	**F**	**Rb**
Temperature (°C)	21.56 ± 0.05	22.02 ± 0.04	20.45 ± 0.08	20.32 ± 0.05
HUmidity (%)	8.07 ± 0.19	9.84 ± 0.23	7.12 ± 0.29	5.08 ± 0.23
pH_{water}	5.39 ± 0.02	6.06 ± 0.02	6.37 ± 0.05	6.38 ± 0.03
Total N (g/kg)	0.66 ± 0.01	1.53 ± 0.02	0.74 ± 0.01	2.09 ± 0.09
Organic C (g/kg)	12.25 ± 0.27	22.66 ± 0.27	13.43 ± 0.20	31.47 ± 1.10
P Olsen (mg/kg)	16.79 ± 0.29	51.01 ± 0.70	18.78 ± 0.69	55.84 ± 1.03
CEC (mmol/kg)	2.69 ± 0.04	5.45 ± 0.06	3.39 ± 0.06	7.80 ± 0.23
K^+ (mmol/kg)	1.91 ± 0.03	8.77 ± 0.19	0.51 ± 0.02	8.47 ± 0.32
Ca^{2+} (mmol/kg)	4.47 ± 0.08	16.86 ± 0.31	9.62 ± 0.28	33.69 ± 1.85
Mg^{2+} (mmol/kg)	1.60 ± 0.03	5.02 ± 0.09	3.75 ± 0.11	8.43 ± 0.43
Na^+ (mmol/kg)	1.42 ± 0.04	3.81 ± 0.09	3.54 ± 0.11	5.63 ± 0.22
CaCO3 (mg/kg)	-	-	0.00 ± 0.00	0.17 ± 0.05
NH_4^+ (mg/kg)	-	-	5.75 ± 0.32	16.85 ± 2.07
NO_3^- (mg/kg)	-	-	2.37 ± 0.11	2.22 ± 0.07

4. Discussion

4.1. Bean-tomato association

At the Adriers (AD) site, we found a contrasted effect of beans on the growth of tomato plants between years. In 2018, the tomato plants in the bean-tomato association were smaller than the other treatments with a lower shoot dry biomass, while they had a higher biomass in 2019, and produced a lower yield of tomato, although not statistically significant. The same pattern was observed in PF in presence of beans, with a lower shoot dry biomass in 2018 and taller plants in 2019 compared to the monoculture. Yet, the tomato yield was not affected both years at PF. We suggest here that a strong competition for nutrients occurred between beans and tomatoes in 2018, *i.e.* the first year of co-cultivation, inducing a negative effect on tomato plant growth, and that this effect was compensated in 2019 by a late fertilizing effect of beans on the soil. Beans fix atmospheric nitrogen (N_2) in root nodules, which is released into the soil through rhizodeposition (Fustec et al. 2010). However, although N rhizodeposition occurs during the growing phase, it increases with plant maturity, as the senescence of roots and nodules increases (Khan et al. 2002; Mahieu et al. 2007; Wichern et al. 2008). Thereby, nitrogen released in the soil by beans in 2018 would have been available and beneficial for the tomato growth in 2019 only. In 2018, the competition for nutrients was probably higher between beans and tomato plants than between plants in the monoculture. Nitrogen is the most limiting nutrient for tomato growth and is taken up in large amount from the soil (Sainju et al. 2003), and we could have expected its content to be higher in presence of beans due to the symbiotic atmospheric nitrogen fixation. Yet, the soil nitrogen content (NO_3^-, NH_4^+ in 2019 and total N both years) was not higher in the bean-tomato association than in the other treatments. On the contrary, the total nitrogen tended to be lower at Adriers. No difference was observed at Pontenx-les-Forges, where no negative impact of bean on tomato growth was found. Furthermore, the gain of total nitrogen during cultivation (between one month after transplantation and harvest) was slightly lower in the bean-tomato association than in TT or LT in 2018 at Adriers, but not in 2019, although it was not significant. This supports our hypothesis of a higher competition for nitrogen between bean and tomato plants in 2018 than in 2019 and is consistent with a greater N uptake by tomato in intercropping (Dalal 1974; Liboon and Harwood 1975). Competition for phosphorus also seems to have occurred. In

2018, significantly more phosphorus was lost in presence of beans than in the monoculture and the leek-tomato association, between one month after transplantation and harvest. This resulted in a slightly lower available phosphorus, but this trend was less marked in 2019. Phosphorus is largely involved in the regulation of N_2 fixation by beans (Graham 1981), and a phosphorous deficiency limits the development and activity of nodules (Graham and Rosas 1979). Hence, our results support a higher competition hypothesis for nutrients in presence of beans, resulting in a lower N rhizodeposition in the soil and in a negative effect of beans on tomato growth in 2018 but not in 2019. Bean and tomato may also compete for water. In 2018, drip irrigation was used during the cropping season, while sprinklers were used in 2019, which likely modified the water regime, reduced the abiotic stress in 2019 and decreased a bean-tomato competition for water.

No significant difference of weed biomass was found between the bean-tomato and the monoculture, but fewer weeds tended to develop in presence of beans, each year and at both sites. Weed development is generally reduced under crops with large canopies such as beans (Colbach et al. 2019), and both farmers reported that the bean-tomato association reduced their weeding time.

4.2. Leek-tomato association

The development of tomato plants was not affected by the presence of the leeks at the AD site. At the PF site in 2019, the leek association had an overall positive effect on tomato performances. Plants were taller and had a higher shoot dry biomass. At both sites, the number of tomatoes per plant was significantly higher than in the monoculture, caused by a higher number of green tomatoes. This higher yield could be explained either by a reduced plant-plant competition or an increased direct or indirect facilitation. Leek can be considered as a weak competitor compared to tomato, due to its low N uptake and its late N demand (Baumann et al. 2001). However, the soil properties did not support the hypothesis of weaker competition for nutrients in presence of leeks. Leeks may also have partially directly favored tomato growth through plant-plant facilitation. Plants from the *Allium* genus release sulphur compounds such as thiosulfinates and disulphides with methyl (DMDS), propyl (DPDS) or propenyl groups (Arnault et al. 2004, 2005), and Arnault et al. (2013) found that plant growth was stimulated in DMDS-treated soil. Previous studies showed that DPDS was more

predominant in leek (Auger et al. 1989; Casella et al. 2013), which could have a similar effect. To our knowledge, no growth-promoting effect of leeks nor of DPDS has been reported in the literature, and the analysis of sulphur compounds, among which the DPDS, on-site or in controlled conditions could provide further information for the understanding of underlying mechanisms. It would also explain the higher weed biomass in presence of leeks on raised beds or flat grounds, in 2018 (visual observation) and 2019 at both sites. Hage-Ahmed et al. (2013) also showed that intercropping tomato with leek can increase the colonization of tomato roots by arbuscular mycorrhizal fungi (AMF), resulting in higher shoot and root biomasses in presence of *Fusarium oxysporum* in soil. Leeks have also been identified as "highly mycotrophic" plants, that is plants with high mycorrhization potential, that facilitate root colonization of "low mycotrophic plants" by mycorrhizal hyphae (Chave 2015; Rodriguez-Heredia et al. 2020). Hence, a higher colonization and mycorrhization of tomato roots may have occurred in the leek-tomato association than in the monoculture, thereby promoting tomato plant growth. Preliminary results of AMF colonization on tomato roots could not confirm this hypothesis (data not shown), nor did the pattern of development of tomatoes. The colonization by AMF and their mycorrhization was shown to accelerate the plant development, inducing an early flowering of tomatoes (Salvioli et al. 2012; González-González et al. 2020), whereas the presence of leeks rather delayed the production and maturation of tomatoes, as indicated by the proportion of red over all tomatoes.

4.3. Permanent organic raised bed

The positive or negative impacts of the presence of beans on tomato plant performances at PF tended to have a higher intensity on flat grounds than on raised beds and, although no significant effect was found, crop associations and the raised bed cultivation showed patterns of interaction in 2018 and in 2019. The yield and the number of red tomatoes per plant in the bean-tomato association were slightly lower on raised beds while it tended to be increased in the leek-tomato association on raised beds, particularly in 2019. On the other hand, the higher mean mass of red tomatoes found on raised bed was probably due to the higher contents of available P, Mg^{2+}, and K^{+}, which are involved in fruit production (Sainju et al. 2003). Previous studies also found that benefits of the nitrogen input by legumes on crops was higher in low- than in high-input systems (Jensen and Hauggaard-Nielsen 2005; Corre-Hellou et al. 2007). This supports our observations on the higher effect of the bean-tomato association on tomato

performances in low resource conditions. Then, Han et al. (2018) showed that organic matter and pH are major factors conditioning DMDS degradation in the soil. It decreases with pH and with high organic matter content. Considering the positive trend of the interaction leek-tomato association and raised bed, the higher organic matter content in raised bed may have reduced the degradation of DMDS or DPDS released by leeks and increased a facilitation effect of leek on tomato production. However, studies on the impact organic permanent raised beds on soil properties are too limited to support our findings.

Raised beds significantly reduced the development of weeds during the cropping season in the monoculture and in the associations. Higher nutrient concentrations could have favored it. However, raised beds were established a few months prior to the experiment and were composed of hay and composted wood, which acted as mulch at the soil surface. Mulch is known to prevent seed germination by limiting the access to light and increasing the soil moisture, which favors seed pathogens (Liebman and Davis 2000). Hence, the germination of seeds from the soil seed bank was probably prevented, and dispersed seeds from the environment did not have the time to constitute a new seedbank in raised beds. A long-term monitoring of permanent raised beds would give more insight on the efficacy of raised beds against weed establishment.

5. Conclusion

The objective of this study was to assess the impacts of crop association and raised bed cultivation on plant performances of tomato. At both study sites, although a competition was observed in 2018, tomato plant performances in presence of beans were as great as in the monoculture in 2019, after one year of co-cultivation. It would be interesting to monitor the evolution of tomato plant performances after several years of bean-tomato associations to check for a reduced bean-tomato competition. In view of these results, using winter varieties of beans would also probably be more suitable to tomato in a rotation than in association to take advantage of the N rhizodeposition and to avoid the competition. Then, a positive effect of the leek-tomato association was found on tomato growth. Mechanisms behind it remain to be determined between a lower competition than in monoculture or a facilitation of tomato plant growth induced by leeks. Soil analyses did not provide a good understanding of those mechanisms. At Pontenx-les-Forges, the raised beds are relatively recent and several years of

experimentation are necessary to confirm assumptions. Nutrient contents in samples are only a picture of the available stocks at a given time, and looking at dynamics showed interesting trends of soil functioning. Coupling these observations with studies on microbial composition and activity and mesofauna or nematode assemblages could provide more information and a better understanding of these mechanisms. Furthermore, yield is not the only criterion to take into account for the adoption of agricultural practices by growers. An assessment of the gains/costs in terms of working time, investment and benefits related to these practices, such as weed reduction could be a major factor of decision that could compensate a potential yield loss.

1

Chapitre 2. Les communautés de nématodes comme indicatrices d'état de santé et des réseaux trophiques du sol en réponse à deux associations de cultures et à la culture sur buttes

Pour cette étude, nous nous sommes intéressés à l'impact écologique des pratiques étudiées sur le sol à une échelle spatiale encore plus fine que lors des précédents chapitres, en se focalisant ici sur un groupe d'organismes appartenant à la microfaune du sol. L'objectif de ce travail était d'identifier les impacts écologiques des associations de cultures et de la culture sur buttes en utilisant les nématodes libres comme indicateurs de l'état du sol et de son fonctionnement. Pour cela, j'ai réalisé un suivi des communautés de nématodes dans la rhizosphère de la tomate lors des deux années d'expérimentation en micro-fermes maraichères.

Ce chapitre présente et discute les résultats de cette expérience sous la forme d'un manuscrit soumis à la revue *Agriculture, Ecosystems & Environment.* Cet article est cours de révision.

Effect of intercropping and organic raised-bed gardening on soil nematode community structure and metabolic footprints in tomato small-scale farming

Jeremy Detrey[a], Didier Bouchon[a], Julia Clause[a,*]

[a] University of Poitiers, Laboratory of Ecology & Biology of Interactions - UMR CNRS 7267, TEAM EES – Ecology Evolution Symbiosis, 5 rue Albert Turpain, TSA, 51106, 86073, Poitiers Cedex 9, France.

* Corresponding author: julia.clause@univ-poitiers.fr

Abstract

In this field study, we compared the composition of the nematode communities in three tomato crop associations – *i.e.* bean-tomato, leek-tomato, monoculture -, and under two soil management systems - raised beds *vs.* flat grounds - to evaluate the impact of intercropping and soil management on the soil health status. The study was conducted in two small-scale farms with different soils (loamy *vs.* sandy loam soil) in south-western France in 2018 and 2019, and sampling was done at the end of the tomato season. Nematode communities were identified to the family level, to which colonizer-persister (c-p) values were assigned, and ecological indices and metabolic footprints were calculated. Communities indicated an enriched environment at both sites (Maturity Index <2) and a dominant bacterial decomposition pathway (Channel Index <50). At the loamy site, the crop association had an overall low effect on nematode communities. The only significant effect was the higher fungivore footprint in both associations compared to the monoculture in 2019. The soil food web was also more structured in 2019 than in 2018. At the sandy site, soil management had a larger impact than the crop association on nematode communities. A higher nematode abundance was observed in raised beds, and the communities indicated a soil enrichment in nutrients, but also a less structured food web. The bean-tomato association affected the plant-parasitic nematodes more than the other nematodes, particularly in flat grounds, in which nematodes indicated a nutrient enrichment. In the same association, an increased herbivore footprint and a decreased structure footprint, were observed in both flat grounds and raised beds. Overall, the analysis of nematode communities revealed a soil disturbance associated with the external addition of organic matter and showed a particular pattern of soil-plant interaction in presence of both tomato plants and beans, which may be linked with soil microbial communities and plant exudates. The diverging patterns of the food web structuration between both sites with also different farming history raise the issue of long-term monitoring experiments to better understand the impacts of farming practices.

Keywords: **Crop association; *Solanum lycopersicum*; Bioindication; Plant Parasitic Index (PPI); Soil food web; Agroecological practices**

1. Introduction

The management of agricultural soil biodiversity is essential for a sustainable food production. The soil biodiversity indeed provides and maintains several ecosystem services such as nutrient cycling and the regulation of soil pathogens (Altieri 1999; Schwartz et al. 2000; Brussaard et al. 2007; Barrios 2007), which are of major interests for the provision of services. As soil organisms temporally respond to changes in soil physical and chemical properties (Doran and Zeiss 2000; Brussaard et al. 2004), they are used as indicators to understand the impact of agricultural practices on overall soil biodiversity and related ecological processes. Among soil organisms, nematodes occupy several trophic levels in the soil food web due to the diversity of their diets (Ingham et al. 1985; Ferris and Bongers 2006). They are involved in the ecosystem functioning by transforming organic matter into available nutrients as well as in the soil pest and pathogen regulation, and they contribute to the soil food web stability through their feeding activity (Yeates 2003). This makes of nematode assemblages an important bioindicator of soil health and of ecosystem disturbances (Ferris et al. 2001; Neher 2001; Ferris 2010a). Several indices based on the analysis of the nematode fauna have been developed to reflect soil conditions such as the Maturity Index, the Structure Index, the Enrichment Index, the Basal Index or the Channel Index (Bongers and Ferris 1999; Ferris et al. 2001). These indices are based both on the trophic structure of the nematode communities and on c-p (colonizer-persister) values, which reflect a range from extreme r- to extreme K strategists (Bongers 1990, 1999). Additional metabolic footprint analyses were developed to better understand the flows of carbon and energy that enter the soil food web (Ferris 2010b). Through those indices, analyses of nematode assemblages are powerful tools to assess the structure, the function, and the resilience of soil food webs.

Although there is a growing interest in research on agroecological practices, studies on soil invertebrates are still scarce, especially in small-scale vegetable farms, where nature-based practices are commonly used. Those practices aim at improving environmental conditions to restore and maintain biodiversity and associated ecological processes and ecosystem services (Wezel et al. 2014). Following that principle, intercropping or permanent raised beds may favor beneficial organisms and prevent crop pests infestation or pathogens onset (Ratnadass et al. 2012; Razze et al. 2016). Intercropping (*i.e.* crop association) involves at least two plants growing together and coexisting for a period of time (Brooker et al. 2015). This practice is

based on plant-plant or plant-fauna interactions for the control of pests and pathogens or for a better management of nutrient cycling and nutrient availability. For example, plant species from the genus *Allium* are known to produce volatile sulphur compounds which can have nematicidal effects when associated with other crops (Huang et al., 2016), while plants from the Fabaceae family fix atmospheric nitrogen in roots through their symbiosis with nitrogen-fixing bacteria. Through root degradation, Fabaceae then supply additional nitrogen to the soil (Fustec et al. 2010). The use of permanent raised beds involves adding a large amount of organic matter on the soil surface to increase the fertility of mounts in which plants are grown. This practice aims to improve soil conditions and to indirectly favor the diversity of organisms, their associated ecological processes and, *in fine*, crop health and yield (Govaerts et al. 2007; Naresh et al. 2012). These practices (crop association and raised-bed gardening) are particularly applied in small-scale farming, where their implementation is easier to achieve. Here, we decided to test the impact of those two practices in a context of tomato cropping, a high-yielding crop with a major economically importance (FAO, 2014). We used two companion crops: leeks and beans. Those two cash crops appeared to be good candidates to be intercropped with tomato plants as they belong respectively to the Alliaceae and Fabaceae families and, as seen above, are likely to impact soil communities.

In this context, the aim of this study was to assess the impact of crop association and raised-bed gardening (hereafter referred as *soil management*) on nematode communities as indicators of the soil health in a small-scale vegetable farm. We hypothesized that nematode assemblages and derived indices differed with intercropping and permanent raised bed practices.

2. Material and methods

2.1. Study sites

A two-year field experiment (2018-2019) was performed under plastic tunnel greenhouses in two organic vegetable small-scale farms in south-western France. The first site was located in Adriers (AD), France (46° 25’ 20.53” N, 0° 75’ 70.95” E; mean annual temperature/rainfall: 12.4°C/0.92 mm) on a sandy loam soil organically which has been cultivated for the last 10 years. The second site was located in Pontenx-les-Forges (PF), France (44° 22’ 84.79” N, -

1.088596 E; mean annual temperature/rainfall: 15.0°C/1.59 mm) on a sandy soil in a reconverted acacia wasteland.

2.2. Experiment design

2.2.1. Site I: Adriers

At the AD site, the response of the nematode community to two crop associations (Bean-Tomato (BT) and Leek-Tomato (LT)) was investigated in comparison to a tomato monoculture (Tomato-Tomato (TT)). For each treatment, three replicated plots (7 m x 1 m) were determined in a total randomized block design (Fig. 1A). A block consisted in a 21 m^2 cropping bed divided into three 7 m x 1 m plots, and blocks were 70 cm apart. The tomato cultivar (*Solanum lycopersicum* cv. 'Coeur de boeuf rouge'; AGROSEMENS, France) was selected for its economic potential as it is commonly found on markets and appreciated by consumers. The leek cultivar (*Allium porum* cv. 'Lancia'; AGROSEMENS, France) and bean cultivar (*Phaseolus vulgaris* cv. 'nanus' HAR19; AGROSEMENS, France) were selected for their summer growing season. All seeds were organic. One month before the start of the experiment, all tomato seedlings were grown, transplanted once, and kept in pots in a nursery at the PF site. Four months before the start of the experiment, leeks were sown in a professional potting soil in a non-heated greenhouse at the AD site. At the start of the experiment, only the most-developed leeks were planted, and their roots and leaves were shortened to favor plant development. Bean seeds were sown directly. The spacing between crops was set up according to the seed company's recommendations (AGROSEMENS; Fig. A.1). One week before planting, composted organic cattle manure (20 $t.ha^{-1}$) was buried into the soil (15-20 cm) using a rototiller. Crops were irrigated by a drip irrigation system (2 hrs, weekly) in 2018 to reduce the risk of mildew, and by sprinklers in 2019. This change improved leek performances. Experimental plots were hand-weeded four times during the growing season. The preceding winter crop consisted in Brassicaceae.

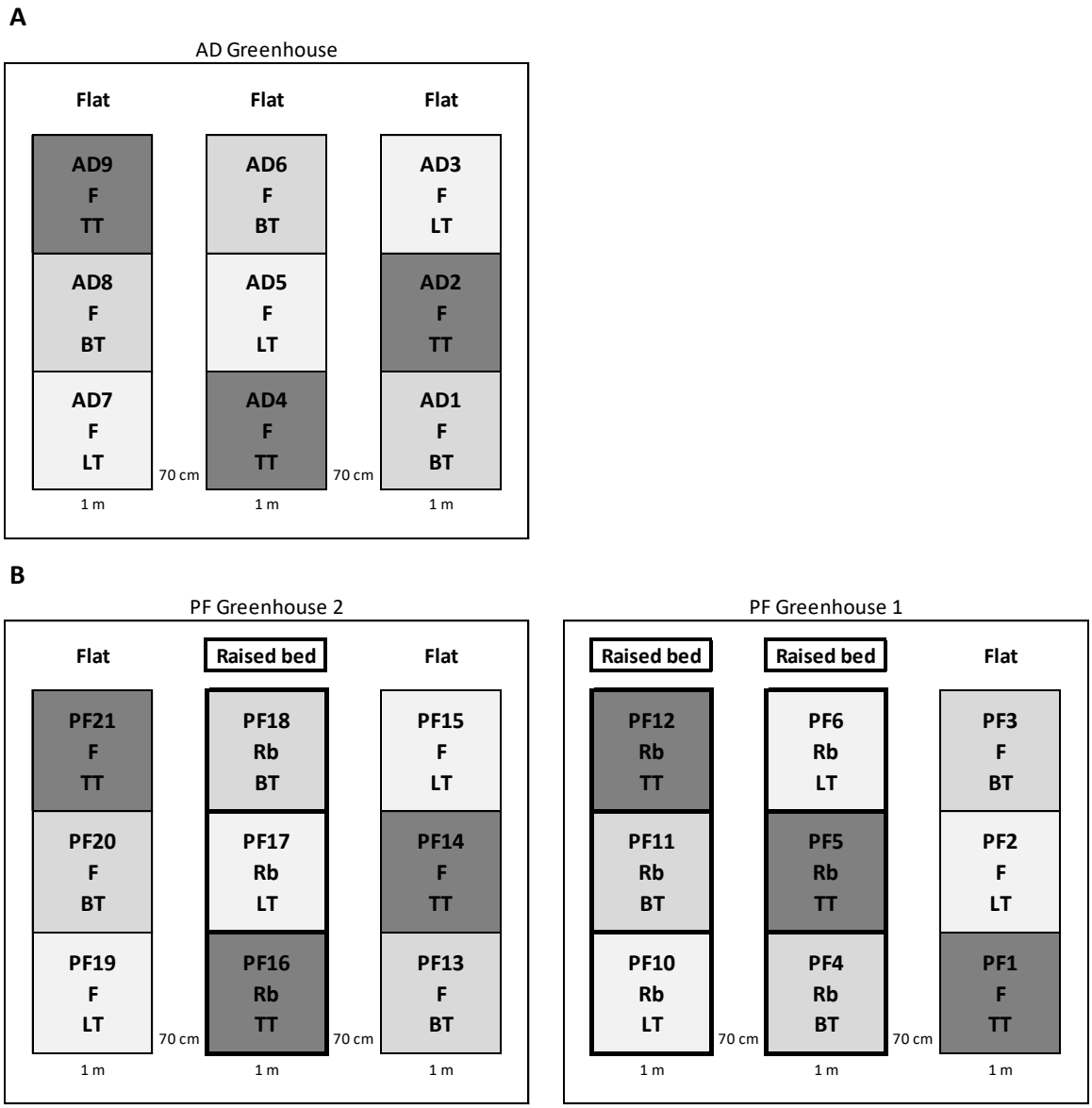

Fig. 1. Experimental design at both study sites: A. Adriers (AD) and B. Pontenx-les-Forges (PF). The three replicates for each crop association were established in a total randomized block design on Flat grounds (F) and Raised beds (Rb). Dark grey: Tomato monoculture (TT), medium grey: Bean-Tomato (BT) and light grey: Leek-Tomato (LT) associations.

2.2.2. Site II: Pontenx-les-Forges

At the PF site, the setup and crop choices for the two associations and the monoculture (BT, LT and TT) were the same as in AD (see §2.3.1). This setup was doubled to test the interaction with different soil managements: permanent organic raised beds (Rb) *vs.* flat ground (F) (Fig 1B). The farmer was interested in using raised beds as a mean to compensate for the sandy soil texture, originally poor in organic matter. Permanent raised beds were prepared by layering hay, horse manure (20 $t.ha^{-1}$) in 2018 or a mixture of horse manure with organic amendment (Vegethumus; FRAYSSINET, France; 20 $t.ha^{-1}$) in 2019 and composted ramial chipped wood. Flat beds were prepared by incorporating these amendments into the soil (15-20 cm) one week before planting. The design for crop associations was the same as in AD for both F and Rb systems, resulting in 18 sampling plots (Fig. 1B). The cultivar and seedling preparations were the same as in AD. Crops were irrigated by a drip irrigation system (2 hrs, weekly in 2018) to reduce the risk of mildew, with an occasional use of sprinklers in case of drought events (2 m^3 every other day), and with sprinklers in 2019. No winter crop was grown between 2018 and 2019.

2.3. Nematode communities analysis

Nematodes were sampled each year in September, during harvest, at both sites. In each plot, two soil samples were taken from the rhizosphere of three randomly-chosen tomato plants with an auger (diam.: 1.9 cm, depth: 20 cm) to analyze nematode communities. The six subsamples of each plot were then pooled. Nematodes were extracted from each plot sample with an Oostenbrick elutriator after taking a 125-mL subsample of fresh soil and followed the AFNOR 23611-4 extraction method. Nematodes in suspension were filtered and collected with a series of three consecutive 45-µm sieves. They were then transferred onto cellulose to allow the remaining nematodes to migrate for 48 hours from soil particles to a water solution. After their migration, nematodes were fixed and preserved in 10 mL of 4 % formaldehyde solution. Solutions were then concentrated to 5 ml, from which 1 ml was taken to estimate nematode abundance and richness with counting dishes under a microscope (x 40). 100 nematodes were identified in each sample at the family level under the microscope (magnification up to 100x) with an identification key (Bongers 1988).

Trophic groups (Yeates 2003) and life history strategies (c-p values from 1 to 5) (Bongers 1990; Bongers and Bongers 1998; Bongers and Ferris 1999) were assigned to each nematode family, and functional indices, food web diagnosis and metabolic footprints were calculated using the Nematode Indicator Joint Analysis (NINJA) (Sieriebriennikov et al. 2014). The Maturity Index (MI) is an indicator of soil disturbance based on the proportion of nematodes belonging to c-p groups ranging from one (early colonizers of new resources) to five (persisters in undisturbed environment) in a given soil sample. MI values range from less than 2.0 in nutrient-enriched disturbed systems to 4.0 in undisturbed environments (Bongers and Ferris 1999). As plant-parasitic nematodes are not included in the calculation of the MI, a separate Maturity Index for plant-parasites (the Plant-Parasitic Index PPI) was computed. The abundance of plant-parasitic nematodes reflects the vigor of their host plants, determined in turn by the system enrichment. Then, the PPI/MI ratio was calculated as a useful indicator of soil fertility (Bongers et al. 1997). The Enrichment Index (EI) refers to the number of opportunistic fungal and bacterial feeders that quickly respond to an input of C and N sources. High EI values indicate an enrichment in organic resources into the soil (N-enriched or depleted). The Structure Index (SI), based on nematode taxa with c-p values from 3 to 5, are an indicator of the length and the resistance of the soil food web. The Channel index (CI) indicates the prevalent decomposition channel in the food web (bacteria-driven vs fungi-driven) based on the proportion of fungivores compared to enrichment-opportunistic bacterivores. The metabolic footprint analysis measures the magnitude of ecosystem functions and services such as carbon and energy flow and entries in the soil food web (Ferris et al. 2001; Ferris 2010b). This is graphically represented as a soil food web analysis and food web conditions using EI (lower trophic levels) and SI (higher trophic levels). The Enrichment footprint is the metabolic footprint of nematodes that rapidly respond to a resource enrichment, while the Structure footprint represents the metabolic footprint of nematodes from higher trophic levels that have regulatory functions in the food web and that are indicative of the abundance of other organisms with similar functions. Finally, the Herbivore and Fungivore footprints refer to the C and energy entering the soil food web through their respective channels (Ferris 2010b).

2.4. Soil properties

Two soil cores (diam.: 4.8 cm; depth: 20 cm) were randomly sampled and pooled per plot for chemical analyses. All soil chemical analyses were performed by a certified laboratory (Laboratoire d'Analyses de la Chambre d'Agriculture du Loiret, France). NH_4^+ and NO_3^- were extracted with a KCl solution and measured by colorimetry (540 nm and 660 nm). Organic matter (OM) was measured by dry combustion (ISO NF 14235). pH was measured with water (1:5 ratio; NF ISO 10390). Total C and N (C_{tot} and N_{tot}) concentrations were measured with a CHN pyrolysis micro-analyzer (NF ISO 10694 and NF ISO 13878). Available phosphorus (P_2O_5) was measured by spectrophotometry using the Olsen method (NF ISO 11263). Cation Exchange Capacity (CEC) was measured with the Metson method (NF X 31-130) and exchangeable cations (K^+, Ca^{2+}, Mg^{2+}, Na^+) were measured using atomic flame emission from ammonium acetate extracts (NF X 31-108). Soil moisture was measured at three random points with a FieldScout TDR 100 meter (12 cm depth; Spectrum Technologies, IL, USA) and values were averaged per plot. Stabilized soil temperature was measured at one random point in the middle of each plot (11 cm depth: HANNA Instruments, France).

2.5. Statistical analyses

All statistical analyses were performed using the R software (R Core Team 2013). As the data met the assumptions of normality and homogeneity of variances, one-way and two-way ANOVAs were performed on the number of nematodes, indices and metabolic footprints to compare the different associations alone (AD) and in interaction with the soil management (PF). When the interaction was not significant, an additive model was used for the two-way ANOVA. Tukey post-hoc tests were performed to compare means. As assumptions were not met for the PPI Index and the herbivore footprint, non-parametric two-way Scheirer-Ray-Hare (SHR) tests were performed. No transformation was applied to the data. Years were not considered in models, as adding this parameter would have reduced the statistical power of tests and increased Type 2 errors.

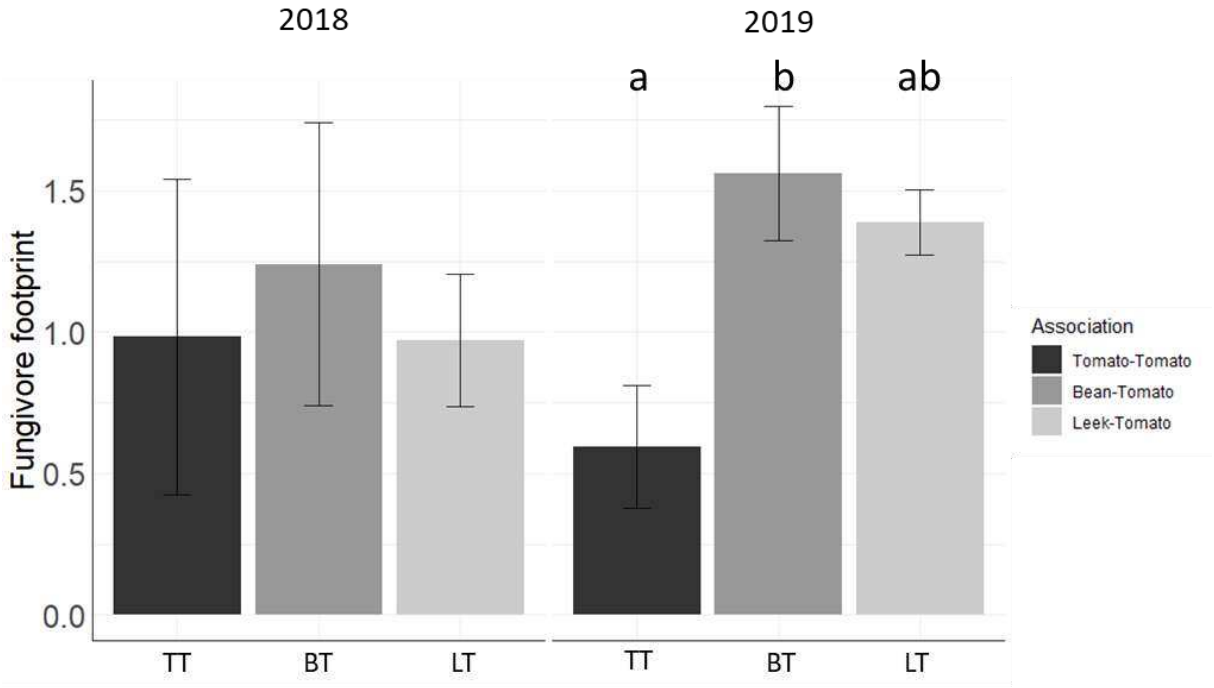

Fig. 2. Fungivore footprint (Mean ± se) for each crop association and for the two years of experimentation at Pontenx-les-Forges (PF). Dark grey: Tomato monoculture (TT), medium grey: Bean-Tomato (BT) and light grey: Leek-Tomato (LT)). Different letters indicate significant differences within each year ($p < 0.05$).

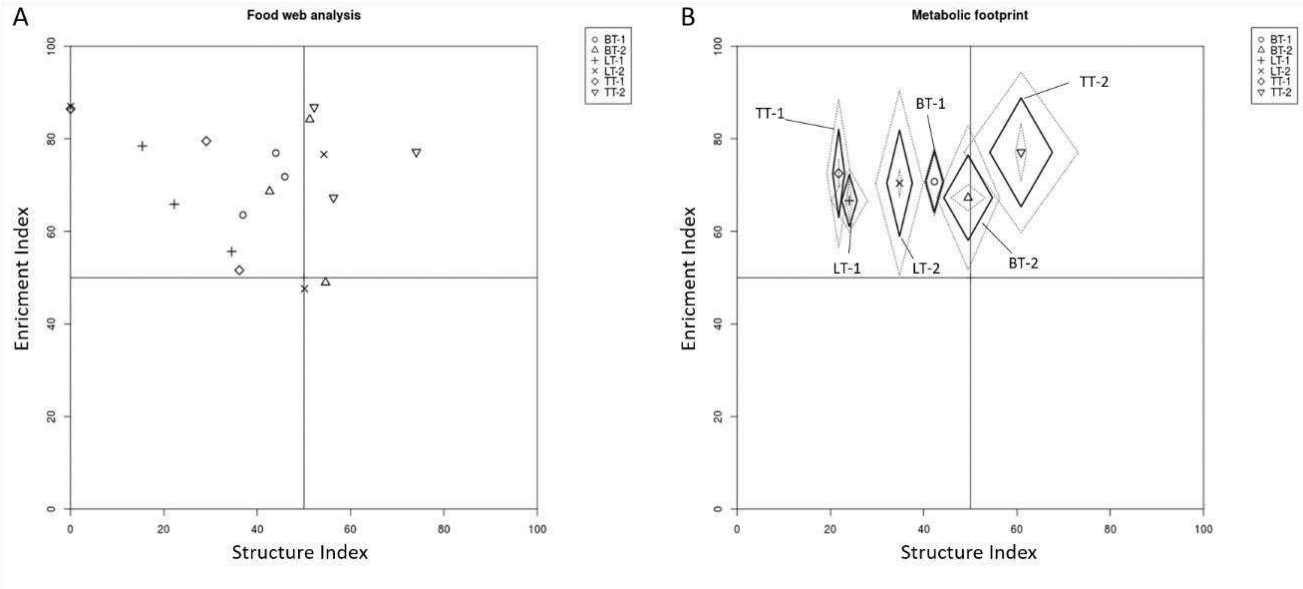

Fig. 3 A. Food web analysis and B. Functional metabolic footprint of nematode communities at Adriers (AD) in the three crop associations: Bean-Tomato (BT), Leek-Tomato (LT) and Tomato monoculture (TT), for the two years of experimentation: 2018 (-1) and 2019 (-2). Vertical axes of each footprint represent the enrichment footprint and horizontal axes the structure footprint. Full lines represent the treatment means and dotted lines represent standard deviations. The nematode functional metabolic footprint is the total area of the two functional (enrichment and structure) footprints.

3. Results

3.1. Site I: Adriers

Ten families of plant-parasitic nematodes and twenty-five families of free-living nematodes were identified in samples collected at AD during the experiment (Table 1). The main families of plant-parasitic nematodes were Tylenchidae and Dolichodoridae, and free-living nematodes were dominated by Cephalobidae and Rhabditidae (Table 1). All indices, metabolic footprints and details on the composition of the nematode community in AD are given in Table 2. For each association (TT, BT and LT) and both years, the Maturity Index was lower than 2.0, indicating a disturbed or enriched environment, while the Channel Index was lower than 50, both years (Table 2), indicating a dominant bacterial decomposition pathway. The only significant effect of the crop association (monoculture or intercropping) was recorded for the fungivore footprint in 2019 (Fig 2; ANOVA, $F_{(2,6)} = 6.84$, $p = 0.02$). The fungivore footprint was significantly higher in the bean-tomato association compared to the tomato monoculture, and a similar trend was recorded in the leek-tomato association although it was not significant. All other parameters (*i.e.* the number of nematodes mL^{-1}, Maturity index (MI), Plant-Parasitic Index (PPI), Enrichment Index (EI), Structure Index (SI), Basal Index (BI) and Channel Index (CI)) were not impacted by the association during both years of the experiment (Table 2). The soil food web analysis (Fig. 3A) confirmed the absence of difference between the associations. In all crop associations, the soil food web was enriched (EI > 50) and tended to be more structured in 2019 than in 2018 (Fig. 3B). In 2018, the soil food web was the most structured in BT and the least in TT, whereas in 2019, it was the most structured in TT. BT presented intermediate values.

Table 1. Nematode family composition by feeding type: p-p (in italics) and c-p classes, family mass average (NINJA; Sieriebriennikov et al., 2014) and relative abundance (Mean % ± se) in the three crop associations (Tomato monoculture (TT), Bean-Tomato (BT) and Leek-Tomato (LT) associations), at Adriers (AD) for the two years of experimentation.

			2018			2019		
Family	***p-p* /c-p class**	**Mass (ug)**	**TT**	**BT**	**LT**	**TT**	**BT**	**LT**
Herbivores								
Ectoparasites								
Dolichodoridae	*3*	0.601	8.0 ± 4.3	12.0 ± 2.2	5.0 ± 1.0	11.3 ± 2.5	11.0 ± 2.7	3.0 ± 0.7
Tylenchorhynchus	*3*	0.234	-	-	0.3 ± 0.2	-	-	-
Trichodoridae	*4*	0.885	0.3 ± 0.2	-	-	-	-	-
Epidermal/root hair feeders								
Tylenchidae	*2*	0.160	21.3 ± 2.7	31.0 ± 4.2	33.7 ± 3.7	11.0 ± 0.6	10.3 ± 0.4	19.3 ± 3.2
Migratory endoparasites								
Anguinidae	*2*	8.798	-	1.3 ± 0.5	-	-	-	-
Pratylenchidae	*3*	2.136	5.0 ± 2.6	2.0 ± 0.6	4.3 ± 1.3	1.3 ± 0.5	1.3 ± 0.8	3.0 ± 1.0
Sedentary parasites								
Achromadoridae	*3*	0.316	-	-	-	1.0 ± 0.6	-	-
Belondiridae	*5*	6.127	-	-	0.7 ± 0.4	-	-	-
Paratylenchidae	*3*	0.055	0.3 ± 0.2	1.7 ± 0.5	1.3 ± 0.5	-	1.7 ± 0.7	-
Hoplolaimidae	*3*	0.527	6.0 ± 0.9	1.0 ± 0.3	1.7 ± 0.4	2.7 ± 0.2	0.3 ± 0.2	2.7 ± 0.8
Rotylenchus	*3*	3.559	-	0.3 ± 0.2	0.3 ± 0.2	-	-	-
Bacterivores								
Acrobeloides	2	0.227	-	1.7 ± 1.0	3.0 ± 1.7	-	-	-
Acrobeles	2	0.600	-	0.3 ± 0.2	-	1.0 ± 0.6	5.0 ± 2.6	-
Alaimidae	4	0.537	-	0.3 ± 0.2	-	1.7 ± 0.2	0.3 ± 0.2	1.0 ± 0.6
Diplogastridae	1	1.591	-	-	0.7 ± 0.2	-	0.3 ± 0.2	-
Diploscapteridae	1	0.261	0.7 ± 0.2	-	0.7 ± 0.2	-	0.7 ± 0.4	0.7 ± 0.2
Diplopeltidae	3	0.726	-	-	-	1.0 ± 0.6	-	-

Cephalobidae	2	0.408	23.3 ± 1.5	19.0 ± 1.9	23.0 ± 5.7	25.0 ± 1.2	22.3 ± 3.6	22.0 ± 2.0
dauer	1	2.846	-	0.3 ± 0.2	-	1.0 ± 0.3	-	-
Leptolaimidae	3	0.640	1.3 ± 0.8	-	-	-	-	-
Monhysteridae	2	0.358	-	-	-	-	0.3 ± 0.2	0.7 ± 0.4
Plectidae	2	0.845	1.0 ± 0.0	1.0 ± 0.3	1.3 ± 0.8	1.3 ± 0.5	2.0 ± 0.9	3.3 ± 1.3
Prismatolaimidae	3	0.460	-	0.3 ± 0.2	-	-	1.0 ± 0.3	0.3 ± 0.2
Panagrolaimidae	1	0.655	1.0 ± 0.3	0.7 ± 0.4	1.0 ± 0.6	1.3 ± 0.4	2.3 ± 1.1	1.0 ± 0.6
Rhabditidae	1	5.037	21 ± 5.4	14.7 ± 0.5	11.7 ± 1.0	26.7 ± 4.6	20.0 ± 4.9	26.0 ± 6.7
Teratocephalidae	3	0.149	-	-	-	0.3 ± 0.2	0.3 ± 0.2	0.7 ± 0.2
Fungivores								
Aphelenchoididae	2	0.191	7.3 ± 2.5	7.7 ± 1.7	5.7 ± 0.5	4.3 ± 0.8	11.3 ± 0.8	10.0 ± 0.9
Aphelenchus	2	0.231	-	-	0.3 ± 0.2	-	-	-
Aphelenchidae	2	0.313	0.3 ± 0.2	-	0.7 ± 0.4	0.3 ± 0.2	1.0 ± 0.3	1.0 ± 0.6
Leptonchidae	4	1.307	-	0.7 ± 0.4	-	-	-	-
Paraphelenchus	2	0.343	-	-	1.0 ± 0.6	-	-	-
Omnivores								
Aporcelaimidae	5	22.727	1.0 ± 0.3	1.0 ± 0.3	1.3 ± 0.8	6.0 ± 2.0	4.0 ± 0.3	1.7 ± 0.5
Neodiplogastridae	1	2.229	1.3 ± 0.5	0.3 ± 0.2	1.0 ± 0.6	-	0.3 ± 0.2	-
Thornenematidae	5	1.183	-	-	-	0.3 ± 0.2	-	-
Predators								
Anatonchidae	4	6.749	-	-	-	0.3 ± 0.2	0.3 ± 0.2	-
Mononchidae	4	5.268	0.7 ± 0.2	2.3 ± 0.8	1.0 ± 0.0	0.7 ± 0.4	1.7 ± 0.7	2.0 ± 1.2
Mylonchulus	4	1.745	-	-	0.3 ± 0.2	-	-	-
Nordiidae	4	2.619	-	0.3 ± 0.2	-	-	0.3 ± 0.2	0.3 ± 0.2
Tripylidae	3	3.488	-	-	-	1.3 ± 0.5	1.0 ± 0.6	1.3 ± 0.8
Tobrilidae	3	6.990	-	-	-	-	0.7 ± 0.4	-

Table 2. Nematode abundances, indices and footprint values, and relative abundances within feeding types, c-p classes for free-living nematodes (CP1 to 5) or p-p classes for herbivorous nematodes (PP1 to 5) of nematodes assemblages (Mean ± se) in the three crop associations (Tomato monoculture (TT), Bean-Tomato (BT) and Leek-Tomato (LT) associations), at Adriers (AD) for the two years of experimentation.

	2018			**2019**		
	TT	**BT**	**LT**	**TT**	**BT**	**LT**
Nematode abundance						
Nematodes.soil ml^{-1}	8.52 ± 0.79	7.19 ± 0.18	7.91 ± 0.65	8.91 ± 1.33	7.80 ± 1.02	11.56 ± 0.95
Nematode indices						
Basal Index (BI)	23.47 ± 4.28	24.11 ± 1.79	29.27 ± 2.59	16.12 ± 2.03	23.53 ± 3.06	21.88 ± 3.69
Channel Index (CI)	14.48 ± 6.36	10.69 ± 2.21	13.10 ± 2.38	5.12 ± 1.62	17.15 ± 4.86	14.59 ± 4.48
Enrichment Index (EI)	72.53 ± 6.15	70.75 ± 2.25	66.64 ± 3.80	77.08 ± 3.26	67.28 ± 5.88	70.40 ± 6.80
Structure Index (SI)	21.75 ± 6.39	42.28 ± 1.57	24.04 ± 3.23	60.88 ± 3.88	49.52 ± 2.06	34.81 ± 10.07
Maturity Index (MI)	1.70 ± 0.11	1.89 ± 0.03	1.81 ± 0.07	1.98 ± 0.11	1.97 ± 0.10	1.84 ± 0.14
Plant Parasitic Index (PPI)	2.47 ± 0.08	2.36 ± 0.06	2.29 ± 0.04	2.58 ± 0.04	2.55 ± 0.04	2.34 ± 0.05
PPI/MI ratio	1.48 ± 0.05	1.25 ± 0.02	1.28 ± 0.07	1.32 ± 0.05	1.31 ± 0.05	1.33 ± 0.14
Metabolic footprints						
Composite footprint	47.74 ± 5.24	41.43 ± 0.45	36.44 ± 2.48	71.57 ± 6.62	57.93 ± 4.93	56.75 ± 7.23
Enrichment footprint	32.14 ± 7.27	22.56 ± 0.88	18.99 ± 1.34	39.74 ± 6.25	31.11 ± 7.20	38.69 ± 9.57
Structure footprint	4.31 ± 1.42	6.39 ± 0.29	5.63 ± 2.50	22.70 ± 6.22	17.64 ± 1.73	9.24 ± 2.67
Herbivore footprint	7.28 ± 1.29	8.93 ± 0.58	7.48 ± 1.51	4.55 ± 0.41	3.92 ± 0.79	4.27 ± 0.18
Bacterivore footprint	34.50 ± 7.48	24.99 ± 0.73	21.65 ± 1.70	44.30 ± 6.24	34.83 ± 7.02	42.15 ± 9.14
Fungivore footprint	0.98 ± 0.32	1.24 ± 0.29	0.97 ± 0.13	0.59 ± 0.13	1.56 ± 0.14	1.39 ± 0.07
Omnivore footprint	4.26 ± 1.27	3.54 ± 1.11	5.12 ± 2.95	19.89 ± 6.66	13.43 ± 1.11	5.49 ± 1.68
Predator footprint	0.72 ± 0.21	2.73 ± 1.02	1.23 ± 0.09	2.24 ± 0.45	4.20 ± 1.06	3.45 ± 1.19
% of total nematodes						
Herbivores	41.00 ± 2.85	49.33 ± 2.69	47.33 ± 6.45	27.33 ± 2.36	24.67 ± 2.83	28.00 ± 2.85
Bacterivores	48.33 ± 4.81	38.33 ± 0.69	41.33 ± 4.99	59.33 ± 3.79	54.67 ± 4.54	55.67 ± 4.19

Fungivores	7.67 ± 2.46	8.33 ± 1.84	7.67 ± 1.07	4.67 ± 1.02	12.33 ± 1.17	11.00 ± 0.33
Omnivores	2.33 ± 0.69	1.33 ± 0.38	2.33 ± 1.35	6.33 ± 1.95	4.33 ± 0.38	1.67 ± 0.51
Predators	0.67 ± 0.19	2.67 ± 1.02	1.33 ± 0.19	2.33 ± 0.38	4.00 ± 1.00	3.67 ± 1.17
% of free-living						
Bacterivores	81.23 ± 5.06	76.57 ± 2.82	78.70 ± 2.93	81.23 ± 2.86	72.00 ± 3.55	76.67 ± 2.84
Fungivores	13.23 ± 4.06	15.57 ± 3.11	15.30 ± 2.66	6.73 ± 1.68	16.73 ± 1.94	15.50 ± 1.01
Omnivores	4.33 ± 1.35	2.87 ± 0.84	3.10 ± 1.79	8.77 ± 2.62	5.70 ± 0.44	2.50 ± 0.80
Predators	1.23 ± 0.36	5.03 ± 1.72	2.87 ± 0.61	3.27 ± 0.56	5.57 ± 1.42	5.30 ± 1.63
CP 1	40.17 ± 8.16	32.17 ± 2.61	30.67 ± 4.35	39.00 ± 5.04	30.23 ± 6.59	36.43 ± 8.35
CP 2	54.60 ± 6.18	58.07 ± 2.90	64.67 ± 3.64	44.77 ± 3.81	56.77 ± 5.04	52.63 ± 5.26
CP 3	2.23 ± 1.29	0.80 ± 0.46	-	3.70 ± 0.67	4.00 ± 0.47	3.63 ± 1.71
CP 4	1.23 ± 0.36	6.90 ± 1.51	2.87 ± 0.61	3.80 ± 0.69	3.67 ± 0.98	4.80 ± 1.60
CP 5	1.77 ± 0.55	2.07 ± 0.64	1.77 ± 1.02	8.77 ± 2.62	5.30 ± 0.47	2.50 ± 0.80
% of herbivores						
Ectoparasites	21.20 ± 10.53	26.13 ± 5.89	10.63 ± 1.35	38.53 ± 5.98	39.27 ± 7.75	10.53 ± 2.36
Epidermal/root hair feeders	53.60 ± 8.15	61.20 ± 5.13	73.60 ± 3.01	42.00 ± 4.36	44.93 ± 4.40	66.27 ± 4.88
Sedentary parasites	0.67 ± 0.38	3.13 ± 0.92	4.20 ± 1.43	3.83 ± 2.21	9.97 ± 4.86	-
Migratory endoparasites	10.33 ± 5.12	7.07 ± 1.08	7.40 ± 2.29	5.73 ± 2.52	4.77 ± 2.75	13.70 ± 5.06
Semi-endoparasites	14.20 ± 1.10	2.43 ± 0.87	4.20 ± 0.31	9.87 ± 0.49	1.07 ± 0.62	9.50 ± 2.75
PP 2	53.60 ± 8.15	63.83 ± 5.58	73.60 ± 3.01	42.00 ± 4.36	44.93 ± 4.40	66.27 ± 4.88
PP 3	45.40 ± 8.67	36.13 ± 5.58	25.27 ± 2.78	58.00 ± 4.36	55.07 ± 4.40	33.73 ± 4.88
PP 4	1.00 ± 0.58	-	-	-	-	-
PP 5	-	-	1.13 ± 0.65	-	-	-

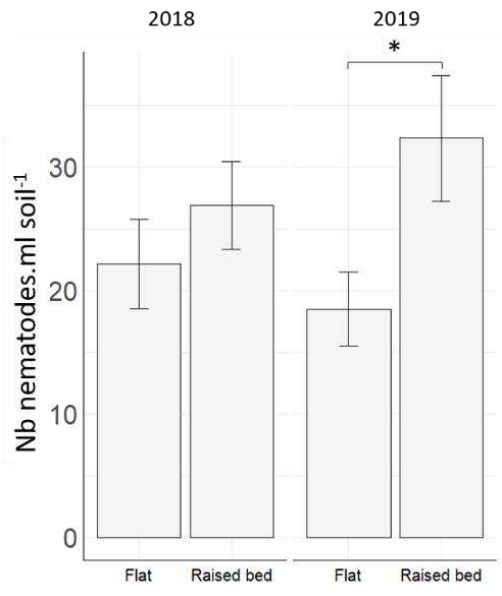

Fig. 4. Nematode abundances per mL of soil (Mean ± se) for each soil management (Flat grounds *vs.* Raised beds), for the two years of experimentation at Pontenx-les-Forges (PF). Significant differences between soil managements within years are indicated with an asterisk (* $p < 0.05$).

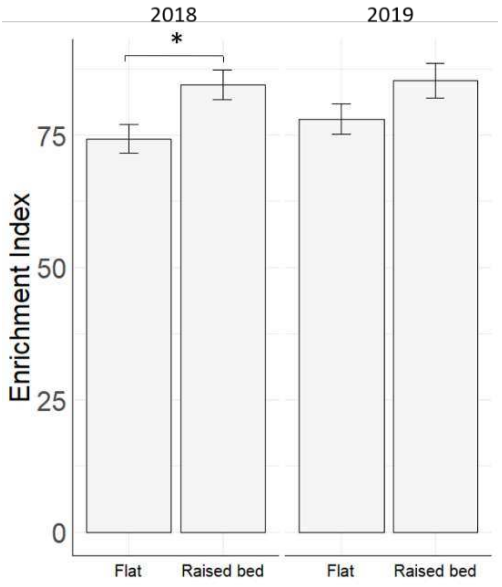

Fig. 5. Soil nematodes food web Enrichment Index (EI) values (Mean ± se) for each soil management (Flat grounds *vs.* Raised beds), for the two years of experimentation at Pontenx-les-Forges (PF). Significant differences between soil managements within years are indicated with an asterisk (* $p < 0.05$).

3.2. Site II: Pontenx-les-Forges

Seven families of plant-parasitic nematodes and twenty-four families of free-living nematodes were identified in the samples collected in PF (Table 3). The main families of plant-parasitic nematodes were Tylenchidae and Trichodoridae. Free-living nematodes were dominated by Cephalobidae, Rhabditidae and Prismatolaimidae. All indices, metabolic footprint and details on the composition of the nematode community are given in Table 4. For each treatment (*i.e.* crop association (TT, BT, LT) × soil management (F *vs.* Rb)), the Maturity Index was lower than 2.5, indicating a disturbed or enriched environment, while the Channel Index was lower than 20, indicating a dominant bacterial decomposition pathway, both years of the experiment (Table 4). Whatever the year, the number of nematodes per mL of soil was significantly higher in raised beds, in 2019 only (Fig. 4; ANOVA, $F_{(1,14)} = 6.57$, $p = 0.02$). A higher abundance of nematodes was still observed in BT in 2019, and particularly in raised beds (Table 4). The Enrichment Index (EI) was significantly higher in raised beds in 2018 but not in 2019 (Fig. 5; ANOVA, $F_{(1,14)} = 6.10$, $p = 0.02$), and it was not impacted by the crop association (Table 4). On the contrary, the Maturity Index (MI) was significantly lower in raised beds compared to the flat ground culture in 2018 (Fig. 6; ANOVA, $F_{(1,14)} = 7.85$, $p = 0.01$) but not in 2019.

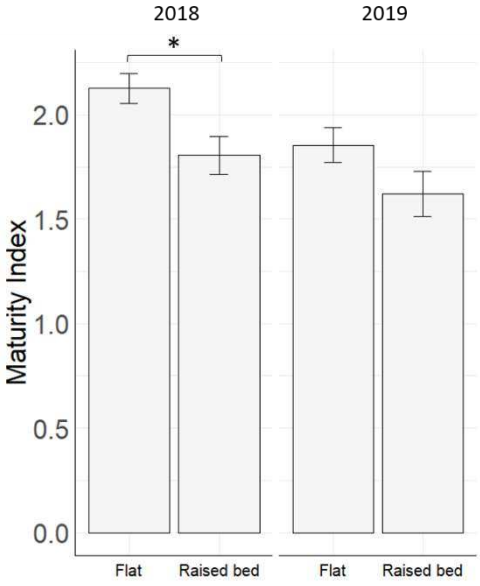

Fig. 6. Soil nematodes food web Maturity Index (MI) (Mean ± se) for each soil management (Flat grounds *vs.* Raised beds), for the two years of experimentation at Pontenx-les-Forges (PF). Significant differences between soil management within years are indicated with asterisks (* $p < 0.05$).

Table 3. Nematode family composition by feeding type: p-p (in italics) and c-p classes, family mass average (NINJA; Sieriebriennikov et al., 2014) and relative abundance (Mean % ± se) in the three crop associations (Tomato monoculture (TT), Bean-Tomato (BT) and Leek-Tomato (LT) associations) and the two soil managements (Flat ground *vs*. Raised bed), at Pontenx-les-Forges (PF) for the two years of experimentation.

			2018					
			Flat ground			**Raised bed**		
Family	***p-p* /c-p class**	**Mass (ug)**	**TT**	**BT**	**LT**	**TT**	**BT**	**LT**
Herbivores								
Ectoparasites								
Dolichodoridae	*3*	0.601	1.0 ± 0.6	-	-	0.3 ± 0.2	2.7 ± 0.5	-
Hemicycliophora	*3*	0.865	-	-	-	-	-	-
Trichodoridae	*4*	0.885	-	15.0 ± 5.0	-	0.3 ± 0.2	0.7 ± 0.2	-
Epidermal/root hair feeders								
Tylenchidae	*2*	0.160	6.7 ± 1.1	14.7 ± 2.2	16.7 ± 1.9	9.7 ± 1.6	11.0 ± 1.5	7.3 ± 0.8
Migratory endoparasites								
Pratylenchidae	*3*	2.136	0.3 ± 0.2	-	-	-	-	2.0 ± 1.2
Sedentary parasites								
Paratylenchidae	*3*	0.055	-	-	-	-	-	0.3 ± 0.2
Hoplolaimidae	*3*	0.527	0.3 ± 0.2	-	-	-	-	-
Bacterivores								
Acrobeloides	2	0.227	-	-	-	0.3 ± 0.2	-	-
Acrobeles	2	0.600	0.3 ± 0.2	0.7 ± 0.4	-	-	-	-
Alaimidae	4	0.537	-	-	1.3 ± 0.8	0.3 ± 0.2	-	-
Diplogastridae	1	1.591	0.7 ± 0.2	0.7 ± 0.4	2.0 ± 0.3	1.0 ± 0.6	2.7 ± 0.5	3.3 ± 0.4
Diploscapteridae	1	0.261	1.7 ± 0.7	3.3 ± 1.4	2.7 ± 0.7	3.3 ± 1.9	10.7 ± 2.4	10.3 ± 2.9
Cephalobidae	2	0.408	23.0 ± 0.6	18.0 ± 2.7	20.3 ± 2.7	14.3 ± 1.8	14.7 ± 3.2	14.0 ± 0.3
dauer	1	2.846	-	-	0.3 ± 0.2	-	-	-
Monhysteridae	2	0.358	-	0.7 ± 0.4	-	-	-	2.7 ± 1.5
Plectidae	2	0.845	3.3 ± 0.5	1.3 ± 0.4	5.3 ± 1.8	0.7 ± 0.2	1.3 ± 0.5	1.0 ± 0.3

Prismatolaimidae	3	0.460	23.3 ± 2.2	18.0 ± 3.0	23.0 ± 1.5	31.7 ± 3.5	13.7 ± 3.9	10.7 ± 0.5
Panagrolaimidae	1	0.655	0.3 ± 0.2	0.3 ± 0.2	-	2.7 ± 1.5	3.3 ± 0.7	9.7 ± 4.2
Rhabditidae	1	5.037	21.3 ± 6.0	15.0 ± 2.6	15.3 ± 4.1	23.3 ± 1.7	21.7 ± 4.5	18.3 ± 1.3
Rhabdolaimidae	3	0.097	-	-	0.7 ± 0.4	-	-	-
Teratocephalus	3	0.078	-	-	-	0.3 ± 0.2	-	-
Teratocephalidae	3	0.149	3.0 ± 0.6	0.7 ± 0.2	5.0 ± 0.9	1.0 ± 0.3	0.7 ± 0.2	0.3 ± 0.2
Wilsonema	2	0.054	0.7 ± 0.2	1.0 ± 0.3	0.3 ± 0.2	-	-	-
Fungivores								
Aphelenchoididae	2	0.191	4.3 ± 2.0	1.7 ± 0.5	2.3 ± 0.8	1.7 ± 0.5	2.3 ± 1.1	2.0 ± 0.3
Aphelenchidae	2	0.313	2.3 ± 0.8	5.7 ± 2.1	2.0 ± 0.6	6.7 ± 1.7	8.0 ± 2.3	14.3 ± 4.6
Leptonchidae	4	1.307	-	-	-	-	-	-
Tylencholaimus	4	0.472	-	-	-	-	-	-
Omnivores								
Aporcelaimidae	5	22.727	3.3 ± 0.7	2.3 ± 0.2	1.0 ± 0.3	0.7 ± 0.2	1.0 ± 0.3	-
Dorylaimidae	4	12.838	-	-	-	-	-	-
Neodiplogastridae	1	2.229	3.7 ± 1.5	1.0 ± 0.0	0.7 ± 0.4	1.0 ± 0.6	4.7 ± 2.1	3.3 ± 0.4
Qudsianematidae	4	2.233	-	-	-	-	-	0.3 ± 0.2
Predators								
Mononchidae	4	5.268	-	-	0.3 ± 0.2	0.3 ± 0.2	0.3 ± 0.2	-
Nordiidae	4	2.619	-	-	-	-	-	-
Onchulidae	3	2.824	-	-	-	-	-	-
Tripylidae	3	3.488	0.3 ± 0.2	-	0.7 ± 0.4	0.3 ± 0.2	0.7 ± 0.4	-

Table 3. (continued)

	2019					
	Flat ground			Raised bed		
Family	**TT**	**BT**	**LT**	**TT**	**BT**	**LT**
Herbivores						
Ectoparasites						
Dolichodoridae	-	0.3 ± 0.2	0.3 ± 0.2	-	-	0.3 ± 0.2
Hemicycliophora	-	-	-	0.3 ± 0.2	-	-
Trichodoridae	0.3 ± 0.2	19.0 ± 2.2	2.0 ± 0.3	-	12.0 ± 3.8	0.7 ± 0.4
Epidermal/root hair feeders						
Tylenchidae	9.3 ± 1.7	6.7 ± 1.5	15.0 ± 2.5	22.3 ± 2.5	27.0 ± 2.6	9.0 ± 2.4
Migratory endoparasites						
Pratylenchidae	0.3 ± 0.2	2.0 ± 0.6	-	0.7 ± 0.2	1.0 ± 0.6	-
Sedentary parasites						
Paratylenchidae	-	-	-	0.3 ± 0.2	-	-
Hoplolaimidae	1.7 ± 0.7	-	-	-	-	-
Bacterivores						
Acrobeloides	-	-	-	-	-	-
Acrobeles	14.3 ± 4.1	5.7 ± 2.0	16.3 ± 7.4	-	-	-
Alaimidae	-	-	-	-	0.3 ± 0.2	-
Diplogastridae	0.3 ± 0.2	-	1.7 ± 0.7	0.3 ± 0.2	1.7 ± 0.2	2.3 ± 1.3
Diploscapteridae	-	-	-	1.0 ± 0.6	1.3 ± 0.5	-
Cephalobidae	12.0 ± 3.0	22.0 ± 2.7	16.7 ± 3.3	13.0 ± 4.3	9.3 ± 1.9	32.0 ± 6.9
dauer	0.3 ± 0.2	-	0.3 ± 0.2	-	-	-
Monhysteridae	-	-	-	0.7 ± 0.4	-	-
Plectidae	0.3 ± 0.2	0.7 ± 0.4	0.3 ± 0.2	-	-	-
Prismatolaimidae	14.0 ± 2.4	4.7 ± 0.5	9.3 ± 0.4	15.3 ± 6.5	3.0 ± 1.0	9.0 ± 1.5
Panagrolaimidae	-	0.3 ± 0.2	2.0 ± 0.9	5.7 ± 2.0	12.3 ± 4.0	-
Rhabditidae	37.3 ± 5.5	31.3 ± 4.2	22.3 ± 2	29.3 ± 3.7	28.0 ± 2.6	35.7 ± 3.4

Rhabdolaimidae	-	-	-	-	-	-
Teratocephalus	-	-	-	-	-	-
Teratocephalidae	0.7 ± 0.4	0.3 ± 0.2	1.3 ± 0.4	0.7 ± 0.4	0.3 ± 0.2	-
Wilsonema	0.3 ± 0.2	-	1.3 ± 0.8	-	-	-
Fungivores						
Aphelenchoididae	0.3 ± 0.2	-	1.7 ± 0.4	1.7 ± 1.0	1.3 ± 0.8	7.0 ± 2.2
Aphelenchidae	4.7 ± 1.4	3.0 ± 0.9	2.7 ± 1	7.0 ± 0.7	1.7 ± 0.5	2.7 ± 1.5
Leptonchidae	0.3 ± 0.2	-	1.0 ± 0.6	-	-	-
Tylencholaimus	-	-	1.0 ± 0.6	-	-	-
Omnivores						
Aporcelaimidae	1.3 ± 0.4	0.3 ± 0.2	3.0 ± 0.6	0.7 ± 0.4	0.7 ± 0.2	1.0 ± 0.6
Dorylaimidae	0.3 ± 0.2	-	-	-	-	-
Neodiplogastridae	-	0.7 ± 0.4	-	0.3 ± 0.2	-	-
Qudsianematidae	-	-	0.3 ± 0.2	-	-	-
Predators						
Mononchidae	-	3.0 ± 1.7	1.3 ± 0.5	-	-	-
Nordiidae	0.3 ± 0.2	-	-	-	-	-
Onchulidae	-	-	-	-	-	0.3 ± 0.2
Tripylidae	1.3 ± 0.5	-	-	0.7 ± 0.4	-	-

Table 4. Nematode abundances, indices and footprint values, and relative abundances within feeding types, c-p classes for free-living nematodes (CP1 to 5) or p-p classes for herbivorous nematodes (PP1 to 5) of nematodes assemblages (Mean ± se) in the three crop associations (Tomato monoculture (TT), Bean-Tomato (BT) and Leek-Tomato (LT) associations) and the two soil managements (Flat ground *vs.* Raised bed), at Pontenx-le-Forges (PF) for the two years of experimentation.

	2018					
	Flat ground			**Raised bed**		
	TT	**BT**	**LT**	**TT**	**BT**	**LT**
Nematode abundance						
Nematodes.soil ml^{-1}	18.64 ± 1.40	25.93 ± 6.34	21.92 ± 2.52	27.56 ± 4.89	29.41 ± 4.57	23.76 ± 1.71
Nematodes indices						
Basal Index BI	14.93 ± 1.11	16.41 ± 2.01	15.73 ± 1.61	10.55 ± 1.66	11.79 ± 3.42	13.34 ± 1.76
Channel Index CI	10.52 ± 3.44	8.26 ± 2.45	5.66 ± 0.58	7.60 ± 2.02	7.65 ± 2.86	9.71 ± 2.99
Enrichment Index EI	75.45 ± 3.00	76.00 ± 1.30	71.48 ± 4.26	82.36 ± 3.25	86.33 ± 3.89	85.08 ± 2.05
Structure Index SI	69.48 ± 1.84	64.91 ± 5.87	72.24 ± 0.65	77.69 ± 1.54	57.91 ± 9.01	44.50 ± 2.11
Maturity Index MI	2.11 ± 0.10	2.09 ± 0.07	2.18 ± 0.08	2.07 ± 0.09	1.72 ± 0.07	1.63 ± 0.04
Plant Parasitic Index PPI	2.12 ± 0.07	2.88 ± 0.22	2.00 ± 0.00	2.07 ± 0.02	2.29 ± 0.04	2.14 ± 0.08
PPI/MI ratio	1.02 ± 0.05	1.37 ± 0.07	0.92 ± 0.04	1.01 ± 0.04	1.35 ± 0.08	1.32 ± 0.08
Metabolic footprints						
Composite footprint	55.46 ± 5.12	43.12 ± 3.57	39.22 ± 4.93	48.07 ± 2.95	49.69 ± 6.70	42.25 ± 2.03
Enrichment footprint	34.40 ± 7.76	23.64 ± 3.41	24.48 ± 5.96	36.37 ± 3.72	38.85 ± 6.06	35.66 ± 1.59
Structure footprint	15.38 ± 2.62	10.76 ± 0.80	8.69 ± 0.89	8.29 ± 0.59	6.54 ± 1.36	2.00 ± 0.14
Herbivore footprint	0.97 ± 0.32	5.20 ± 1.19	1.28 ± 0.15	0.90 ± 0.17	1.58 ± 0.10	1.68 ± 0.70
Bacterivore footprint	39.83 ± 8.47	28.79 ± 3.88	32.78 ± 4.86	42.81 ± 2.79	39.54 ± 6.78	36.45 ± 1.77
Fungivore footprint	0.77 ± 0.21	0.72 ± 0.24	0.48 ± 0.05	0.81 ± 0.13	1.01 ± 0.33	1.53 ± 0.37
Omnivore footprint	13.63 ± 2.80	8.41 ± 0.64	3.78 ± 0.87	2.92 ± 0.92	6.66 ± 0.79	2.59 ± 0.34
Predator footprint	0.27 ± 0.16	-	0.90 ± 0.52	0.63 ± 0.36	0.90 ± 0.52	-
% of total nematodes						
Herbivores	8.33 ± 1.84	29.67 ± 2.87	16.67 ± 1.90	10.33 ± 1.84	14.33 ± 1.17	9.67 ± 2.12

Bacterivores	77.67 ± 5.35	59.67 ± 3.29	76.33 ± 2.04	79.00 ± 2.60	68.67 ± 4.48	70.33 ± 3.86
Fungivores	6.67 ± 1.50	7.33 ± 2.50	4.33 ± 0.19	8.33 ± 1.50	10.33 ± 3.24	16.33 ± 4.29
Omnivores	7.00 ± 1.86	3.33 ± 0.19	1.67 ± 0.19	1.67 ± 0.69	5.67 ± 1.84	3.67 ± 0.51
Predators	0.33 ± 0.19	-	1.00 ± 0.58	0.67 ± 0.38	1.00 ± 0.58	-
% of free-living						
Bacterivores	84.23 ± 4.19	84.93 ± 3.27	91.57 ± 1.03	88.10 ± 2.34	79.90 ± 4.19	78.20 ± 4.76
Fungivores	7.50 ± 1.78	10.30 ± 3.44	5.20 ± 0.23	9.33 ± 1.78	12.37 ± 4.00	17.70 ± 4.45
Omnivores	7.90 ± 2.20	4.73 ± 0.16	2.03 ± 0.27	1.80 ± 0.72	6.60 ± 2.14	4.07 ± 0.57
Predators	0.40 ± 0.23	-	1.17 ± 0.67	0.77 ± 0.44	1.17 ± 0.67	-
CP 1	29.73 ± 4.82	28.63 ± 1.26	25.10 ± 4.66	34.20 ± 6.09	49.87 ± 5.40	50.23 ± 4.07
CP 2	37.30 ± 2.03	40.47 ± 4.67	36.37 ± 2.53	26.73 ± 3.28	31.33 ± 7.60	37.20 ± 3.96
CP 3	29.23 ± 2.40	27.63 ± 5.49	35.40 ± 2.03	37.60 ± 4.07	17.27 ± 4.12	12.17 ± 0.19
CP 4	-	-	1.90 ± 0.78	0.73 ± 0.21	0.40 ± 0.23	0.37 ± 0.21
CP 5	3.70 ± 0.79	3.30 ± 0.17	1.23 ± 0.44	0.73 ± 0.21	1.13 ± 0.37	-
% of herbivores						
Ectoparasites	7.13 ± 4.12	44.13 ± 11.20	-	4.93 ± 1.43	24.70 ± 4.17	-
Epidermal/root hair feeders	88.10 ± 6.87	55.87 ± 11.20	100.00 ± 0.00	95.07 ± 1.43	75.30 ± 4.17	86.27 ± 7.93
Sedentary parasites	-	-	-	-	-	1.97 ± 1.14
Migratory endoparasites	2.37 ± 1.37	-	-	-	-	11.77 ± 6.79
Semi-endoparasites	2.37 ± 1.37	-	-	-	-	-
PP 2	88.10 ± 6.87	55.87 ± 11.20	100.00 ± 0.00	95.07 ± 1.43	75.30 ± 4.17	86.27 ± 7.93
PP 3	11.90 ± 6.87	-	-	2.57 ± 1.48	20.50 ± 4.31	13.73 ± 7.93
PP 4	-	44.13 ± 11.20	-	2.37 ± 1.37	4.23 ± 1.25	-
PP 5	-	-	-	-	-	-

Table 4. (continued)

	2019					
	Flat ground			Raised bed		
	TT	BT	LT	TT	BT	LT
Nematode abundance						
Nematodes.soil ml^{-1}	15.92 ± 0.70	21.47 ± 5.08	18.09 ± 2.59	25.80 ± 1.96	46.67 ± 4.46	24.53 ± 5.34
Nematodes indices						
Basal Index BI	14.07 ± 2.03	16.95 ± 1.20	19.01 ± 2.24	10.38 ± 1.69	7.81 ± 2.45	19.07 ± 3.62
Channel Index CI	4.57 ± 1.71	2.09 ± 0.69	4.11 ± 0.80	7.54 ± 2.52	1.95 ± 0.59	6.67 ± 1.23
Enrichment Index EI	80.92 ± 3.80	79.88 ± 1.52	73.34 ± 3.38	86.04 ± 2.55	91.49 ± 2.73	78.32 ± 3.87
Structure Index SI	59.10 ± 2.04	36.74 ± 9.21	60.13 ± 2.17	57.86 ± 8.75	50.62 ± 4.76	40.36 ± 8.02
Maturity Index MI	1.82 ± 0.10	1.74 ± 0.10	2.00 ± 0.04	1.75 ± 0.15	1.40 ± 0.08	1.72 ± 0.07
Plant Parasitic Index PPI	2.27 ± 0.09	3.49 ± 0.08	2.27 ± 0.04	2.06 ± 0.01	2.51 ± 0.13	2.12 ± 0.05
PPI/MI ratio	1.28 ± 0.11	2.05 ± 0.12	1.14 ± 0.03	1.23 ± 0.10	1.82 ± 0.11	1.25 ± 0.08
Metabolic footprints						
Composite footprint	69.36 ± 6.19	62.30 ± 3.57	55.74 ± 1.59	54.30 ± 5.71	54.62 ± 4.06	64.21 ± 3.79
Enrichment footprint	54.01 ± 7.86	45.38 ± 5.88	33.93 ± 3.03	44.58 ± 5.48	44.46 ± 4.67	53.12 ± 5.42
Structure footprint	8.93 ± 1.70	5.15 ± 2.59	13.71 ± 1.55	5.36 ± 0.89	2.79 ± 0.63	5.03 ± 2.01
Herbivore footprint	1.30 ± 0.10	6.84 ± 0.75	1.77 ± 0.24	2.19 ± 0.24	5.89 ± 1.26	0.94 ± 0.25
Bacterivore footprint	61.07 ± 7.38	50.36 ± 5.99	41.47 ± 1.98	48.30 ± 4.64	46.22 ± 4.33	58.60 ± 4.97
Fungivore footprint	0.58 ± 0.08	0.26 ± 0.08	0.99 ± 0.37	0.84 ± 0.18	0.32 ± 0.12	1.15 ± 0.17
Omnivore footprint	5.12 ± 1.52	1.58 ± 0.91	10.07 ± 1.85	2.44 ± 1.20	2.20 ± 0.64	3.30 ± 1.90
Predator footprint	1.29 ± 0.41	3.24 ± 1.87	1.44 ± 0.55	0.54 ± 0.31	-	0.23 ± 0.13
% of total nematodes						
Herbivores	11.67 ± 1.02	28.00 ± 3.46	17.33 ± 2.69	23.67 ± 2.41	40.00 ± 6.33	10.00 ± 2.65
Bacterivores	79.67 ± 2.41	65.00 ± 4.48	71.67 ± 2.71	66.00 ± 2.33	56.33 ± 5.54	79.00 ± 3.84
Fungivores	5.33 ± 1.35	3.00 ± 0.88	6.33 ± 1.92	8.67 ± 1.58	3.00 ± 1.00	9.67 ± 0.96

Omnivores	1.67 ± 0.51	1.00 ± 0.58	3.33 ± 0.51	1.00 ± 0.33	0.67 ± 0.19	1.00 ± 0.58
Predators	1.67 ± 0.51	3.00 ± 1.73	1.33 ± 0.51	0.67 ± 0.38	-	0.33 ± 0.19
% of free-living						
Bacterivores	90.13 ± 2.08	89.80 ± 2.36	86.73 ± 1.66	86.47 ± 1.27	94.27 ± 1.17	87.53 ± 1.92
Fungivores	6.10 ± 1.53	4.13 ± 1.28	7.63 ± 2.27	11.33 ± 1.91	4.73 ± 1.37	10.93 ± 1.33
Omnivores	1.90 ± 0.59	1.50 ± 0.87	3.97 ± 0.49	1.37 ± 0.49	1.00 ± 0.31	1.20 ± 0.69
Predators	1.87 ± 0.57	4.53 ± 2.62	1.73 ± 0.71	0.83 ± 0.48	-	0.37 ± 0.21
CP 1	42.97 ± 6.25	44.00 ± 3.58	32.53 ± 3.55	49.30 ± 8.53	70.10 ± 6.77	42.50 ± 5.66
CP 2	36.23 ± 3.25	43.90 ± 2.21	46.43 ± 3.78	28.60 ± 3.86	22.97 ± 5.88	45.57 ± 6.54
CP 3	18.17 ± 3.07	7.03 ± 1.06	12.97 ± 0.56	21.10 ± 8.35	5.13 ± 1.51	10.70 ± 1.94
CP 4	1.13 ± 0.37	4.53 ± 2.62	4.50 ± 1.21	-	0.77 ± 0.44	-
CP 5	1.53 ± 0.44	0.50 ± 0.29	3.57 ± 0.59	0.97 ± 0.56	1.00 ± 0.31	1.20 ± 0.69
% of herbivores						
Ectoparasites	3.03 ± 1.75	71.20 ± 4.49	14.67 ± 1.55	1.77 ± 1.02	24.20 ± 6.27	7.20 ± 2.58
Epidermal/root hair feeders	76.20 ± 9.19	21.83 ± 3.34	85.33 ± 1.55	93.80 ± 1.28	73.57 ± 6.41	92.80 ± 2.58
Sedentary parasites	-	-	-	1.67 ± 0.96	-	-
Migratory endoparasites	3.70 ± 2.14	6.97 ± 1.50	-	2.80 ± 0.89	2.23 ± 1.29	-
Semi-endoparasites	17.03 ± 7.98	-	-	-	-	-
PP 2	76.20 ± 9.19	21.83 ± 3.34	85.33 ± 1.55	93.80 ± 1.28	73.57 ± 6.41	92.80 ± 2.58
PP 3	20.77 ± 10.12	7.93 ± 2.03	2.07 ± 1.19	6.20 ± 1.28	2.23 ± 1.29	2.07 ± 1.19
PP 4	3.03 ± 1.75	70.20 ± 5.06	12.57 ± 2.32	-	24.20 ± 6.27	5.13 ± 2.96
PP 5	-	-	-	-	-	-

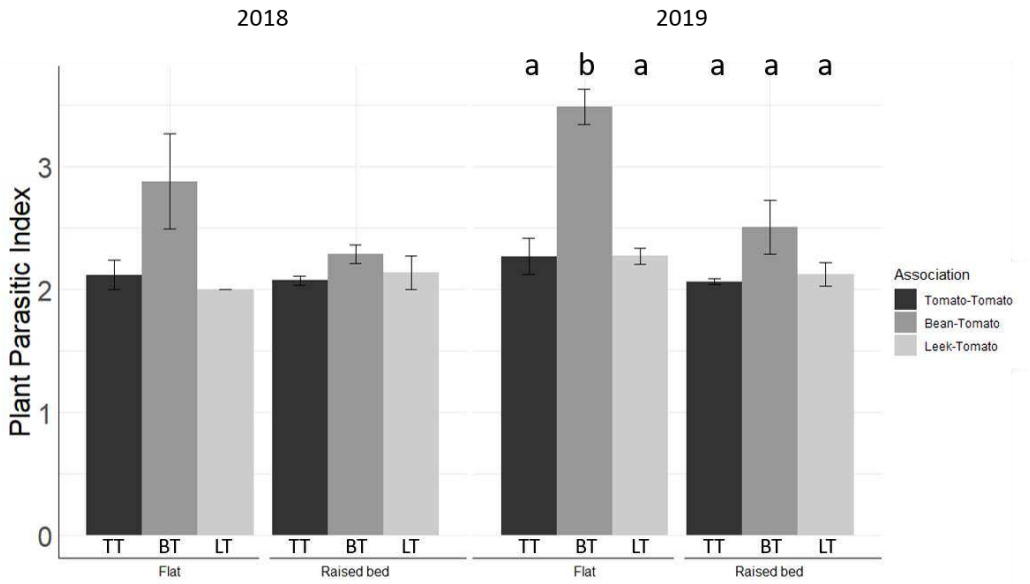

Fig. 7. Soil nematodes food web Plant-Parasitic Index (PPI) (Mean ± se) for each crop association and for each soil management (Flat grounds *vs.* Raised beds), for the two years of experimentation at Pontenx-les-Forges (PF). Dark grey: Tomato monoculture (TT), medium grey: Bean-Tomato (BT) and light grey: Leek-Tomato (LT) associations. Different letters indicate significant differences between treatments within each year ($p < 0.05$).

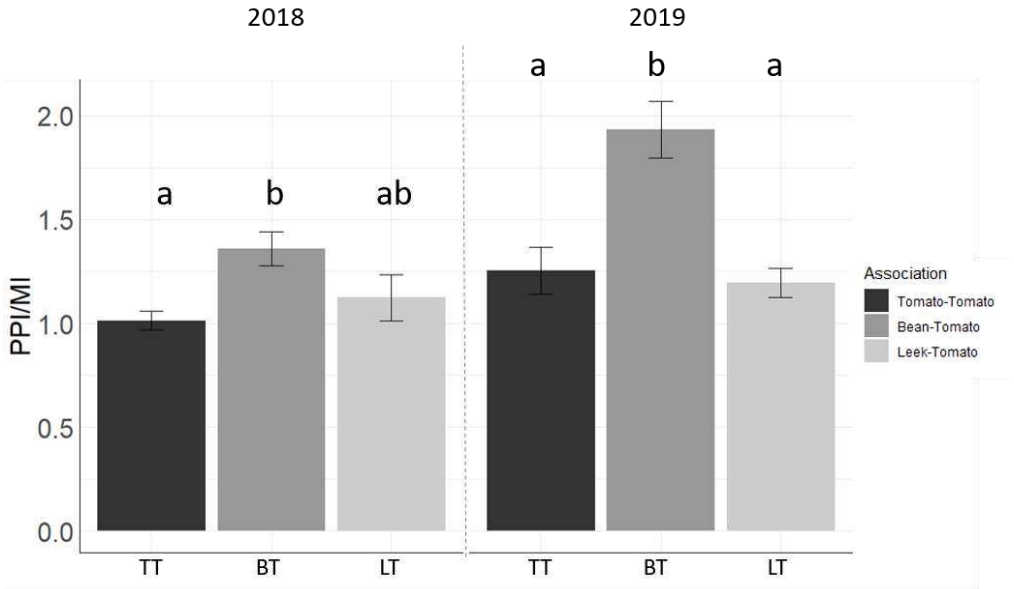

Fig. 8. Soil nematodes food web Plant-Parasitic Index / Maturity Index ratio (PPI/MI) values (Mean ± se) for each crop association, for the two years of experimentation at Pontenx-les-Forges (PF). Dark grey: Tomato monoculture (TT), medium grey: Bean-Tomato (BT) and light grey: Leek-Tomato (LT) associations. Different letters indicate significant differences between crop associations within each year ($p < 0.05$).

The crop association and the soil management had a significant interactive effect on the Plant-Parasitic Index (PPI) in 2019 but not in 2018 (Fig. 7; ANOVA, $F_{(5,12)} = 6.16$, $p = 0.01$). The PPI was higher in BT in flat grounds (Fig 7; ANOVA, $F_{(2,14)} = 14.77$, $p < 0.001$) but not in raised beds. Overall, the PPI was lower in raised beds than in flat grounds (ANOVA, $F_{(1,14)} = 9.85$, $p = 0.007$). In 2018, the PPI was significantly higher in BT (SHR; df = 2; H = 9.17; p = 0.01), while raised beds had no impact. Similarly, the PPI/MI ratio was significantly higher in BT both in 2018 (Fig. 8; ANOVA, $F_{(2,14)} = 4.58$, $p = 0.02$) and in 2019 (ANOVA, $F_{(2,14)} = 13.01$, $p < 0.001$). The herbivore footprint was also higher in BT, although this trend was only significant in 2019 (Fig. 9; $SHR_{(2, 12)}$, H = 9.92, p = 0.007). The Structure footprint was impacted by the soil management (Fig. 10A; ANOVA; $F_{(1,14)} = 11.54$; $p = 0.004$) and by the association (Fig. 10B; ANOVA, $F_{(2,14)} = 4.50$, $p = 0.03$) in 2018 only, but no interaction was found. This Structure footprint was lower in LT compared to TT, while intermediate values were obtained in BT (Fig. 10A, Table 4), and it was lower in raised beds than in flat grounds (Fig. 10B, Table 4). Finally, the soil food web analysis showed that, at PF, the soil food webs were enriched by all treatments (EI > 50; Fig. 11A). No clear pattern was visible, although raised beds tended to be more enriched than flat grounds. The soil food webs were overall less structured in 2019 than in 2018 for all treatments (Fig. 11B), and the Structure Index seemed to be more impacted by the crop associations and the soil management than the Enrichment Index.

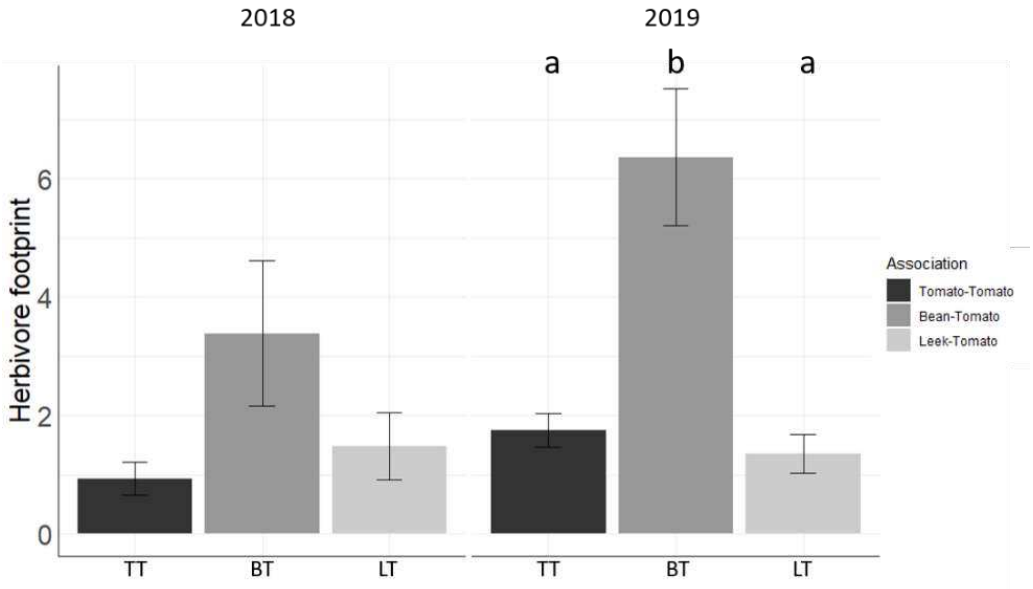

Fig. 9. Soil nematodes food web herbivore footprint values (Mean ± se) for each crop association, for the two years of experimentation at Pontenx-les-Forges (PF). Dark grey: Tomato monoculture (TT), medium grey: Bean-Tomato (BT) and light grey: Leek-Tomato (LT) associations. Different letters indicate significant differences between crop associations within each year ($p < 0.05$).

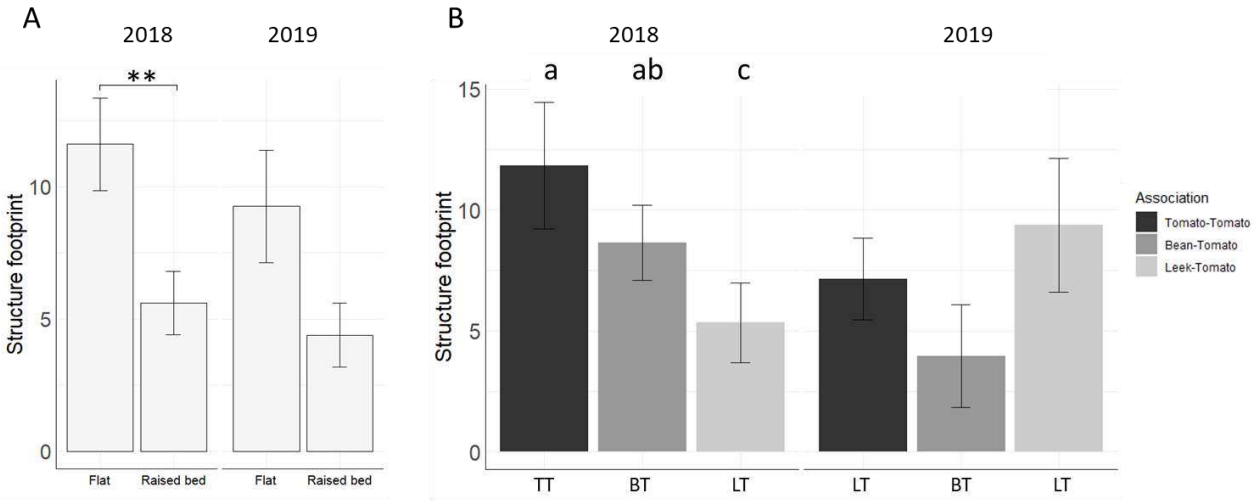

Fig. 10. Soil nematodes food web structure footprint values (Mean ± se) A.for each soil management (Flat grounds *vs.* Raised beds) and B. for each crop associations, for the two years of experimentation at Pontenx-les-Forges (PF). Dark grey: Tomato monoculture (TT), medium grey: Bean-Tomato (BT) and light grey: Leek-Tomato (LT). Different letters indicate significant differences between crop associations within each year ($p < 0.05$), and significant differences between soil managements within years were indicated with asterisks (** $p < 0.01$).

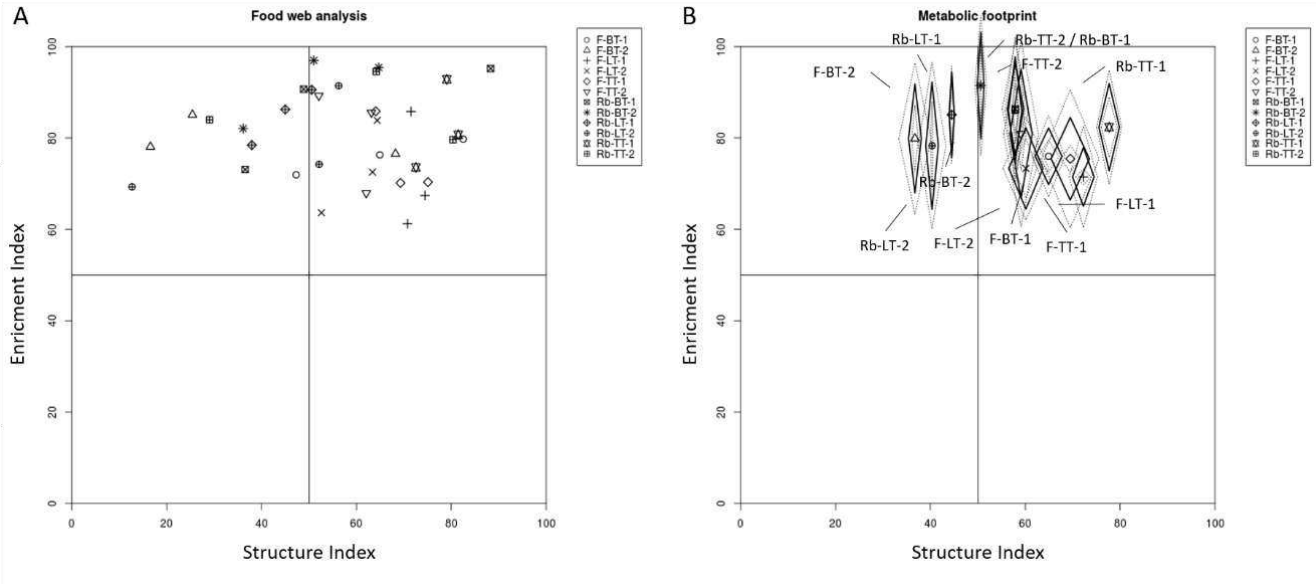

Fig. 11 A. Food web analysis and B. Functional metabolic footprint of nematode communities in Pontenx-les-Forges (PF) under two soil managements: Flat grounds (F) and Raised beds (Rb), and three crop associations: Bean-Tomato (BT), Leek-Tomato (LT) and Tomato monoculture (TT) for the two years of experimentation: 2018 (-1) and 2019 (-2). Vertical axes of each footprint represent the enrichment footprint and horizontal axes represent the structure footprint. Full lines represent the treatment means and dotted lines represent standard deviations. The nematode functional metabolic footprint is the total area of the two functional (enrichment and structure) footprints.

4. Discussion

In this study, we used nematode communities as indicators to investigate the impact of crop associations (bean-tomato and leek-tomato) and of a raised-bed gardening (*i.e.* soil management) on the soil health and the soil food web. Within nematode communities, the most abundant families belonged to the bacteria-feeding nematode group, dominated by Cephalobidae and Rhabditidae. This was consistent with the low values of the Channel Index recorded for each treatment at both sites, which indicated a dominance of the bacterial decomposition pathway (Ferris et al. 2001), and with the fact that those families are the most represented families in cropped sites (Yeates 2003). Our results showed that this pathway was not driven neither by the crop association nor by the soil management. Both sites were also characterized by a low Maturity Index, which is also commonly found in agricultural soils and characterizes a disturbed soil (Bongers 1990). Interestingly, the proportion of Rhabditidae was higher in 2019 compared to 2018 at both sites (Table 1 and Table 3). Such increase of Rhabditidae has been commonly attributed to a resource pulse (Yeates 2003), here explained by the recent conversion from a wasteland of acacia trees into a vegetable garden at Pontenx-les-Forges, but not at Adriers, where farming has been continuous for 10 years. At Adriers, changes in the nematode communities betFween 2018 and 2019 may have been induced by the presence of crucifers as winter crops. Crucifers are known to suppress plant-parasitic nematodes through changes in soil microfauna and microflora, and are associated with an increase of bacterial-feeding and of non-pathogenic nematodes communities (Couëdel et al. 2019). Additionally, at the same site, the proportion of plant-parasitic nematodes, dominated by Tylenchidae and Pratylenchidae, tended to decrease in 2019 (Table 1), which was consistent with previous results, in which free-living nematodes were less sensitive to the toxins of cruciferous crops than plant-parasitic nematodes (Stirling and Stirling 2003).

Overall, we found that raised beds had a higher and more systematic impact on soil functioning than crop associations. The higher abundance of nematodes on raised beds was only significant in 2019, which indicates that one-year-old raised beds are sufficient to observe differences in nematode populations. It is likely that setting up raised beds negatively impacted nematodes of higher trophic levels (with higher c-p values) that are more sensitive to physical disturbances (Ferris et al. 2001) and that need time to recolonize the environment. Indeed, although soil management did not impact the Structure Index (SI), a lower structure

footprint was recorded in raised beds. This lower structure footprint in raised beds compared to the flat grounds indicated not only a lower proportion of predatory nematodes but also of other organisms such as mites with a similar function (see Ferris, 2010b). Moreover, the higher Enrichment Index (EI) recorded in raised beds suggested higher resources for bacterivores and fungivores, which could be expected considering the additional input of organic matter (OM), as showed by Dupont et al. (2009) (Table B.1). This also supports the lower MI recorded in raised beds. However, the low abundance of fungivorous nematodes both in raised beds and in flat grounds indicated that the supplied OM was more beneficial to enrichment-opportunists such as bacterivorous Rhabditidae than to fungivorous nematodes. This is consistent with a recent meta-analysis for bacterivores, but not for fungivores (D'Hose et al., 2018). The lower MI recorded in raised beds compared to the flat grounds was surprisingly not associated with a higher PPI, which is not consistent with Bongers et al. (1997), who showed that MI and PPI were negatively correlated. However, the disturbance induced by the raised bed set up could have negatively affected both indices during the first years. Thus, long-term experiments on raised beds are needed to better understand the impact of these soil management practices on nematode communities.

Regarding the effect of crop association on nematode assemblages, we showed that the bean-tomato association presented the highest impact on nematodes. The bean-tomato association at PF did not reduce the MI but significantly increased the PPI, thus increasing the PPI/MI ratio, an indicator of soil fertility (Bongers et al. 1997). Therefore, the higher PPI/MI ratio in BT compared to the monoculture supported the hypothesis that the use of bean as intercrop increased soil fertility (Fustec et al. 2010). However, the analysis of soil nitrogen content did not support this hypothesis (Table B.1), nor the absence of impact on the EI, where nitrogen-fixing plants could have favored bacterial feeders (Djigal et al. 2012). We argue that plant-parasitic nematodes are responsive to improved conditions induced by the bean-tomato association, and not or to a lesser extent in the tomato monoculture or the leek-tomato association at the PF site. Those improved conditions may be linked with root exudates of beans or of tomato plants induced by the presence of beans. For example, exudates of *Medicago trunculata* (Fabaceae) and tomato were both shown to attract *Meloidogyne* spp. (Tylenchidae) (Čepulytė et al., 2018) and both plants are known to be sensitive to root-knot nematodes. This is confirmed by the higher proportion of PP5 such as ectoparasitic

Trichodoridae, which were particularly abundant in BT in 2019, and by the higher herbivore footprint that indicated higher quantities of C and energy entering the soil food web through herbivores (Ferris 2010b). The bean-tomato association particularly impacted plant-parasitic nematodes in a context of low concentrations of soil nitrogen and phosphorus, as shown by the results obtained at PF in flat grounds (Table B.1). This pattern was not observed at AD, probably because soil nitrogen and phosphorus concentrations were higher. D'Hose et al. (2018) found no significant impact of organic amendment on plant-parasitic nematodes compared to mineral fertilization, but mentioned one study in which it decreased their population. This was also the case in our experiment, as adding a hay/manure/compost raised bed decreased the plant-parasitic index within the bean-tomato association.

Surprisingly, we found a relatively low impact of the leek-tomato association on the nematode community at both sites, except a higher fungivore footprint at AD in 2019, due to a higher abundance of fungivores and particularly of Aphelenchoididae in LT and BT (Table 1). We found no reference of a specific *Allium*-Aphelenchoididae interaction. At PF, a lower structure footprint was found in presence of leeks in 2018, but this effect did not persist in 2019. As *Allium* species are known to produce nematicidal compounds (Arnault et al. 2013), we expected that the presence of leeks would induce significant changes in the nematode assemblages.

The length and the resistance of the soil food web indicated by the Structure Index (Bongers and Bongers 1998) did not clearly differentiate treatments. The analysis of the fauna profile confirmed that crop associations did not strongly impact nematode communities at AD, while differences were more visible at PF. The Structure Index of the nematode community profile tended to increase for each treatment between 2018 and 2019 at AD whereas, the reverse trend was observed at PF. This suggests that the nematode communities in long-term cropped systems (here, at AD) do not react in the same way as in recent systems (here, at PF). The farming history likely influenced the sampled communities: they were more stable at AD, while they were disrupted at PF due to the recent implementation of crops from acacia and the recent setup of raised beds. Long-term monitoring could provide more evidence.

5. Conclusion

Our monitoring of nematode communities revealed that they were more impacted by raised-bed gardening with manure, hay and compost than by tomato crop associations. Nematode communities were dominated by bacterial feeders that indicated a physical disturbance and a low maturity of the community. Patterns of soil enrichment were already visible through nematode communities after one year of practice. The impact of the crop association varied between sites and, at one site, the bean-tomato association affected plant-parasitic nematodes more than the other groups, while the leek-tomato association had a low and inconsistent effect. Plant-parasitic nematodes revealed that the bean-tomato association increased soil fertility in nutrient-poor conditions, and that it favored the development of herbivore nematodes. Nematode communities responded differently to crop associations under different agricultural histories, and long-term experiments are still needed to assess the long-term impacts of raised beds, crop associations and mixed agroecological practices in general on free-living nematode communities. We also suggest the use of other taxa such as microarthropods to better understand the impact of crop association and raised-bed gardening on soil functioning, trophic networks and soil-plant interactions.

6. Acknowledgments

We thank B. Giffard, B. Joubart and G. Darrieutort for giving us access to the equipment and premises for the extraction of the sampled nematodes at Bordeaux Sciences Agro. We thank J. Charry and J. Fournier, the farmers, for their collaboration, for giving us access to their farms and for managing the crops during the experiment. Finally, we thank I. Giraud, J. Doidy, L. Maurousset, N. Pourtau and C. Vriet for their help in the field for sampling and F. Gros for the proofreading of the English language.

Chapitre 3. Expérimentation *ex situ* : interactions entre organismes du sol et association de cultures

Lors des précédents chapitres, un effet peu marqué de la présence du poireau a été observé sur les communautés de nématodes libres du sol dans la rhizosphère des plants de tomate en culture associée. Cependant, les Alliacées sont connues pour représenter une alternative dans la lutte contre les pathogènes du sol en raison de leurs propriétés allélopathiques. Par ailleurs, les interactions entre les organismes du sol et les plantes peuvent parfois être complexes en système naturel et ainsi limiter les effets et la compréhension des mécanismes étudiés. Ainsi, nous avons menés une expérience en system simplifié au laboratoire EBI de Mai à Juillet 2019, pour étudier le rôle potentiel de contrôle du poireau, associé à la tomate, sur l'un des principaux ravageurs dans la culture de tomates, les nématodes à galles du genre *Meloidogyne.* L'effet du poireau sur *M. incognita* a été testé seul et en interaction avec deux organismes identifiés comme ayant aussi un potentiel de contrôle sur *M. incognita* et souvent présent en milieu agricole : le champignon mycorhizien (*R. irregularis*) et des vers de terre épigé (*E. andrei*).

Dans le cadre de cette expérience menée en parallèle à celle *in situ*, j'ai pu co-encadrer un stagiaire de Master 2, Valentin Cognard, qui a largement contribué au suivi des plantes sous serre et à l'acquisition des résultats.

Le manuscrit de ce chapitre a été soumis à la revue *Plant & Soil*.

Growth and root-knot nematode infection of tomato are influenced by mycorrhizal fungi and earthworms in intercropping cultivation system with leeks

Jeremy Detrey[a], Valentin Cognard[a], Caroline Djian-Caporalino[c], Nathalie Marteu[c], Joan Doidy[b], Nathalie Pourtau[b], Cecile Vriet[b], Laurence Mauroussset[b], Didier Bouchon[a], Julia Clause[a,*]

[a] University of Poitiers, Ecology & Biology of Interactions - UMR CNRS 7267, TEAM EES – Ecology Evolution Symbiosis, 5 rue Albert Turpain, TSA, 51106, 86073, Poitiers Cedex 9, France.
[b] University of Poitiers, Ecology & Biology of Interactions - UMR CNRS 7267, TEAM SEVE - Sugar & Ecology Plants-environment, 5 rue Albert Turpain, TSA, 51106,86073, Poitiers Cedex 9, France.
[c] INRAE, Université Côte d'Azur, CNRS, Institut Sophia Agrobiotech, 06903 Sophia Antipolis, France *

Abstract

Aims: In a greenhouse experiment, we investigated the influence of leek (*Allium porrum*) intercropping, mycorrhizal fungi and earthworms on the root-knot nematode infection by *Meloidogyne incognita* and associated growth and development of tomato plants (*Solanum lycopersicum*).

Methods: Plants were grown in pots, intercropped with leeks or in monoculture, in which earthworms and/or mycorrhizal fungi were introduced, totaling 10 treatments. The effects of both factors were assessed i) by counting the galls induced by the nematodes and the number of layings on roots, and ii) by estimating plant growth and development through their height change, shoot and root dry biomasses and flowering.

Results: Tomato growth was increased in the leek intercropping compared to the monoculture, probably due to a lower plant-plant competition, although a facilitation effect cannot be excluded. The presence of leeks did not reduce the number of galls (per g of root), but a lower number of egg masses (per g of root) was found in the leek intercropping compared to the monoculture, suggesting an inhibition of the reproduction of *M. incognita*. The presence of *Rhizophagus irregularis* increased the infestation of *M. incognita*, while that of *Eisenia andrei* tended to reduce it, and their presence altered plant parameters in comparison to treatments with root-knot nematodes only.

Conclusions: The competition between the two tomato plants in the monoculture treatments undoubtedly influenced the patterns of reduced plant growth, early flowering and RKN infection. However, stimulating impacts of leek on plant growth and inhibitory effects on nematode reproductive cycle cannot be excluded. Altered patterns of plant growth and development in presence of AMF and/or earthworms in presence of RKN suggest that plant-soil organisms interactions play an indirect role in the nematode-crop interaction.

Keywords: Crop association; biological control; soil biodiversity; *Meloidogyne incognita*; *Eisenia andrei*; *Rhizophagus irregularis*

Abbreviations

AMF: Arbuscular Mycorrhizal Fungi
EW: Earthworms
LT / TT : Leak-Tomato association / Tomato-Tomato (monoculture)
RKN : Root-knot nematodes

1. Introduction

Root-knot nematodes (RKN) from the genus *Meloidogyne* are considered as pests of primary importance in agriculture and the top-ten nematodes in the world based on scientific and economic importance (Jones et al., 2013). As endoparasites of plants, they carry out a part or all of their life cycle in the root tissues to feed and reproduce (Hoefferlin et al. 2018). These nematodes will induce galls on roots from which egg masses are laid, and eggs are then released into the soil. Under a favorable environment, they develop into juveniles which, as soon as they hatch, will infect the roots of the same or other neighbouring host plants, thereby inducing the formation of new galls (Eisenback and Triantaphyllou 1991; Moens et al. 2009). Thus, through series of reproduction cycles, the soil infestation by these nematodes can reach 100,000 to 200,000 eggs/kg of soil (Blancard 2009). Yield reductions have been estimated between 12 and 21 % for all cultivated plants (Hoefferlin et al. 2018), and up to 100 % yield losses were recorded on untreated susceptible tomato varieties (Wesemael et al. 2011; Jones et al. 2013). Among the methods developed to control plant-parasitic nematodes, chemical control based on pesticides is commonly used in intensive conventional agriculture, despite its cost and unsustainability (Neves et al. 2009; Cheng et al. 2015). However, due to increasing restrictions to limit environmental impacts, physical and/or biological control (a.k.a. biocontrol) alternatives are being developed for a more sustainable agriculture. Biocontrol approaches rely on “natural enemies, antagonists or competitors and other self-replicating biotic entities” (Kenis et al. 2012), and on molecules from natural origin (French Ministry of Agriculture 2020).

Among alternatives to chemicals for pest control, intercropping can be considered alone or combined to other practices in integrated pest management (Smith and McSorley 2000; Djian-Caporalino et al. 2019). The simultaneous presence of several plant species in the same area offers significant advantages, such as improved nutrition or protection against pests (Yarou 2017). Plant species from the *Allium* genus, for example, are known for their biocidal effects by releasing sulphur compounds such as thiosulfinates and disulphides with methyl (DMDS), propyl (DPDS) or propenyl groups (Arnault et al. 2004, 2005). These volatile compounds released in root exudates have an inhibitory effect on the hatchability of RKN (Li et al. 2018). Extracts can be used alone efficiently against RKN (Tada et al. 1988) and associations of *Allium sp*. with other crops also produced nematicidal effects (Huang et al., 2016).

The diversity of soil organisms is also particularly important and often neglected in pest control (Fournil et al. 2018). Indeed, the diversity of soil organisms induces ecological niches that are more favorable to the development of plants and unfavorable to plant pests (bacteria, fungi or nematodes), whose populations decline or stabilize below a tolerable threshold (Baker 1991; Barrios 2007). Endomycorrhizal fungi, and particularly arbuscular mycorrhizal fungi (AMF), establish symbiosis with plant roots, colonizing the majority (74%) of plant species (Smith and Read 2010; Van Der Heijden et al. 2015). This mutualistic interaction is mainly known to promote water, sugar and nutrient exchanges between the plant and the fungal partners. Besides, mycorrhizal fungi also enhance soil structure and foster diversified and stable microbial communities, preventing the proliferation of pathogenic propagules (Pozo and Azcón-Aguilar 2007; Sosa-Hernández et al. 2019). AMF can physically protect roots in the rhizosphere acting like a barrier against microorganisms and invertebrates, or acting inside roots by releasing fungal compounds (Simard and Durall 2004; Song et al. 2010). For example, the AMF *Funneliformis mosseae* (formerly *Glomus mosseae*) has already been shown to reduce RKN infection on mycorrhized tomato roots (Vos et al., 2012, 2013). Understanding the interactions between AMF and nematodes is an important challenge to reduce crop yield losses due to nematodes (Djian-Caporalino et al. 2009; Schouteden et al. 2015). Earthworms are also important components of agroecosystems, as they stimulate plant growth by increasing soil fertility *via* earthworm casts and by promoting microbiological activity (Blouin et al. 2013; van Groenigen et al. 2015). Their presence can also limit the activity of pests such as the epi-endogeic *Amynthas corticis* reducing thrip attacks on tomato plants (Xiao et al. 2019). Rostami et al. (2014) also showed in an *in vitro* experiment that the application of *Eisenia fetida* earthworm products (liquid from vermicompost, coelomic fluids and water-soluble compounds from earthworm skin) inhibited the hatching of *Meloidogyne javanica* eggs in cucumbers and had larvicidal effects. Few studies were conducted on the combined effects of soil organisms and plant-parasitic nematode populations and on their impact on crops. Among them, Hua et al. (2010) showed that the combined presence of AMF and earthworms reduced the number of plant-parasitic nematodes compared to the fungus alone in a polluted soil, mostly driven by an earthworm effect.

Tomato (*Solanum lycopersicum*) is one of the world's most economically important high-yielding crop and is susceptible to soil-borne pathogens such as RKN (FAO, 2014). In a context of vegetable gardening, agroecological practices relying on plant-plant and plant-soil

organisms' interactions could limit the populations of RKN, and/or reduce their impacts on tomato plant growth and production. Among candidates, co-cultivation of tomato crops with another cash crop from the genus *Allium* such as leek (*Allium porrum* L.), in which DPDS is predominant (Auger et al. 1989; Casella et al. 2013), represents a potential tool to control RKN. Using an experimental greenhouse set-up, we investigated the impact of leek, arbuscular mycorrhizal fungi (*Rhizophagus irregularis)* and compost earthworms (*Eisenia andrei*), alone and in combination, on the control of RKN (*Meloidogyne incognita* Kofoid & White) and on the development of tomato plants.

2. Material and methods

2.1. Study system

The tomato cultivar (var. 'Coeur de boeuf rouge'; AGROSEMENS, France) was selected for its economic potential, as it is commonly found on markets and appreciated by consumers. Seeds were organically produced and, according to the supplier, the variety is not known to exhibit any resistance against *Meloidogyne incognita*. The leek cultivar (var. 'Lancia'; AGROSEMENS, France) was selected for its ability to grow during summer in order to be intercropped with tomato. Tomato plants were infected by a solution containing eggs of a pure population of *Meloidogyne incognita*, provided by the Institute Sophia Agrobiotech-INRAE, France.

Rhizophagus irregularis (DAOM 197198 inoculum; Agronutrition, France) was selected to investigate the effect of Arbuscular Mycorrhizal Fungi (AMF). Due to its wide commercial distribution among farmers for field inoculation, this species is likely to be present in many agricultural landscapes (Savary et al. 2018). It can be purchased in high concentration as pure inoculum and can be easily transported in a sterile environment. Finally, the epigeic earthworm species *Eisenia andrei* Savigny (Vers la Terre, Pezenas, France) was chosen to test an 'earthworm effect'. Known as compost worm, it feeds on decaying organic matter, lives in the soil litter and the top soil and was commonly found in agrosystems due to the use of compost as manure by farmers.

2.2. Experimental design

To measure the effects of leek intercropping, AMF and earthworms alone and in combination on the biocontrol of RKN infestation, we set up a balanced two-factor randomized experiment. The two factors were 1) "Association" (*i.e.* intercropping) with two levels: tomato monoculture or leek-tomato, 2) "Soil organisms" with 5 levels: control with no additional soil organisms (Control), presence of the RKN *M. incognita* only, presence of RKN and arbuscular mycorrhizal fungi (AMF) *R. irregularis* (RKN/AMF), presence of RKN and the compost earthworm *E. andrei* (RKN/EW), presence of RKN, AMF and earthworms (RKN/AMF/EW). The combination of both factors resulted in 10 treatments, with 5 biological replicates (n=5), totalling 50 pots. As tomato was the target plant, leek monocropping was not tested.

The experiment was carried out from May to July 2019 at the University of Poitiers, France (46°33'55.3", N 0°22'57.3"E) under ventilated greenhouse conditions (24.5°C average temperature, natural day/night cycle, 45 % average humidity). The experimental soil was collected from the topsoil (0-40 cm) of a grassland in an organic vegetable farm (46°15'07.1"N, 0°45'25.5"E; Adriers, France). The sandy loam soil was sieved through a 4 mm diameter mesh to remove coarse fragments and macrofauna. To prevent the presence of potential nematodes (cysts, eggs, larvae, adults) and other contaminating organisms, the soil was autoclaved two months before the beginning of the experiment (two cycles of 20 min at 120°C, 1 bar pressure). The initial soil characteristics were: organic matter (OM) = 3.32 %, pH_{KCl} = 6.21, N_{tot} = 0.14 %, C_{tot} = 1.93 %, available P = 94 g/kg, CEC = 6.28 cmol/g, Ca^{2+} = 1721 g/kg, Mg^{2+} = 327 g/kg, Na^{+} = 25.3 g/kg, K^{+} = 240 g/kg.

Tomato seedlings were prepared by sowing seeds on moist filter paper in Petri dishes and transplanted 5 days later in 9 x 9 cm pots filled with autoclaved soil. Upon transplanting, 40 seedlings corresponding to the RKN/AMF and RKN/AMF/EW treatments for the monoculture (TT) and the leek-tomato association (LT) were inoculated with a 1 mL solution containing 1000 spores.mL^{-1} of the AMF *R. irregularis.* Thirty supplementary seedlings were used to weekly check the tomato root colonization by AMF. When tomato root colonization by AMF was confirmed, tomato seedlings were transplanted in the 3.5 L microcosm pots filled with soil infested with nematodes eggs (RKN) or not (Control), with associated plants (tomato or leeks) and with soil organisms (EW and/or AMF). Leek seeds were sown and grown on peat soil for 6 weeks in an organic vegetable farm (Chez Paulet, Adriers) then placed in

experimental greenhouse conditions for additional 36 days before being transplanted with the tomato plant. Upon this first transplantation, leaves and roots of leeks were cut to favor their growth in pots, and absence of AMF colonization was checked on leek roots before transplantation.

In order to be as representative of field conditions as possible, where the crop density of a monoculture can be twice as high as that of an intercropped crop, two tomato plants were set in a single pot in the tomato monoculture condition, and only one in the leek-tomato association. No treatment with one plant and no leek was done, as a co-cultivation effect rather than a single-plant effect was tested. Furthermore, the same quantity of inoculum of RKN was applied to pots of both TT and LT, without considering the tomato plant density. At the start of the experiment (t_0), tomato plants (11 weeks old) were individually transplanted into plastic pots (upper diameter 20 cm, lower diameter 16 cm, height 15 cm) filled with homogenized experimental soil with either another tomato plant or two leeks. Before the transplantation, soil of treatments containing nematodes were inoculated with 5,000 eggs of *M. incognita* by pipetting 1 mL of egg solution (5,000 eggs.mL^{-1}; Institute Sophia Agrobiotech-INRAE, France), and soil was mixed to homogenize egg concentration. For AMF treatments, tomato plants had been previously inoculated with *R. irregularis* 8 weeks before being transplanted. Eight individuals of *E. andrei* (total average fresh weight: 0.30 ± 0.04 g) were gently introduced below the soil surface, and 5 g of dry grass litter (*Avena fatua*, *Deschampsia cespitosa*, *Anisantha sterilis* and *Brachyopodium sylvaticum*) were added to the soil surface. The earthworm density was determined from the density observed upon sieving the soil, and the rewetted litter provided food and protection for earthworms. It also aimed at reducing evaporation throughout the experiment. Extra tomato plants were prepared to check for RKN infestation and completion of their reproductive cycle (7 weeks, 20°C) during the experiment. All pots were transferred to greenhouse conditions and a tomato plant was randomly selected in TT treatments for monitoring changes in plant height. Monitoring started on May 22nd (t_0) and ended on July 7th (t_7). Plants were watered 2 to 3 times/day as heat conditions increased outside the greenhouse. To prevent the leaching and loss of RKN, plants were watered from the top through 2-3 short water shoots, adjusted according to soil moisture, and underpot dishes were checked for dryness. Due to the colonization time of AMF and the additional time for nematodes to complete their cycle, the experiment was extended after the flowering. No sign of nutrient deficiency was observed.

2.3. Sampling

After the final recording of plant measurements at week 7 (t_7), plants were harvested. Shoots of the monitored tomato plants were cut at the ground level and roots were gently separated from the soil and from other roots systems. Shoots were set aside and oven-dried (70°C, 3 days) and soil samples were collected and stored at 4°C for chemical analysis. Root systems were washed in three consecutive baths and were gently dried on a filter paper. Similar root samples were collected on each root system to check and quantify the AMF colonization. The remaining root systems were then weighed and stored at 4 °C for nematode analyses.

2.4. Measurements

2.4.1. Plant growth and development

All plant measurements were performed on the unique tomato plant in the leek-tomato association, and on the tagged tomato plant in the tomato monoculture. From the start to the end of the experiment (t_0 to t_7), tomato plant height was measured weekly from the stem base to the apical meristem and the number of flowers was counted. To estimate the changes in plant growth through tomato shoots, we calculated the weekly difference between the plant height (t_x) and the initial plant height (t_0). At the end of experiment, shoot and root dry biomasses were weighed and plant height was measured.

2.4.2. Root-knot nematode infestation level

After being cleaned from soil, fresh tomato root systems were weighed and colored in a solution of eosin B (15 min, 4.5 g.L-1)(Hooper et al. 2005). The solution of eosin B stains egg masses in red and facilitates counting. Root systems were then washed in two successive baths for root and gall discoloration, and both galls and egg masses were counted. Due to the very large number of galls per root system (estimated from 2,000 to 10,000 galls over the entire root system), the measurement of infestation by RKN was systematically performed on a sub-sample of the root system (5 % fresh weight of tomato root system). All counts were then multiplied by 20 to consider the infestation on the entire root system. The level of RKN infestation was measured by counting the total number of galls, the total number of egg masses (*i.e.* eggs that were laid on galls) and the number of galls with multiple egg masses, which indicates that more than one nematode had penetrated and reproduced in the same

gall (*i.e.* > 1 egg mass per gall). All those measurements were done blindly with a binocular microscope. Control tomato roots were checked and no RKN was found.

2.4.3. AMF root colonization and earthworm counts

To estimate mycorrhizal colonization, tomato root systems were collected and AMF colonization rates were determined using "the vinegar ink" staining protocol (Vierheilig et al. 1998). Fresh clean root samples were digested in 10% KOH at 70°C for 20 min, rinsed several times with distilled water, stained at 70°C for 15 min in vinegar:ink solution (95:5, v:v) and distained in 8% acetic acid for 5 min. For light microscopy, 30 1 cm-long root fragments were mounted on glass slides. Mycorrhizal rates (frequency of colonization by mycorrhizal fungi [F%], intensity of mycorrhizal fungi colonization out of all 30 root fragments [M%] and intensity of mycorrhizal fungal colonization in colonized root fragments only [m%]) were calculated using the Mycocalc software (http://www2.dijon.inra.fr/mychintec/Mycocalc-prg/download.html ; Trouvelot et al., 1986). Recovered earthworms from each mesocosm were counted and weighed.

2.5. Soil properties

All soil physicochemical properties were performed by a certified laboratory (Laboratoire d'Analyses Chambre d'Agriculture du Loiret, France). NH_4^+ and NO_3^- were extracted with a KCl solution and measured by colorimetry (540 nm and 660 nm). Organic matter (OM) was measured by dry combustion (ISO NF 14235). pH was determined with water (1:5 ratio; NF ISO 10390). Total C and N (C_{tot} and N_{tot}) concentrations were measured with a CHN pyrolysis micro-analyzer (NF ISO 10694 and NF ISO 13878). Available phosphorus (P_2O_5) was measured by spectrophotometry using the Olsen method (NF ISO 11263). Cation Exchange Capacity (CEC) was measured with the Metson method (NF X 31-130) and exchangeable cations (K^+, Ca^{2+}, Mg^{2+}, Na^+) were measured using atomic flame emission from ammonium acetate extracts (NF X 31-108).

2.6. Data analysis

All statistical analyses were performed using R (R Core Team 2013). Nematode infestation variables (*i.e.* total number of galls, total number of egg masses, and number of galls with multiple egg masses) were standardized per root dry biomass. Within each culture type (TT or LT), the impact of soil organisms on plants and RKN infestations was assessed with a one-way ANOVA after checking for normality and homogeneity of variances. Significant differences between treatments were assessed using Tukey's post-hoc tests. Comparisons of grand means between TT and LT (combination of all treatments within association or monoculture, excluding the control treatment for nematode variables) were performed using a one-way Multivariate ANalysis Of VAriance (MANOVA) to highlight an effect of leeks.

To assess the effect intensity of treatments on plants and/or RKN infestation, log Response Ratios (LnRR) were calculated. First, LnRRs (LnRR #1) were calculated to assess the response of plant variables to the introduction of RKN alone in comparison to controls, within TT or LT: LnRR ($variable_i$ = ln($variable_i$ / mean(control)), where *i* is the tomato individual in the considered treatment (n=5) and mean(control) is the mean value of all individuals (n=5) in the control. LnRRs (LnRR #2) were then calculated to assess the response of plants and nematode infestation to the introduction of AMF and earthworms alone or in interaction in comparison to nematodes alone, within TT or LT : LnRR($variable_i$ = ln($variable_i$ / mean(RKN)), where *i* is the tomato plant individual and mean(RKN) is the mean value of all individuals in the RKN treatment (n=5). Third, LnRRs (LnRR #3) were calculated to assess the effect intensity of the leek-tomato association compared to the tomato monoculture (TT) on plant and nematode infestation for each 'soil organisms' treatment: LnRR($variable_i$ = ln($variable_i$ / mean(TT)), where *i* is the tomato individual from the LT association (n=5) and mean(TT) is the mean value of all individuals (n=5) in the tomato monoculture. LnRR > 0, LnRR < 0 and LnRR = 0 mean a positive, negative and neutral effect respectively. The deviation from 0 was tested with t-tests. In order to assess the overall impact of treatments on plant growth and RKN infestation and an eventual link with differences in soil properties, a principal component analysis (PCA) was performed using the *FactoMineR* and the *ade4* R packages (Dray and Dufour 2007; Lê et al. 2008). Variables that were highly correlated and did not provide any additional information were removed and general patterns of variance were determined from the 8 following variables: 5 measures of plant growth and development (height increase, shoot biomass, root

biomass, number of flowers, first flowering day) and 3 measures of RKN infestation (total number of galls, total number of egg masses and number of galls with multiple egg masses, all calculated per gram of dry root). 7 soil properties and 3 soil organisms parameters (number of earthworms remaining in pots and AMF colonization of tomato roots) were added as illustrative variables (see ESM 3 for data). As the study focused on the biocontrol of RKN and because nematode-free control treatments highly impacted the results of the PCA analysis, controls were removed from the analyses. A between–within classes analysis was then performed on the PCA to quantify to what extent the association, the soil organisms or the interaction of both factors affected plants and root infestation by RKN. This method allows hierarchizing factors that contribute to the recorded variation. The between-classes analysis examined the differences between TT and LT or between soil organisms, whereas the within-classes analysis examines the remaining variation after the class effect has been removed (Dray and Dufour 2007). The statistical significance of the between classes PCA was tested using a Monte-Carlo test based on 999-permutations.

3. Results

3.1. Plant growth and development

3.1.1. Tomato height change and biomass

Within both TT and LT association, the impact of RKN alone and in combination with other soil organisms on plant growth varied. The presence of RKN alone significantly reduced the tomato height increase compared to control plants in LT but not in the monoculture (Fig. 1A, ESM 1 Table S1). A similar pattern was observed for the shoot biomass (Fig. 1B), for which the negative effect of adding RKN was confirmed by the Log Response Ratio #1 (data not shown; t-test, df = 4, t = -3.12, P = 0.03). No significant effect of RKN and associated galls was found on the root biomass in presence of RKN only compared to the control treatment (ESM 1, Table S1). Overall, the height increase and shoot biomass were lower in presence of all soil organisms (ANOVA, df = 4, F = 4.4, P = 0.01 and df = 4, F = 3.5, P = 0.03 respectively; Fig. 1A and 1B) in LT only. The highest increase of height was recorded in controls and was significantly lower in presence of RKN alone or in combination with earthworms, and intermediate values were recorded in presence of AMF (Fig. 1). The highest shoot biomass was observed in control and the lowest in the RKN/AMF combination (Fig. 1A). No effect of

soil organisms was found on the height increase or shoot biomass in the monoculture (Fig. 1). Combining AMF and earthworms treatments (RKN/EW/AMF) had a strong positive effect on the height increase in LT (LnRR #2; t-test, df = 4, t = 4.18, *P* = 0.01; Fig. 2A, ESM 1 Table S2), while it had no effect in the monoculture. The addition of earthworms (RKN/EW) significantly reduced the tomato height increase in TT (t-test, df = 4, t = -4.54, *P* = 0.01; Fig. 2A), while it had no effect in LT. The addition of AMF had no significant effect on increase of plant height, while the addition of AMF and earthworms, alone or in combination had no effect on root and shoot biomasses in both TT and LT (ESM 1 Table S2).

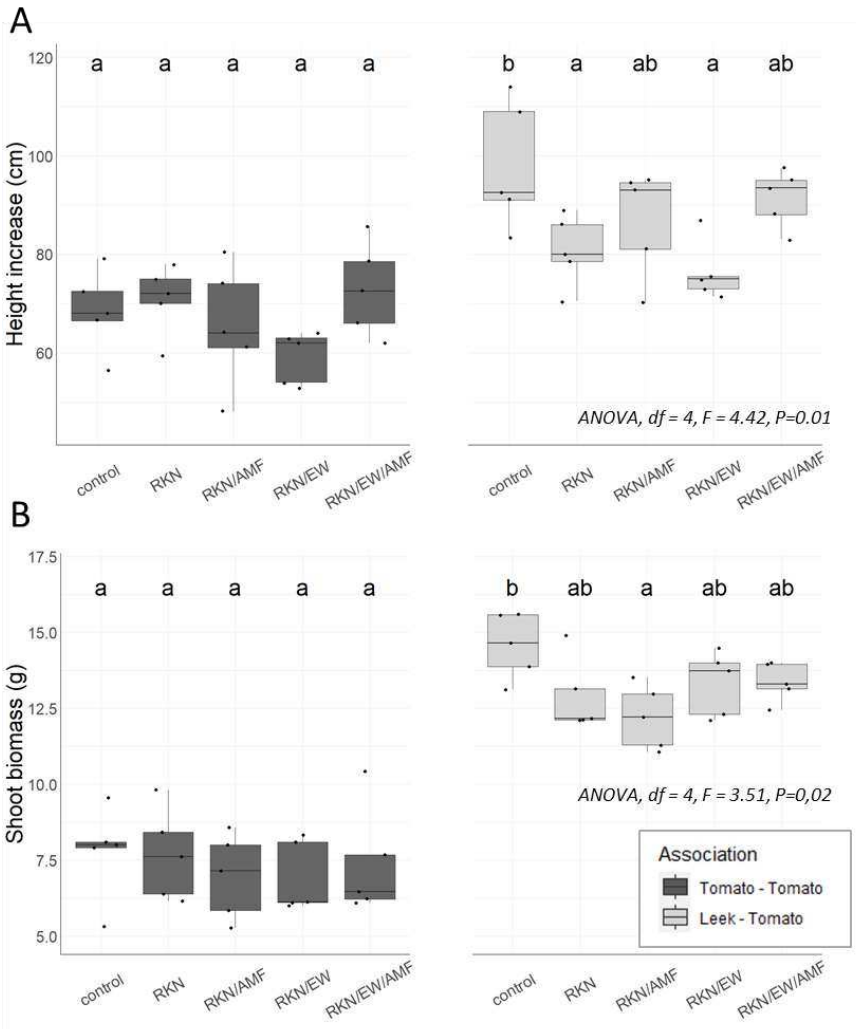

Fig. 1 A. Height increase (final height – initial height) and B. shoot dry biomass of tomato plants at the end of the experiment (t7) for each of the five treatments in the two plant associations: Tomato monoculture (dark grey) and Leek-Tomato association (light grey). Control: without soil organisms, RKN: with *Meloidogyne incognita*, RKN/AMF: with *M. incognita* and arbuscular mycorrhizal fungi (AMF) *Rhizophagus irregularis*, RKN/EW: with *M. incognita*, and earthworms (EW) *Eisenia andrei*, RKN/EW/AMF: *M. incognita, E. andrei* and *R. irregularis*. Different letters indicate significant differences between treatments within each plant association ($P < 0.05$).

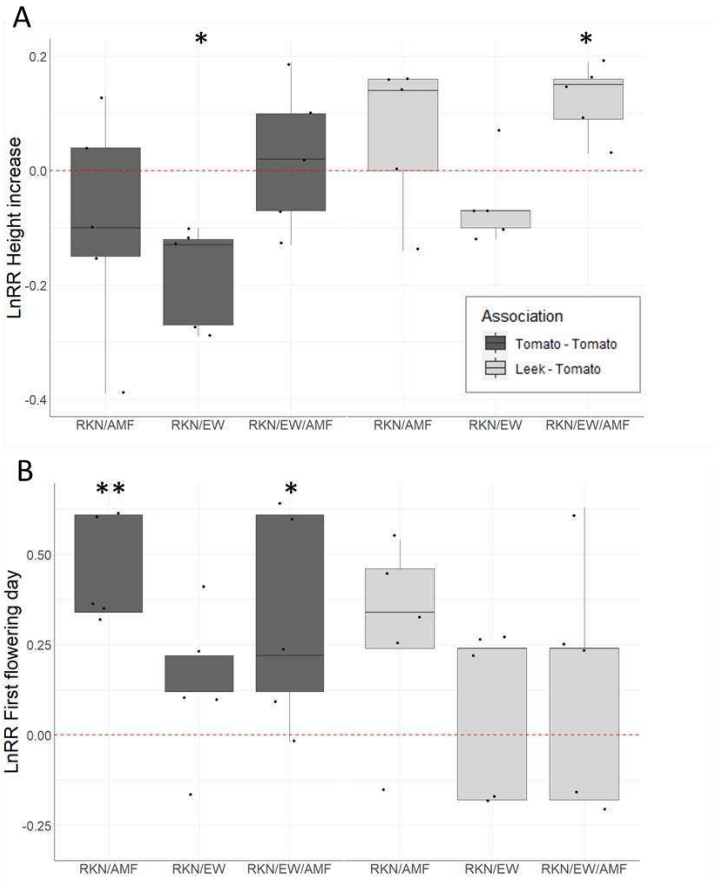

Fig. 2. Effect intensity of adding earthworms (EW) and arbuscular mycorrhizal fungi (AMF) alone or in interaction to RKN on A. the tomato height increase and B. the first flowering day, within the two plant associations: Tomato monoculture and Leek-Tomato association. The effect intensity is indicated by the Log Response-Ratio (LnRR = Ln(Treatment/RKN). The dotted line represents a null effect of each treatment (LnRR = 0). Negative values indicate a negative effect; positive values indicate a positive effect. The deviation from 0 was tested with a one-sample t-test and significant effects were indicated with asterisks (* $P < 0.05$, ** $P < 0.01$).

3.1.1. Flowering

The presence of RKN only did not impact the flowering (LnRR #1, data not shown) in TT or in LT. However, adding AMF to RKN delayed the flowering, (t-test, df = 4, t = 6.85, $P = 0.002$), in the tomato monoculture only (LnRR #2, Fig. 2B). Within both TT and LT, adding AMF and earthworms, alone or in interaction (RKN/EW/AMF) had no effect on the number of flowers (ESM 1 Table 2).

The comparisons between TT and LT showed a overall higher number and an earlier appearance of flowers in LT (MANOVA, df = 1, F = 24.40, $P < 0.001$ and F = 9.90, $P = 0.03$ respectively; ESM 1 Table S1). Despite a general trend in all treatments, the positive effect of LT association on the number of flowers was significant in the RKN/EW/AMF combination only (LnRR #2; t-test, df = 4, t = 5.5, $P = 0.007$; Fig. 3D, ESM 1 Table S3), while its effect on the early flowering was significant in the control only (t-test, df = 4, t = -4.7, $P = 0.009$; Fig. 3E).

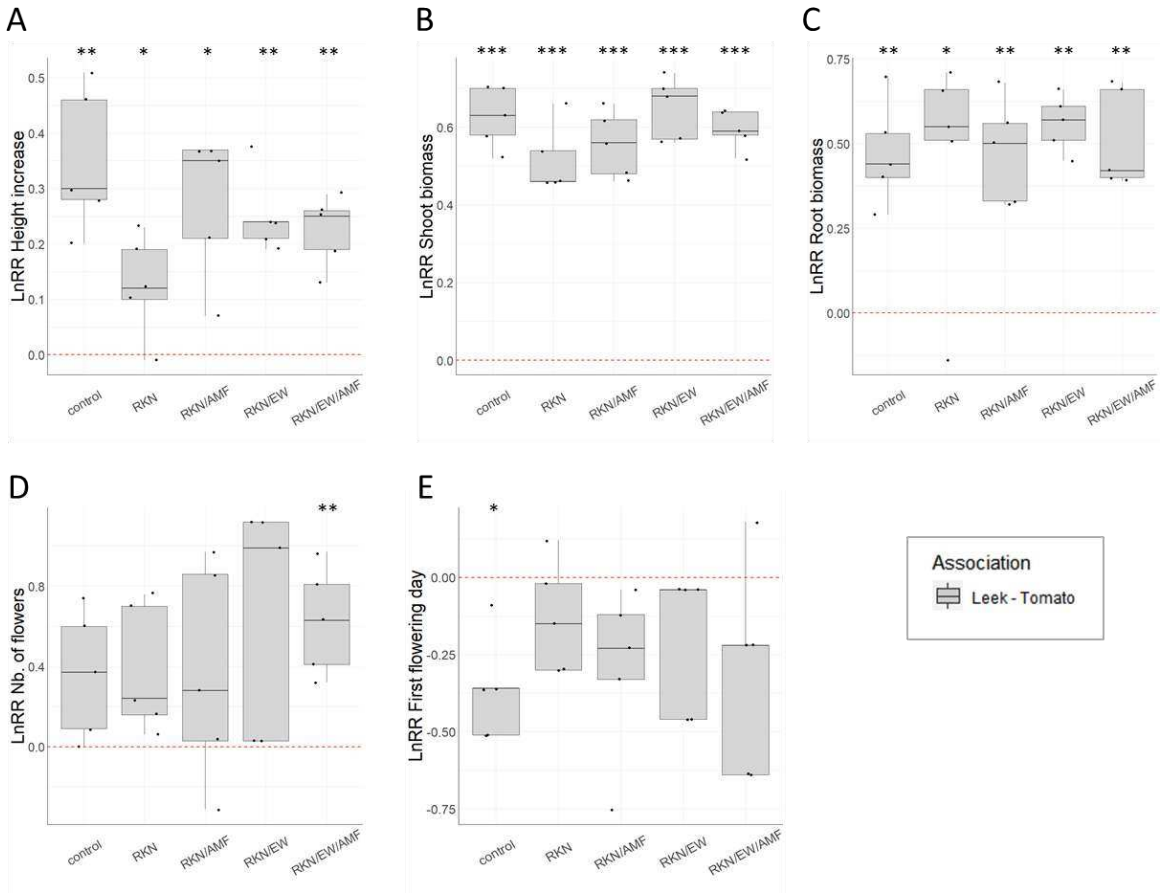

Fig. 3. Effect intensity of using the leek-tomato association on the tomato A. height increase; B. shoot biomass; C. root biomass; D. number of flowers; E. first flowering day, compared to the tomato monoculture, in absence (control) or in presence of RKN, and with earthworms (EW) or arbuscular mycorrhizal fungi (AMF) alone or in interaction, represented by the Log Response-Ratio (LnRR = Ln(LT/TT). The dotted line represents a null effect of each treatment (LnRR = 0). Negative values indicate a negative effect; positive values indicate a positive effect. The deviation from 0 was tested with a one-sample t-test and significant effects were indicated with asterisks (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$).

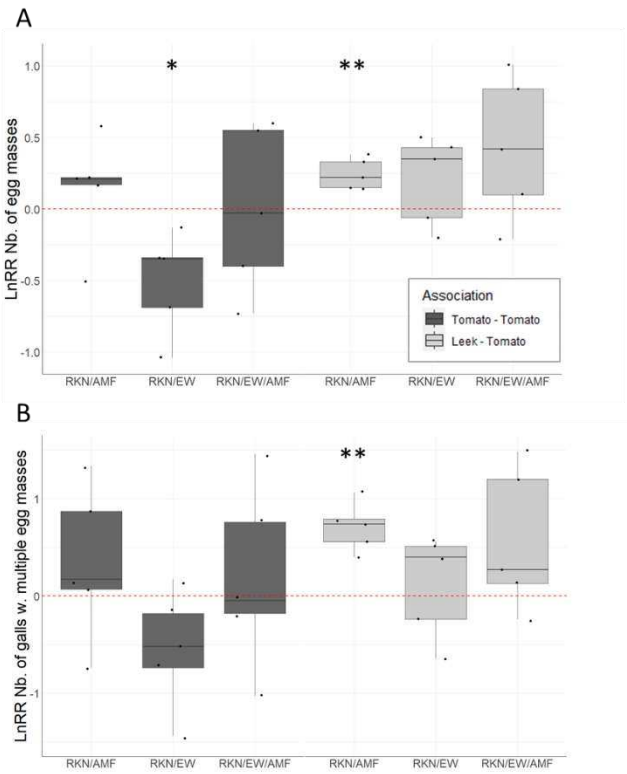

Fig. 4 Effect intensity of adding earthworms (EW) and arbuscular mycorrhizal fungi (AMF) alone or in interaction to root-knot nematodes (RKN) on A. the number of egg masses on tomato roots and B. the number of galls with multiple egg masses, within two plant associations: Tomato monoculture and Leek-Tomato association, represented by the Log Response-Ratio (LnRR = Ln(Treatment/RKN). The dotted line represents a null effect of each treatment (LnRR = 0). Negative values indicate a negative effect; positive values indicate a positive effect. The deviation from 0 was tested with a one-sample t-test and significant effects were indicated with asterisks (* $P < 0.05$, ** $P < 0.01$).

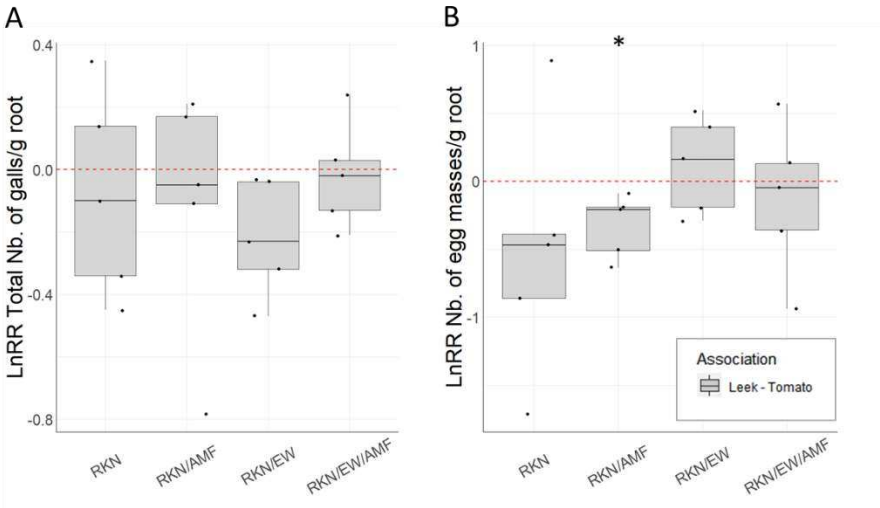

Fig. 5. Effect intensity of using the leek-tomato association on A. the total number of galls per gram of dry tomato root and B. the number of egg masses per gram of dry tomato root, compared to the tomato monoculture, in presence of nematodes alone (RKN), or with earthworms (EW) or arbuscular mycorrhizal fungi (AMF) alone or in interaction, represented by the Log Response-Ratio (LnRR = Ln(LT/TT)) for each treatment. The dotted line represents a null effect of each treatment (LnRR = 0). Negative values mean negative effect; positive values mean positive effect. The deviation from 0 was tested with one-sample t-test and significant effects were indicated with asterisks (* $P < 0.05$).

3.2. Root-knot nematode infestation

Adding other soil organisms to RKN was first considered. Within the tomato monoculture, adding earthworms to RKN decreased the total number of egg masses in tomato roots compared to treatments with RKN only (LnrRR #2; t-test, df = 4, t = -3.16, *P* = 0.03; Fig 4A, ESM 2 Table S4). However, no difference was recorded for the number of egg masses per gram of dry root biomass. Adding earthworms and AMF alone or in combination had no effect on any of the other parameters of RKN infestation in the tomato monoculture (ESM 2 Table S4). In LT, only the addition of AMF alone to RKN increased the number of egg masses (t-test, df = 4, t = 5.2, *P* = 0.007; Fig. 4A) and the number of galls with multiple egg masses (t-test, df = 4, t = 6.36, *P* = 0.003; Fig. 4B), compared to treatments with RKN only. No effect was observed on any of the other variables regarding the RKN infestation per gram of dry root biomass in the leek-tomato association (ESM 2 Table S4).

The presence of leeks with RKN strongly increased the number of galls on tomato roots compared to the same treatment in the tomato monoculture (t-test, df = 4, t = 4.8, *P* = 0.009) but it did not impact the total number of egg masses or the number of galls with multiple egg masses (ESM 2 Table S5). No effect was observed on the total number of galls per gram of dry root biomass (Fig. 5), despite a negative trend in the total number of egg masses per gram of dry root (Fig. 5B). In presence of AMF alone with RKN, the presence of leeks did not influence the total number of galls but significantly increased the total number of egg masses (t-test, df = 4, t = 3.6, *P* = 0.022) and the number of galls with multiple egg masses (t-test, df = 4, t = 3.19, *P* = 0.017; ESM 2 Table S5). On the other hand, relative to the dry root biomass, only having AMF alone in the presence of leeks significantly decreased the number of egg masses (t-test, df = 4, t = -3.1, *P* = 0.035; Fig. 5B). In presence of earthworms alone, the association with leeks strongly increased the total number of galls (t-test, df = 4, t = 6.2, *P* = 0.003), the number of egg masses (t-test, df = 4, t = 5.6, *P* = 0.005) and the number of galls with multiple egg masses, to a lesser extent (t-test, df = 4, t = 3.5, *P* = 0.025; ESM 2 Table S5). However, per gram of dry root, the total number of galls, the number of egg masses and the number of galls with multiple egg masses were not affected (Fig. 5). Finally, the association with leeks strongly increased the total number of galls when in presence of both earthworms and AMF (t-test, df = 4, t = 5.6, *P* = 0.005) but no effect was found on other variables and per gram of dry root (ESM 2 Table S5). The comparisons between TT and LT with all soil organisms combined

showed an overall significantly higher total number of galls, total number of egg masses and number of galls with multiple egg masses with leeks (MANOVA, df = 1, $P < 0.001$, $P < 0.01$ and $P = 0.03$ respectively). However, differences between TT and LT for these variables were cancelled out when data were normalised with the dry root biomass (MANOVA, $P > 0.05$; ESM 2 Table S6).

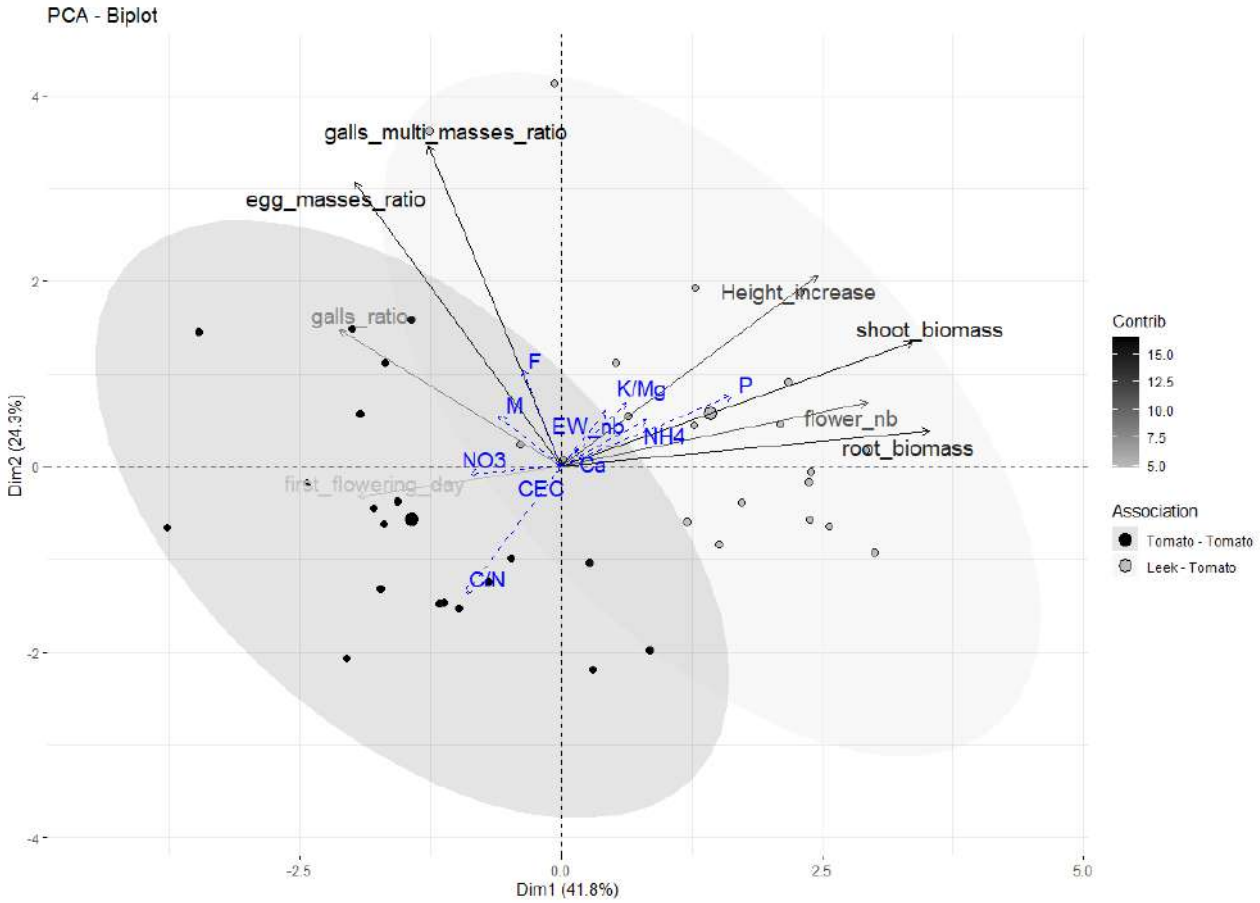

Fig. 6. Correlation circle of the Principal Component Analysis (PCA) on 50 individuals and eight variables on tomato plant performances and nematode infestation. Grey levels indicate the level of contribution of each variable to the circle of correlation. Ten variables (physicochemical, AMF colonization rate and number of earthworms remaining in pots) were added on the circle of correlation as illustrative variables (blue). Ellipses indicate the centre of gravity for each association (Dark grey: Tomato monoculture; light grey: Leek-Tomato).

3.3. Soil organisms, associations and soil properties

The within-between analyses performed on the Principal Component Analysis (PCA) based on plant responses and the RKN infestation showed that the impact of the association was greater than that of soil organisms (Fig. 6, ESM 3). 30.15 % of the total variation was explained by differences between TT and LT association, while a weak part of the total variation (9.56 %) was explained by differences between soil organisms (ESM 3 Fig. S2; Table S7). Differences between soils organisms explained 69.48 % of the variation within TT and LT association, although they were not clearly segregated (ESM 3 Fig. S2). The root biomass (r = 0.89), the shoot biomass (r = 0.85), the number of flowers (r = 0.74) and height increase (r = 0.62) were strongly and positively correlated to the first axis (41.8 % of the total variance), and the number of galls per gram of tomato root (r = -0.53), the number of egg masses per gram of tomato root (r = -0.49) and to the first flowering day (r = -0.49) were negatively correlated (ESM 3 Table S8). This first axis clearly segregated leek-tomato-associated samples from the monoculture samples and was associated with a gradient of plant growth and development. The number of galls with multiple egg masses per gram of tomato root (r = 0.87) and the number of egg masses per gram of root (r = 0.77) were positively correlated to the second axis (24.3 % of the total variance) (ESM3 Table S8). Although they did not contribute to the PCA axes, soil properties differed with treatments (ESM 3 Table S9). The soil content in PO_4^{3-} was positively correlated with the axis 1, and the C:N ratio was negatively correlated with the axis 2. The earthworm number and AMF root colonization were not correlated with any axes, but AMF root colonization was positively correlated to RKN infestation variables, while earthworms were positively correlated to plant variables.

4. Discussion

In this greenhouse experiment, the leek-tomato association was studied in mesocosms to investigate the role of leek, AMF and epigeic earthworms on the biocontrol of *M. incognita* root-knot nematodes and their impact on tomato plant growth and development, in comparison to a tomato monoculture. We found that the effect of the association was stronger on plants than the RKN infestation and that, although patterns were mainly explained by the leek-tomato association, soil organisms explained some variations within the tomato monoculture and the leek-tomato association.

4.1. Plant growth and development

Higher tomato plant height, shoot and root biomasses were found in the leek-tomato association compared to the tomato monoculture, as well as more flowers and an earlier flowering. We argue that both plant-plant competition and facilitation were involved here. Plant height and root mass are known to be reduced with as little as two plants per pot and as early as 8 days post-transplant (Stamp et al. 2004), and plant density impacts plant flowering (Papadopoulos and Pararajasingham 1997). In the monoculture, the shade induced by the larger canopy of tomato plants could have increased the competition for light, and thereby reduced the aboveground biomass, increased the flower abortion, reduced the number of flowers or delayed the flower initiation (Papadopoulos and Pararajasingham, 1997). However, the authors also reported that plant height can be also be increased at high density due to photomorphogenic mechanisms that increase light interception by leaves. Hence, although greenhouse conditions were controlled and pots were regularly spatially reallocated, a direct effect of competition for light within pots cannot be excluded, particularly on biomasses and plant development. In maize, Hammer et al. (2009) reported no direct effect of the increased canopy architecture through increased density on crop biomass, but suggested an indirect effect through the allocation of assimilates and water and nutrient uptakes. Root biomass was reduced and height was favored over root biomass over a 25-day post-transplant period in a context of tomato-tomato competition (Stamp et al. 2004). Here, root biomass was lower in the monoculture compared to the leek-tomato association, 100 days post-tranplant. This lower root biomass was likely partially caused by the development of two root systems of tomato for an extended period of time in a restricted substrate volume (3.5 L). The length of the experiment was indeed constrained by the required colonization of mycorrhizal fungi and the additional completion of the nematode reproduction cycle. Two or more plants compete for space and nutrients and may develop costly extra roots to capture remaining available resources, thereby increasing the rooting volume and modifying the root architecture, and affecting shoot growth and the plant development. The increased rooting and associated cost in presence of competitors is refered to as the ‘tragedy of the commons’ (Gersani et al. 2001). It has not been tested in tomatoes to our knowledge, and it was also not the objective of our study. However, as suggested by Semchenko et al. (2007) “exploring larger substrate volumes to acquire the same amount of resources in the ‘root competition’

treatment as in the 'no root competition' treatment may make growth in larger volumes less efficient", and different rooting strategies may have impacted below and aboveground biomasses. The authors found that a competition effect may be confounded with a self-inhibition effect on constrained space for oat plants, and that plants inefficiently placed roots in large substrate volumes shared with roots of competitors (Semchenko et al., 2007). Contrary to previous experiments that compared tomato plant densities of 2 vs. 1, our experiment compared two types of potential competitors: tomato vs. leek. Experiments on leek competition in intercropping are scarce. Yet, they show that shallow-rooted leek is a poor competitor compared to large-rooted celery, and that it tends to have a low N uptake, partly due to its late N demand (Baumann et al. 2001). Although its growth was facilitated by deeper-rooted dyer's woad in another experiment (Xie and Kristensen 2017), leek in our pot experiment was probably dominated by tomato, which supports a larger effect of the leek-tomato treatment on root biomass compared to the monoculture than that on the height increase. Thereby, similar soil contents in NO_3^- or NH_4^+ in controls of LT and TT associations would indicate that the tomato in presence of leeks took up as much as two tomato plants in the monoculture. The higher available phosphorus (P) content in the soil of the leek-tomato association would suggest that the two tomato plants took up more for phosphorus in the monoculture. No sign of P deficiency was observed at any time on leaves. Previous experiments showed that the use of *Allium sativum* residues increased the growth of lettuce and eggplant when intercropped (Han et al., 2013; Wang et al., 2015), and that the use of mulch of onion and garlic increased tomato plant growth, while the inoculation of dimethyl disulfide (DMDS) increased root biomass (unpublished data). Our experiment targeted the inoculation of soil organisms in a context of intercropping (or co-cultivation). Hence, no tomato was grown alone in pots. Comparing the effect of a single tomato and of leek-tomato intercropping on tomato growth and development and measuring root exudates would help disentangle mechanisms of plant-plant interaction.

In this context of plant-plant interaction, the height increase and shoot biomasses of tomato were lower in presence of RKN alone (RKN) after 7 weeks compared to the control treatment in the leek-tomato association only. It means that the potentially stimulating or biocontrol effect of leek was not sufficient to prevent the negative effect of RKN on tomato growth. This higher effect of nematodes can also be explain by patterns of infestation on tomato roots in

each treatment. The initial population density of *M. incognita* and the level of egg inoculum are important factors of damage to tomato plants (Chindo and Khan 1988; Refaei et al. 2007). Kayani et al. (2017) showed that cucumber growth was negatively correlated to all inoculum densities, 12 weeks after inoculation of J2 juveniles. As we used an equal density of eggs in the nematode inoculum in both TT and LT associations (5,000 eggs/pot) in our 7-week experiment, the density of RKN infecting each plant was divided in two in the monoculture due to the presence of two tomato plants. In the situation in which hatching was not inhibited, the same density of nematode juveniles targeted a single plant in the leek-tomato treatment. As a result, the infestation fo RKN impacted the nutrient acquisition by plants, as shown by soil available nutrients, and tomato growth and development.

When compared to the treatment with RKN alone, the presence of AMF alone with RKN had no effect on tomato growth in the monoculture and had a slight positive effect in the leek-tomato association, which was clearer in presence of earthworms (Fig. 2A). AMF are known to promote plant growth, particularly by improving the efficiency of N and P uptake (Plenchette et al. 1983; Candido et al. 2015; Bona et al. 2017; Ziane et al. 2017). According to the PCA (Fig. 6), no relation was found between the AMF colonization and the soil P availability, indicating that a higher colonization did not increase the P uptake. Facelli et al. (2010) showed that *R. irregularis* limited tomato growth and P uptake when it was inoculated alone, which was probably close to our conditions, since no other AMF was inoculated and the soil was autoclaved two months prior to the experiment to avoid nematode contaminations. On the other hand, the frequency of colonization was associated with the number of galls and, instead of reducing the nematode infestation, the root penetration of hyphae may have favored it in a context of tomato-tomato competition, thereby indirectly altering plant growth. The presence of AMF in the monoculture also induced a later flowering than with RKN alone or even than the control treatment, which is contrary to previous results that showed an early flowering in presence of AMF (Salvioli et al. 2012; González-González et al. 2020). In presence of leeks, the inoculation of AMF had a positive effect on plant height compared to RKN alone. Root colonization by AMF was not enhanced compared to that in the monoculture and it cannot explain the increased height. The mitigating effect of AMF in presence of RKN may be due to a modified nutrient uptake efficiency or the production of molecules that increased the plant tolerance to damages induced by RKN (Hol and Cook 2005), which were not tested here.

Finally, although earthworms are known to increase nutrient mineralization and plant growth (Scheu 2003; Xiao et al. 2018), their presence alone further reduced the plant height increase compared to RKN alone, particularly in the monoculture. They had no significant impact on shoot and biomasses. Our results are not consistent with Xiao et al. (2018), who showed a positive effect of earthworms alone on plant growth and resistance against herbivorous nematodes. This negative effect may be direct through the damage of roots caused by grazing or by the movement of earthworm through a denser root system. Root biomass was indeed slightly but unsignificantly reduced in the tomato monoculture but not in the leek-tomato association in RKN/EW treatments. The impact can also be indirect through modifications of soil properties. Lower NH_4^+ and higher NO_3^- contents were found in the soil of the monoculture in which earthworms were present alone with RKN. Nitrifying bacteria may also have been stimulated by the presence of earthworm and/or their higher mortality and could have competed with plant root for ammonium (Verhagen et al. 1994), although Borgognone et al. (2013) showed a detrimental effect of a high NH_4^+/NO_3^- ratio on tomato. Earthworms alone did not promote plant growth in presence of RKN but seemed to variably interact with AMF in favor of plant growth and development.

4.2. Root-knot nematode infestation

A overall higher total number of galls was found on tomato roots in presence of leeks, due to the more developed tomato root systems in the leek-tomato association. However, no difference on the total number of galls per gram of tomato root was observed between the leek-tomato association and the monoculture, implying that leeks did not reduce RKN infestation on tomato roots but did not increase it neither. The presence of leeks reduced the number of egg masses per gram of tomato root in treatments with RKN alone, and this effect was significant when AMF were present. Lower concentrations of allelochemicals produced by tomato in a context of higher plant competition may have caused reduced plant defenses and an increased infestation, compared to a leek-tomato system dominated by tomato (Stamp et al., 2004). Leeks are also known to contain and to release thiosulfinates (Freeman 1975; Wang et al. 2008b) that are rapidly degraded in the soil and are transformed into disulfides such as dimethyl disulfide (DMDS) or dipropyl disulfides (DPDS) (Auger et al. 1989; Dugravot et al. 2005; Casella et al. 2013; Arnault et al. 2013). DMDS and DPDS are more stable in the soil than thiosulfinates, and these three compounds have biocidal and particularly nematicidal

effects (Tada et al. 1988; Arnault et al. 2004; Zanón et al. 2014; Yan et al. 2019). Although DMDS was known to be a more effective/toxic pesticide than DPDS (Arnault et al. 2004; Reddy 2012), DPDS is more predominant in leek (Auger et al. 1989; Casella et al. 2013). Here, disulfides released by leeks into the soil were not sufficient to reduce the tomato root infestation by *M. incognita*, but may have reduced their establishment or induced an inhibition of its reproduction through an 'intoxication' at the larval stage or an inhibition of their reproductive cycle. With the exception of the study by Tada et al. (1988), studies are lacking on the potential effect of disulfides and particularly DPDS on RKN *M. incognita* and on their establishment in tomato roots.

The presence of AMF *R. irregularis* did not reduce the root infestation by *M. incognita*. This is not consistent with previous results (Talavera et al. 2001; Sharma and Sharma 2015). On the contrary, the presence of *R. irregularis* tended to increase the number of egg masses and the number of galls with multiple egg masses on tomato roots. This result was surprising compared to previous observations where AMF reduced RKN penetration by altering host root exudation and by inducing systemic defence as shown by Vos et al. (2012, 2013). In this experiment, the introduction of AMF in microcosms was achieved by inoculating a pure AMF spore solution (*in vitro* inoculum) on freshly sprouted tomato roots, while Vos et al. (2012, 2013) used an AMF infected soil (conventional inoculum). Also, Vos et al. (2012, 2013) used the AMF species *Funneliformis mosseae* (formerly *Glomus mosseae* BEG12) while we inoculated *R. irregularis*. Both AMF could have a specific mode of action, with *F. mosseae* being a better inoculum for biocontrol while *R. irregularis* would be a better inoculum to promote plant nutrition. The enhanced growth phenotype of AMF-treated tomato was possibly due to their better acclimation to RKN infestation, to which they would resist longer. This means that more *M. incognita* reproductive cycles can occur in mycorrhized hosts, whereas non-mycorrhized plants will not withstand the development of RKN, as roots and shoots grow poorly and plants rapidly die due to the infestation. Here, our experiments highlight the current challenge in developing efficient inoculum with appropriate selection of plant host/fungus combinations adapted to the environmental conditions and needs of the farmers (Rouphael et al. 2015).

The presence of earthworms had no effect on tomato root infestation by RKN, although a reduction of egg masses was observed in the monoculture. Previous studies showed a

nematicidal effect of the use of earthworms produce *in vitro* (Rostami et al. 2014). The earthworm density (c. 250 individuals.m^{-2} here) was probably too low to observe their direct impact in natural soil and, although epigeic earthworms were chosen because of their ubiquity in farming systems and their tolerance to higher temperatures (Lee 1985), stressful greenhouse conditions with a repeated peak of temperature (twice; up to 42°C), likely impacted earthworm behaviour and effects. Earthworms release olfactory compounds when they die, which could have impacted egg mass laying. Instead of epigeic species, anecic species, whose effect on soil properties is often larger than that of other ecological groups, or endogeic species that live in the rhizosphere should be considered in similar studies.

5. Conclusion

In this greenhouse experiment, we tested the impact of the leek-tomato association, of AMF and of an epigeic earthworm on tomato plant growth and development and on the control of RKN, in comparison to a tomato monoculture. The competition between the two tomato plants in the monoculture treatments undoubtedly influenced the patterns of reduced plant growth, early flowering and RKN infection. However, stimulating impacts of leek on plant growth and inhibitory effects on nematode reproductive cycle cannot be excluded. Analyses of tomato and leek root exudates in presence of a single plant and leek-tomato intercropping would help to disentangle those effects. Contrary to previous studies, the inoculation of AMF did not reduce the development of the RKN *M. incognita* but rather increased it, and the addition of epigeic earthworms tended to reduce RKN egg mass laying on roots, yet non-significantly. Their presence altered patterns of plant growth and development in presence of RKN, which suggests that plant-soil organisms interactions play an indirect role in the nematode-crop interaction.

Discussion générale et perspectives

1

L'objectif principal de ce travail de thèse était d'explorer la réponse d'organismes du sol en tant qu'indicateur de son fonctionnement, et d'une plante cible d'importance économique majeure à deux pratiques agroécologiques, l'association de cultures et la culture sur buttes, dans un contexte de micro-fermes maraichères. Les questions abordées dans ce manuscrit étaient les suivantes :

- *Les pratiques étudiées ont-elles un effet sur :*
    - *Les performances végétales de la tomate ? (Chapitre 1)*
    - *Les communautés de nématodes indicatrices de l'état de santé et du fonctionnement du sol ? (Chapitre 2)*
- *Le poireau, en association avec d'autres organismes du sol ou non, permet-il un contrôle des nématodes à galles sur les racines de tomates et influence-t-il le développement de la plante ? (Chapitre 3)*

Dans un premier temps, les résultats de chaque chapitre seront synthétisés et discutés séparément. Puis, dans une seconde partie, l'ensemble de ces résultats sera discuté dans une synthèse générale de ces différents travaux.

1

Synthèse des résultats

1. Effet des pratiques sur les performances de la tomate (Chapitre 1)

Dans ce chapitre, nous avons exploré les réponses des performances végétales de la tomate (développement et rendement) à deux pratiques agroécologiques. Deux associations de cultures (haricot-tomate et poireau-tomate) ont été étudiées et comparées à une monoculture de tomate, soit sur sol plat, soit sur buttes de culture permanentes.

Les résultats montrent des effets assez contrastés des associations de cultures en fonction du site et de l'année. Cependant, des tendances générales peuvent être identifiées et discutées concernant les effets de la mise en place de ces associations. L'association avec le haricot a tendance à avoir un effet négatif sur le développement et le rendement de la tomate lors de la première année de production, tandis que le développement des tomates semble être favorisé la seconde année. Nous suggérons ici qu'une compétition entre tomates et haricots a eu lieu la première année de culture, à l'origine du plus faible développement des plants de tomates observé. La capacité de rhizodéposition du haricot, c'est-à-dire sa capacité à secréter ou libérer des composés organiques dans le sol par détachement de cellules des racines, par exsudation racinaire, lysats cellulaires, mucilage ou décomposition de débris racinaires (Lynch and Whipps 1990), est connue pour augmenter avec la maturité de la plante (Khan et al. 2002; Mahieu et al. 2007; Wichern et al. 2008). On peut donc ici emmètre l'hypothèses que la quantité d'azote libérée dans le sol par le haricot était probablement trop faible en 2018 pour être bénéfique à la tomate, tandis qu'en 2019 les plants de tomates auraient pu bénéficier des apports du haricot de l'année précédente. Par ailleurs, les analyses des propriétés du sol confirment l'hypothèse d'une plus forte compétition entre tomates et haricots lors de la première année. Néanmoins, il est surprenant de ne pas observer de plus grandes quantités d'azote dans le sol en présence de haricot, ni au moment de la récolte, ni d'une année sur l'autre.

Concernant la culture en association avec le poireau, la croissance et le rendement de la tomate sur les deux sites ont tendance à être plus performants. En effet, mis à part la seconde année à Adriers, les plants de tomates associés aux poireaux tendent à être plus grands avec une biomasse plus élevée, et à produire plus de fruits par plant. Cependant, cette

augmentation de la production de tomate est corrélée à une plus grosse quantité de tomates vertes à la récolte finale, la quantité de tomates rouges par plant n'étant pas modifiée. Etant donné que le poireau est une plante peu compétitrice (Baumann et al. 2001), sa présence pourrait induire une plus faible compétition entre les pieds de tomate, dont la densité est deux fois moindre qu'en monoculture. Ces observations sont plutôt surprenantes car aucun effet positif du poireau sur la croissance des tomates n'a été rencontré dans la littérature. Enfin, bien que les mesures soient assez variables, une biomasse légèrement plus grande d'adventices est observée dans l'association poireau-tomate alors que l'inverse est observé dans l'association haricot-tomate.

La mise en place des buttes de culture à Pontenx-les-Forges avait pour objectif principal de compenser la texture sableuse du sol, initialement pauvre en matière organique. Nous avons donc ici confirmé une augmentation significative de la concentration en éléments minéraux dans les buttes de culture (P disponible, K^+, Mg^{2+}, Ca^+, Na^{2+}, pH, N_{total} et $C_{organique}$). Cependant, mise à part une taille moyenne de tomate plus élevée, une meilleure croissance ou un meilleur rendement des plants de tomate n'est pas enregistré dans les cultures en butte. Néanmoins, les cultures en buttes permettent de réduire significativement le développement des adventices par rapport à la culture sur plat, et ce quelle que soit l'association considérée. Bien que peu d'interactions soient trouvées entre l'association de culture et la culture sur buttes, des tendances se dégagent et mériteraient de plus amples investigations. En effet, la combinaison d'une culture en association avec le poireau et sur butte, semble favoriser d'avantage les performances de la tomate, tandis que, en accord avec de précédentes études (Jensen and Hauggaard-Nielsen 2005; Corre-Hellou et al. 2007), la culture en association avec le haricot semble davantage favoriser les performances de la tomate en milieu pauvre, c'est-à-dire ici sur sol plat.

A travers cette étude, nous mettons en avant certains effets bénéfiques de la culture du haricot et du poireau sur les performances de la tomate, lorsqu'ils sont associés à cette dernière. En même temps, nous montrons que la culture sur buttes permet un enrichissement en éléments minéraux du sol, bien que les performances végétales des tomates ne soient pas améliorées par cet enrichissement. Néanmoins, deux années d'expérimentation ne suffisent pas pour conclure quant aux effets respectifs de ces pratiques mais apportent des éléments de réflexion sur les avantages de leur adoption. Multiplier les observations à plus long terme

et sur d'autres exploitations permettrait de valider les tendances observées ici, et d'affiner la compréhension des mécanismes en jeu. A terme, les résultats obtenus, s'ils se confirment, permettraient d'apporter des éléments d'aide à la décision sur l'adoption ces pratiques par les agriculteurs, ainsi que sur leur mise en place.

2. Les nématodes libres du sol indicateurs d'état de santé de de fonctionnement du sol (Chapitre 2)

Au cours de ce chapitre, nous nous sommes intéressés à la réponse des communautés de nématodes, à l'association de culture et la culture sur buttes, en tant que bioindicateurs du fonctionnement du sol.

Bien que différentes communautés de nématodes soient observées sur chaque site d'étude, elles sont majoritairement composées d'espèces bactérivores. Par ailleurs, les indices des voies de décomposition associés à ces communautés indiquaient une décomposition de la matière organique assurée majoritairement par voie bactérienne plutôt que fongique. De plus, les faibles indices de maturité des chaines trophiques observés dans chaque site témoignent d'un sol perturbé, caractéristique des zones agricoles. Néanmoins, les communautés de nématodes du sol ne répondent pas de manière similaire aux associations de culture dans les deux sites. À Adriers, la culture en association n'a quasiment pas d'effet sur les communautés de nématodes identifiées, tandis que celles-ci sont plus impactées à Pontenx-les-Forges, notamment dans l'association haricot-tomate. Cette différence entre sites est probablement liée à l'historique différent d'utilisation du sol entre chaque site. En effet, les serres à Adriers sont utilisées en agriculture biologique depuis une dizaine d'années, tandis qu'a Pontenx-les-Forges l'activité de maraichage a commencé en 2018, après la conversion d'une friche d'acacia en parcelle cultivable. La plus longue activité agricole à Adriers aurait probablement induit une composition des communautés de nématodes plus stable qu'à Pontenx-les-Forges, c'est-à-dire ici moins sensible aux perturbations induites par la mise en place d'associations de cultures. En effet, une plus grande abondance de nématodes provenant de famille de nématodes sensibles aux perturbations est observé à Pontenx-les-Forges.

Une augmentation de la proportion de nématodes phytoparasites est aussi observée en association de culture avec le haricot à Pontenx-les-Forges, ce qui témoigne ici d'une

augmentation de la fertilité de sol (Bongers et al. 1997). Par ailleurs, cette réponse est plus importante en culture sur sol plat, dans des conditions pauvres en nutriments. Dans les deux sites étudiés, les haricots ont tendance à avoir un effet plus marqué sur les communautés de nématodes que les poireaux. Cette observation est surprenante, car en raison de la présence de composés soufrés potentiellement biocides et nématicides dans les tissus du poireau(Arnault et al. 2005, 2013), on pouvait s'attendre à une modification plus importante de la structure des communautés de nématodes, avec notamment une abondance plus faible. La réponse des nématodes à la présence de poireaux a tout de même abouti à une forte réduction de l'empreinte métabolique associée aux nématodes impliqués dans la structure des chaines trophiques du sol à Pontenx-les-Forges en 2018, ce qui se traduit aussi par une plus faible abondance d'organismes ayant aussi une fonction de régulation dans les réseaux trophiques, tels que notamment les organismes prédateurs (Ferris 2010b).

Enfin, la culture en buttes a un effet plus fort et plus systématique que la culture en association sur le fonctionnement du sol. D'une part, une plus forte abondance de nématodes est observée dans les buttes de culture, ce qui témoigne de conditions plus favorables à leur développement. D'autre part, les communautés de nématodes dans les buttes indiquent aussi un enrichissement du sol, et des réseaux trophiques plus perturbés, sûrement liés à la mise en place récente des buttes de culture (2018).

Ainsi, l'analyse des communautés de nématodes du sol nous permet de mettre en évidence une augmentation de la fertilité du sol induite par la culture en association avec le haricot, et plus particulièrement dans un sol moins riche en nutriments comme la culture su sol plat à Pontenx-les-Forges, tandis que le poireau semble n'avoir que peu d'effet. Enfin, nous observons une modification des communautés de nématodes en réponse à un enrichissement du sol induit par la culture sur buttes.

3. Le poireau potentiel agent de contrôle des nématodes à galles ? (Chapitre 3)

Dans ce chapitre, nous avons évalué au cours d'une expérience en système simplifié, la capacité de contrôle du poireau, sur un des principaux ravageurs dans la culture de tomates. L'effet biocontrôle du poireau contre les nématodes à galles de l'espèce *Meloidogyne incognita* a été évalué seul et en interaction avec le champignon mycorhizien *Rhizophagus*

irregularis et le vers de terre *Eisenia andrei* qui ont également montré des propriétés de contrôle biologique envers ce nématode.

Premièrement, une meilleure croissance (accroissement de taille et de biomasse) est observée chez les plants de tomates cultivés en association avec le poireau. Les performances plus réduites des tomates en monoculture sont probablement dues à une compétition plus importante. Cependant, il est probable que d'autres facteurs interviennent dans cette observation. En effet, une compétition entre tomates serait caractérisée par un accroissement du développement racinaire pour compenser le faible niveau de ressources, en permettant une meilleure exploration et acquisition de nutriments dans les microporosités du sol. Or les racines de tomates en monoculture ont une biomasse inférieure à celle des plants associés au poireau. Par ailleurs, les analyses de sol ne révèlent pas de plus faibles quantités de nutriments en monoculture, ce à quoi l'on pourrait s'attendre en cas de compétition plus intense pour l'acquisition des nutriments. Nous émettons ici l'hypothèse que le poireau induit une facilitation du développement de la tomate en raison des composés soufrés (tels que le DPDS et le DMDS) qu'il peut libérer, et dont des effets positifs sur la croissance des plantes ont déjà pu être observés (Arnault et al. 2013).

Le biocontrôle potentiel du poireau sur les nématodes à galle ne permet pas ici de réduire la pénétration des racines de tomates par les nématodes, et donc réduire le nombre de galles observées. Cependant, un plus petit nombre de pontes est observé à la surface des galles sur les systèmes racinaires des tomates. Cette observation nous ont ici permis d'émettre l'hypothèse que le poireau aurait effectivement un effet de control sur les nématodes à galles *M. incognita*, an agissant soit sur la survie de nématodes dans les racines de tomate, soit sur sa reproduction. De plus amples investigations permettraient de tester cette hypothèse. Néanmoins, contrairement à ce qui a pu être observé dans la littérature, le champignon mycorhizien *Rhizophagus irregularis* et le vers de terre *Eisenia andrei*, testés en interaction avec le poireau en culture associée, n'ont pas eu d'effets prononcés sur le contrôle des nématodes à galles.

1

Synthèse générale

Effet de l'historique des pratiques culturales

Au cours de ce travail de thèse, nous avons analysé les impacts écologiques de deux associations et de la culture sur buttes lors de leur mise en place en micro-fermes maraichères sur différentes composantes de l'écosystème. Dans un premier temps, nous avons observé que les deux sites d'étude ne répondaient pas toujours de manière similaire à la mise en place de ces pratiques. L'analyse des communautés de nématodes nous a ici permis de mettre en évidence l'importance de l'historique de culture sur la réponse de ces organismes aux nouvelles sources de perturbations, telles qu'ici la mise en place de cultures en association et sur buttes. Les zones agricoles sont caractérisées par des sols perturbés (Bongers 1990), notamment en conséquence de l'utilisation d'amendement ou bien du travail du sol, mais aussi dû aux successions végétales, généralement rapides et soutenues en milieu agricole. Les communautés d'organismes du sol, qui répondent temporellement aux perturbations, sont ainsi modifiées en fonction de l'intensité, de la fréquence, mais aussi de la durée de ces perturbations. Ainsi différents types d'assemblages d'organismes dans le sol vont d'une part induire un fonctionnement différent du sol, et d'autre, part vont répondre de manières différentes à une même perturbation tels qu'ici la mise en place de nouvelle pratique agricole (Kibblewhite et al. 2008). Malgré les différences de réponses observées entre les sites, l'objectif de ce travail de thèse ne visait pas à faire une comparaison des réponses entre sites mais à dégager des tendances générales de la mise en place de ces pratiques à la fois sur les plantes cultivées, notamment ici la tomate, ainsi que sur le sol, et son fonctionnement.

Bien que, comme nous venons de l'aborder, les effets de ces pratiques sont parfois contrastés, l'analyse des différentes composantes du système sol-plante-faune nous a permis d'avoir une compréhension plus globale des impacts écologiques de ces pratiques sur le système cultivé.

Impacts écologiques des pratiques agroécologiques

Association haricot-tomate

Grâce à l'expérimentation de terrain nous avons pu observer un effet positif de l'association haricot-tomate sur la fertilité du sol, notamment au cours de la deuxième année de culture. En effet, l'augmentation de la proportion de phytoparasites dans la communauté de nématodes est identifiée comme une réponse à une augmentation de la fertilité du sol pour les plantes (Bongers et al. 1997). Par ailleurs, en accord avec Jensen and Hauggaard_Nielson (2005), nos observations ont montré que l'effet du haricot était d'autant plus visible que le sol était plus riche en nutriments. Cette interprétation est vérifiée d'une part par une réponse plus importante des nématodes phytoparasites dans les cultures sur plat (sur sol sableux) que dans les buttes de cultures, mais aussi par l'analyses des performances végétales de la tomate qui avaient aussi tendance à être meilleur en culture sur sol plat.

Étonnamment, les analyses des propriétés physicochimiques ne nous ont pas permis d'observer une augmentation du taux d'azote dans le sol au cours des deux années d'expérimentation. Pourtant, les légumineuses (telles que le haricot) sont connues pour fixer l'azote atmosphérique dans leurs racines et peuvent enrichir le sol de composés azotés, *via* le phénomène de rhizodéposition, dans et ainsi induire une augmentation de la quantité d'azote (Graham 1981; Fustec et al. 2010). L'analyse des communautés de nématodes s'est donc ici révélée efficace pour mettre en évidence cet enrichissement par le haricot, également visible *in fine* sur les performances de la tomate, soulignant ainsi leur efficacité comme bioindicateurs du fonctionnement du sol (Bongers and Ferris 1999; Neher 2001).

Bien qu'un effet favorable du haricot ait été observé sur la fertilité du sol, son application semble être contrainte à un sol limité en nutriments (tels que le sol plat à Pontenx-les-Forges). En effet, sur un plus riche en nutriment comme par exemple à Adriers ou sur les buttes de culture à Pontenx-les forges la présence du haricot pourrait être préjudiciable pour la culture de la tomate en induisant une compétition pour les nutriments. Il serait néanmoins intéressant de tester le potentiel de fertilization du sol par le haricot sur les performances de la tomate lors de rotations de culture soit d'une année sur l'autre, soit au cours de la même année en utilisant des variétés d'hiver. Cependant, comme cet enrichissement est ici associé à une augmentation de la proportion de de nématodes phytoparasites, cet effet pourrait être

préjudiciable aux les plantes cultivées à long terme. En effet, en se nourrissant sur les plantes, les nématodes phytoparasites peuvent entrainer une diminution de leurs performances, ce qui pourrait ainsi annuler les potentiels effets bénéfiques de l'enrichissement du sol. Un suivi à plus long terme de ces communautés de nématodes et des performances végétales de la tomate permettrait une meilleure évaluation du potentiel de l'association avec le haricot. Enfin, l'utilisation d'autres bioindicateurs que les nématodes pourrait aussi apporter des informations utiles pour une meilleure compréhension des effets, que l'on observe, de l'enrichissement du sol par le haricot.

Association poireau-tomate

Relativement peu d'effets de l'association poireau-tomate ont été observés sur les organismes du sol. En effet, lors de l'expérimentation de terrain, les communautés de nématodes étaient relativement peu affectées par la présence des poireaux. Cependant, la culture en association avec le poireau est tout de même corrélée à une plus faible empreinte métabolique des chaines trophiques en 2018 sur le site de Pontenx-les-Forges. Cette mesure fait référence à une fonction de régulation dans les chaines trophiques par les nématodes prédateurs. Elle indique aussi une plus faible proportion d'organismes autres que nématodes ayant aussi une fonction de régulation dans les chaines trophiques du sol (Ferris 2010b). Néanmoins, la présence du poireau n'a pas d'impact sur les nématodes phytoparasites alors que des effets de régulation étaient attendus, compte tenu des propriétés nématicides des composés soufrés des *Allium* identifiées dans la littérature (Arnault et al. 2005). Lors de l'expérience en laboratoire la présence du poireau n'a pas eu d'effet sur l'infestation des racines de tomates par *M. incognita*, mais a cependant permit une réduction de sa capacité de reproduction. Plusieurs hypothèses explicatives sont envisagées mais n'ont pas été testées dans le cadre de ce travail de thèse : la présence du poireau pourrait affecter la survie des nématodes dans les racines de tomate *via* la sécrétion de composés soufrés auxquels les nématodes auraient été exposés lors de leur déplacement vers les racines. Alternativement, le poireau pourrait affecter les nématodes dans les racines de tomate, soit en inhibant la reproduction, soit en la retardant. Identifier et mesurer la présence des composés soufrés dans le sol permettrait ici de tester cette hypothèse. Cependant, cette analyse n'a pu être réalisée lors de ce travail de thèse. Néanmoins, l'ensemble de ces observations semblent remettre en question le potentiel rôle de régulation du poireau sur les organismes du sol.

Les résultats de nos expérimentations de terrain (Chapitre 1) et en laboratoire (Chapitre 3), nous ont permis d'observer de meilleures performances végétales de la tomate lorsque celles-ci étaient associées aux poireaux. Dans un premier temps, l'hypothèse d'une compétition plus intense entre les pieds de tomates en monoculture est fortement suspectée, et notamment lors de l'expérience en laboratoire où la taille des pots a pu constituer une contrainte forte pour le développement des plants (Poorter et al. 2012). Cependant, l'analyse des propriétés physicochimiques du sol et des biomasses racinaires ne montre pas de traces d'une compétition plus intense entre les tomates en monoculture dans les deux séries expérimentales (Stamp et al. 2004). Ces observations suggèrent une facilitation du développement de la tomate induite par la présence des poireaux. Deux principaux arguments appuient cette hypothèse.

Premièrement, certaines plantes comme le poireau ou l'oignon, sont qualifiées de mycorhizotrophes, en raison de leur haut potentiel de mycorhization (IJdo et al. 2011; Chave 2015). Ces plantes sont connues pour être « donneuses de mycorhizes » et ainsi favoriser la mycorhization des racines des plantes alentours, phénomène particulièrement avantageux pour des plantes à faible potentiel, comme les tomates (Schroeder and Janos 2004; Rodriguez-Heredia et al. 2020). La symbiose entre racines et champignons mycorhiziens (mycorhizes) est largement reconnue aujourd'hui pour ses capacités à favoriser la nutrition minérale et hydrique des végétaux, favorisant ainsi leur croissance (Mosse 1973; Artursson et al. 2006; Miransari 2010). Ainsi les meilleures performances de la tomate observées sur le terrain peuvent être induites par une mycorhization plus importante des plants de tomates associés aux poireaux. Nous avons d'ailleurs entrepris d'évaluer la mycorhization des racines de tomates lors de l'expérimentation de terrain en 2018. Cependant, en raison des différentes espèces de champignons indigènes qui colonisaient aussi les racines et malgré l'aide de mycologues, de nombreuses difficultés ont été rencontrées dans l'identification des champignons mycorhiziens ne nous permettant pas de tester cette hypothèse. Au vu des temps nécessaires à l'échantillonnage et à l'identification, et de la faible pertinence des résultats obtenus, cette mesure n'a pas été reconduite en 2019. De plus, cette hypothèse n'a pu être vérifiée lors de l'expérimentation en laboratoire car les spores de champignons mycorhiziens ont été inoculées dans le sol des jeunes plants de tomate. Les poireaux (non mycorhizés) ont été transplantés après que la colonisation des racines de tomates eut été

observée, et n'ont donc pas pu induire une meilleure colonisation des racines de tomates. Les racines des plants de tomates associées aux poireaux ne présentaient donc pas un taux supérieur de colonisation mycorhizienne malgré une plus forte croissance.

Dans un second temps, nous émettons l'hypothèses que l'effet de facilitation du poireau puisse être aussi induit par des molécules émises par le poireau. Arnault et al. (2013) ont notamment observé une croissance végétale stimulée par l'inoculation de DMDS issus d'oignons dans le sol. D'un autre côté, les auteurs observent qu'après l'incorporation de résidus d'*Allium* (poireau et oignon) dans le sol, du DPDS (un des composés prédominants dans le poireau) était fréquemment retrouvé jusqu'à un mois après l'incorporation (Auger et al. 1989; Casella et al. 2013). Cependant, à notre connaissance, aucun effet du DPDS sur la croissance des plantes n'a été rapporté dans la littérature.

Afin d'évaluer si le poireau a effectivement un effet facilitant sur le développement de la tomate, ou si les plus faibles performances des tomates en monoculture ont été induites par une compétition plus intense entre les plants de tomates, il serait intéressant de comparer les performances de plants de tomates isolés à celles de plants cultivés avec des poireaux. Des analyses de sol pourraient être réalisées sur le sol où le poireau était présent afin d'identifier d'éventuelles molécules soufrées (notamment DPDS et DMDS). Ces molécules pourraient être impliquées à la fois dans la facilitation du développement de la tomate et dans le contrôle des organismes du sol comme le nématode à galles *M. incognita*. Pour vérifier cette hypothèse, l'effet d'extraits de poireau pourraient être testé sur la survie et la reproduction *M. incognita* dans le cadre d'une application de biocontrôle, comme cela a pu être fait sur *P. ultimum*, un autre pathogène du sol (Arnault et al. 2013). Si ces tests révélaient un potentiel biocontrôle du poireau sur les nématodes à galles, son application sur le terrain pourrait être envisagé dans des zones agricoles où la présence de *M. incognita* a été identifiée, soit *via* des associations soit *via* des rotations de cultures avec le poireau.

Culture sur buttes

Les analyses des propriétés physicochimiques du sol, combinées à l'analyse des communautés de nématodes, nous ont permis de vérifier un enrichissement du sol en nutriments dans les buttes de culture. La proportion de nématodes « colonisateurs » dans les

communautés, qui sont connus pour répondre de manière rapide à un enrichissement du milieu, était en effet plus importante sur les buttes de culture. La forte proportion de ces nématodes bactérivores dans les buttes de culture, peut être interprétée comme la conséquence d'une plus grande abondance de microorganismes, probablement induite par une plus grande quantité de matière organique dans le sol. De plus, la forte abondance de nématodes permet de mettre en avant l'effet bénéfique des buttes de culture pour le soutien d'une activité biologique dans le sol. Les analyses préliminaires d'autres organismes indicateurs du fonctionnement du sol tels que les collemboles et les acariens nous ont permis d'observer des réponses variables à la culture sur buttes. En effet, une plus grande abondance d'acariens a été observée sur buttes en 2019, tandis que l'abondance de collemboles n'était pas significativement modifiée (Rapport de Master 2 Manon Gauclin 2020). La présence de ces deux groupes d'organismes, en permettant d'augmenter le fractionnement de la matière organique dans le sol, est généralement associée à la décomposition de la matière organique et à la stabilité du milieu. Ainsi un meilleur fractionnement de la matière organique permet d'augmenter la surface de contact entre cette dernière et les microorganismes, augmentant ainsi leurs ressources. Par ailleurs, l'aptitude du sol à soutenir la croissance des plantes dépend de facteurs environnementaux, physiques et chimiques liés à la nutrition des plantes et sont intimement associés à la matière organique du sol par l'activité des microorganismes (Henis 1986). Une analyse plus détaillée de la réponse des communautés de collemboles à la culture sur butte pourrait donc permettre une compréhension plus globale de l'effet de cette pratique sur le sol. Étant donné que les buttes de cultures étaient relativement récentes, un suivi à plus long terme pourrait nous permettre de mesurer si cet enrichissement du sol est persistant dans le temps, et entraîne de meilleures performances des plantes cultivées.

Bien qu'un enrichissement du sol ait été observé, il est surprenant d'observer que les buttes de cultures n'ont que peu d'effets sur les performances végétales de la tomate. Néanmoins, des tomates en moyenne plus grosses sont tout de même observées sur les buttes de cultures mais sans que cela n'affecte le rendement global de la plantation. De plus, comme dans les associations poireau-tomate et haricot-tomate, la maturation des tomates avait tendance à être plus tardive. Toutefois la culture en butte n'a été menée que sur un seul site expérimental (PF). Il est donc difficile de vérifier si ces observations sont bien dues à la culture sur buttes ou si elles sont induites par une différence de climat entre les sites. D'un autre côté,

les buttes de culture ont permis une réduction significative du développement des adventices en 2019 en agissant à la manière d'un paillis, faisant physiquement office de barrière pour l'accès à la lumière des banques de graines du sol en réduisant ainsi leur germination. Toutefois, les buttes de culture consistent en un apport de matière organique (foin, bois composté et fumier) au-dessus du sol sableux, et n'ont été mise en place que récemment (2018). On pourrait donc s'attendre à ce que la banque de graines d'adventices apportée par les buttes de culture soit plus pauvre que celle du sol plat, où un plus grand nombre de générations d'adventices se sont succédé. Bien que plusieurs années d'expérimentation soient encore nécessaires pour pouvoir confirmer ces observations, la réduction des adventices sur les buttes de culture pourrait s'avérer être un critère de décision pour les agriculteurs dans l'adoption de cette pratique.

Apports de la thèse et perspectives

Au cours de ce travail de thèse nous avons essayé de contribuer à un manque d'information identifié dans la littérature sur les impacts écologiques de la mise en place de pratiques agroécologiques en micro-fermes maraichères. Nous avons apporté ici des éléments de compréhension sur les conséquences écologiques de la mise en place de deux associations de cultures et buttes de cuture sur une partie de la composante biologique du sol, et tenté de déterminer les avantages et/ou inconvénients de ces pratiques pour la cuture de tomate. Nos observations soutiennent davantage l'importance de la prise en compte des organismes bioindicateurs dans l'étude du fonctionnement du sol. Nous avons ici mis en évidence un enrichissement du sol par la mise en place d'une association haricot-tomate, notamment visible à travers les communautés de nématodes. Cet enrichissement est potentiellement bénéfique à long terme à la culture de tomate. De plus, nous apportons ici des pistes de réflexion sur les avantages d'une association poireau-tomate. Un potentiel effet de facilitation du poireau sur la croissance et la production de la tomate, ainsi qu'un effet de biocontrôle du poireau sur un des ravageurs les plus important de la tomate, le nématode à galles *M.incognita,* ont pu être mis en évidence. D'autre part, nous avons ici contribué à fournir des informations, relativement peu présentes dans la littérature, quant au rôle des buttes de culture sur l'enrichissement du sol ainsi que sur la réponse des organismes du sol à cet enrichissement. Cependant ces expérimentations nécessitent encore d'être approfondies notamment sur le long terme. Par ailleurs, seules les performances végétales de la tomate ont

ici été prises en compte dans l'évaluation agronomique des pratiques étudiées. Or, l'évaluation des performances des plantes associées (ici le haricot et le poireau), en termes de rendement et notamment dans un contexte de culture sur buttes, pourrait permettre de déterminer plus précisément les avantages et les inconvénients de l'adoption de ces pratiques par les agriculteurs

Si un des objectifs de ce travail était de prendre en compte plusieurs composantes de l'agrosystème pour en étudier le fonctionnement, sa mise en place et la gestion du suivi ont nécessité une quantité de travail considérable. La préparation des sessions de terrain, d'échantillonnage, de conservation des échantillons, d'identification, de manipulation, etc… ont permis d'acquérir un jeu de données important, et les résultats présentés dans ce manuscrit ne représentent pas l'intégralité du travail qui a été effectué. De nombreuses données reste encore à exploiter telles que la diversité et l'abondance des arthropodes récoltés (notamment carabes, stage Master 1, Louise Maris), mais aussi l'analyse des communautés de microarthropodes (collemboles et acariens), ainsi que la détermination et l'analyse des trait fonctionnels associés à ces modèles. Par ailleurs, les analyses qualitatives et quantitatives des microorganismes du sol par génomique environnementale, en prévision, nous apporteront une meilleure compréhension des impacts des pratiques sur le fonctionnement biologique du sol, et devraient nous permettre de confirmer certaines interprétations présentées plus haut, à une échelle encore plus fine. D'autre part, comme cela a déjà été abordé au cours de cette synthèse générale, un suivi à plus long terme permettrait également une meilleure compréhension des mécanismes à l'origine des effets des pratiques étudiées sur le fonctionnement du sol en contexte de micro-fermes maraichères.

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Appendices

Introduction - Agroecological practices and biodiversity in vegetable farming

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#1 permacultur* OR agroecolog* OR agro-ecolog*
AND
#2 ecolog* OR biodiversity
AND
#3 intercrop* OR mix*crop* OR mix*-crop* OR mix*-culture* OR poly*crop* OR poly*-crop* OR poly*culture* OR poly*-culture* OR mulch* OR raised-bed$ OR raised-bed* OR permanent-bed$ OR permanent-bed* OR cover*-crop* OR rotat*-crop* OR rotat*-cultur* OR rotat*-vegetabl* OR rotat* W/1 crop* OR rotat* W/1 cultur* OR rotat* W/2 vegetabl* OR reduc*-till* OR conservat*-till* OR no-till* OR zero-till* OR minimum-till* OR organic-till* OR agroecolog*-infrastructur* OR agro-ecolog*-infrastructur*
AND
#4 vegetabl* OR vegetabl*-garden* OR market-garden* OR truck-garden*
AND
#5 microfarm* OR micro-farm* OR small* W/1 farm* OR small*farm* OR small-farm* OR small-hold* OR small*hold*

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ID	Authors	Year	Country of study	Farm type†	Field of study 1	Field of study 2	Ecosystem service 1	Ecosystem service 2	Practice 1‡	Practice 2‡	Practice 3‡	Practice 4‡
1	Adams et al.	2017	USA	Exp	Ecology	-	Biodiversity	-	Tillage	Rotation	-	-
2	Ali et al.	2019	China	Exp	Ecology	-	Biodiversity	-	CC (incorp)	Rotation	-	-
3	Altieri et al	2011	Brazil	Microfarm	Agronomy	-	Biocontrol	Production	CC (mulch)	-	-	-
4	Bal et al.	2014	USA	Exp	Ecology	-	Biocontrol	-	Tillage	CC (mulch)	Amendment	-
5	Bal et al.	2017	USA	Exp	Ecology	-	Biocontrol	-	Tillage	CC (mulch)	-	-
6	Baumann et al.	2001	Switzerland	Exp	Ecology	Agronomy	Biocontrol	-	Intercrop	-	-	-
7	Bietila et al.	2017	USA	Exp	Agronomy	Ecology	Biocontrol	-	CC (mulch)	-	-	-
8	Bourassa et al.	2008	Canada	Field	Ecology	-	Biodiversity	-	Amendment	Rotation	Tillage	CC (mulch)
9	Bowles et al.	2014	USA	Field	Ecology	-	Biofertilization	-	Amendment	CC (incorp)	-	-
10	Brainard et al.	2016	USA	Field	Ecology	Agronomy	Biocontrol	Production	Tillage	CC (mulch)	-	-
11	Brennan & Acosta-Martinez	2017	USA	Exp	Ecology	Pedology	Biofertilization	-	Amendment	CC (incorp)	-	-
12	Buckland et al.	2013	USA	Field	Ecology	Agronomy	Biocontrol	Production	Amendment	Rotation	-	-
13	Bulluck III et al.	2002	USA	Field	Ecology	Pedology	Biocontrol	Production	Amendment	CC (incorp)	-	-
14	Burgio et al.	2015	Italy	Exp	Ecology	-	Biodiversity	-	Rotation	Amendment	Tillage	-
15	Cai et al.	2007	China	Field	Ecology	-	Biodiversity	-	Intercrop	-	-	-
16	Campanelli et al.	2019	Italy	Exp	Agronomy	-	Biocontrol	-	CC (mulch)	Tillage	-	-
17	Canali et al.	2015	Italy	Exp	Agronomy	Ecology	Biocontrol	Production	Intercrop	CC (living)	-	-
18	Canali et al.	2013	Italy	Exp	Agronomy	Economy	Biocontrol	Biodiversity	CC (mulch)	CC (incorp)	Tillage	-
19	Ciaccia et al.	2019	Italy	Exp	Agronomy	Ecology	Production	Biofertilization	Amendment	CC (incorp)	CC (mulch)	Rotation
20	Ciaccia et al.	2016	Denmark, Italy	Exp	Agronomy	Ecology	Biocontrol	-	CC (living)	-	-	-
21	Ciaccia et al.	2020	Italy	Exp	Ecology	-	Biodiversity	Biocontrol	CC (mulch)	Tillage		
22	Claudius-Cole et al.	2016	Nigeria	Exp	Ecology	Agronomy	Biocontrol	-	CC (living)	Intercrop	-	-
23	Depalo et al.	2016	Denmark, Italy, Germany, Slovenia	Field	Ecology	-	Biocontrol	-	CC (living)	Intercrop	-	-
24	Djian-Caporalino et al.	2019	France	Multiple	Ecology	Sociology	Biocontrol	-	Rotation	Intercrop	CC (living)	CC (incorp)
25	Eyre et al.	2011	United Kingdom	Exp	Ecology	-	Biocontrol	Biodiversity	Rotation	Amendment	-	-
26	George et al.	2012	United Kingdom	Exp	Ecology	-	Biocontrol	-	Intercrop	-	-	-
27	George et al.	2019	United Kingdom	Microfarm	Agronomy		Biocontrol	-	Intercrop	-	-	-
28	Héraux et al.	2005	USA	Multiple	Ecology	Agronomy	Biocontrol	Production	CC (mulch)	Amendment	-	-
29	Hooks et al.	1998	Italy, Slovenia, Denmark, Germany	Exp	Ecology	Agronomy	Biocontrol	Production	CC (living)	-	-	-
30	Hummel et al.	2002a	USA	Exp	Ecology	-	Biocontrol	-	Tillage	CC (living)	Rotation	Intercrop
31	Hummel et al.	2002b	USA	Exp	Ecology	Agronomy	Biocontrol	Production	Tillage	Amendment	Rotation	CC (living)
32	Hurej & Twardowski	2006	Poland	Exp	Ecology	-	Biodiversity	-	Intercrop	-	-	-

Table S2. (*continued*)

33	Jokela & Nair	2016	USA	Exp	Agronomy	Ecology	Production	Biofertilization	Tillage	Amendment	CC (incorp)	CC (mulch)
34	Kokalis-Burelle et al	2017	USA	Exp	Ecology	-	Biodiversity	-	CC (incorp)	Raised Bed	Tillage	-
35	Lee et al.	2013	Republic of Korea	Field	Ecology	-	Biodiversity	-	Amendment	Tillage	-	-
36	Li et al.	2014	China	Exp	Ecology	Agronomy	Biocontrol	Biofertilization	Intercrop	Amendment	-	-
37	Lundquist et al.	1999	USA	Exp	Ecology	Pedology	Biodiversity	-	Amendment	-	-	-
38	Madzaric et al	2017	Italy	Exp	Ecology	-	Biodiversity	-	Amendment	CC (mulch)	CC (incorp)	Rotation
39	Madzaric et al.	2018	Italy	Field	Ecology	-	Biodiversity	-	Amendment	Rotation	-	-
40	Magagnoli et al.	2017a	Italy	Exp	Ecology	Agronomy	Biocontrol	-	CC (mulch)	CC (incorp)	-	-
41	Magagnoli et al.	2017b	Italy	Exp	Ecology	-	Biocontrol	-	CC (mulch)	CC (incorp)	-	-
42	Mahanta et al.	2017	India	Exp	Ecology	Agronomy	Biofertilization	Production	Amendment	-	-	-
43	Marinari et al.	2015	Italy	Exp	Ecology	Agronomy	Biofertilization	-	CC (mulch)	-	-	-
44	Maul et al.	2014	USA	Exp	Ecology	-	Biodiversity	-	CC (living)	Rotation	-	-
45	Mohler et al.	2018	USA	Exp	Ecology	-	Biocontrol	-	Rotation	CC (incorp)	Tillage	-
46	Munyuli et al.	2007	Uganda, Dem Rep Congo	Microfarm	Ecology	-	Biocontrol	-	Intercrop	-	-	-
47	Mutisaya	2016	Kenya	Exp	Ecology	Agronomy	Biocontrol	Production	Intercrop	-	-	-
48	Navarrete et al.	2016	France	Multiple	Ecology	Sociology	Biocontrol	-	CC (living)	Rotation	-	-
49	Navarro-Miro et al.	2019	Denmark, Italy, Spain, Estonia, Slovenia	Exp	Ecology	Agronomy	Biocontrol	Biodiversity	Tillage	CC (mulch)	CC (incorp)	-
50	Night et al.	2011	Rwanda	Field	Ecology	Agronomy	Biocontrol	-	Intercrop	-	-	-
51	Nyawade et al.	2019	Kenya	Microfarm	Pedology	Ecology	Biofertilization	OM degradation	Intercrop	Amendment	-	-
52	Parsons et al.	2007	Canada	Exp	Ecology	Agronomy	Biocontrol	Production	Intercrop	-	-	-
53	Pereira et al.	2010	Brazil	Exp	Ecology	-	Biocontrol	-	Tillage	CC (mulch)	-	-
54	Pitan & Filani	2014	Nigeria	Exp	Ecology	Agronomy	Biocontrol	Production	Intercrop	-	-	-
55	Pitan & Olantunde	2006	Nigeria	Exp	Ecology	Agronomy	Biocontrol	Production	Intercrop	-	-	-
56	Ponge et al.	2013	USA	Field	Ecology	Agronomy	Biocontrol	-	Amendment	Rotation	-	-
57	Powers et al.	1994	Honduras	Exp	Ecology	Agronomy	Biofertilization	Biocontrol	Intercrop	-	-	-
58	Pullaro et al.	2006	USA	Exp	Ecology	Agronomy	Biocontrol	Production	CC (mulch)	-	-	-
59	Quinn	2016	USA	Exp	Ecology	Agronomy	Biocontrol	-	Tillage	CC (mulch)	-	-
60	Ratnadass et al.	2014	Niger	Exp	Ecology	Agronomy	Biocontrol	Production	Intercrop	-	-	-
61	Razze et al.	2016	USA	Exp	Ecology	Agronomy	Biocontrol	Production	Intercrop	CC (living)	-	-
62	Sanchez-Moreno et al.	2006	USA	Exp	Ecology	-	Biodiversity	-	Tillage	Rotation	CC (mulch)	CC (incorp)
63	Schmidt et al.	2017	Germany, Sweden, Italy, Switzerland	Exp	Ecology	-	Biocontrol	-	Tillage	Rotation	Amendment	CC (incorp)
64	Silveira et al.	2009	Brazil	Field	Ecology	-	Biocontrol	-	Intercrop	-	-	-
65	Smukler et al.	2008	USA	Field	Agronomy	Ecology	Production	Biocontrol	Amendment	Tillage	Irrigation	-
66	Sujayanand	2015	India	Exp	Ecology	-	Biocontrol	-	Intercrop	-	-	-

Table S2. *(continued)*

67	Tamm et al.	2018	Estonia	Exp	Pedology	Agronomy	Biofertilization	-	CC (incorp)	CC (mulch)	-	-
68	Testani et al.	2019	Italy	Exp	Ecology	Agronomy	Biocontrol	Production	CC (mulch)	CC (incorp)	Tillage	-
69	Trdan et al.	2008	Slovenia	Exp	Agronomy	Ecology	Biocontrol	-	CC (mulch)	-	-	-
70	Trefas & Van Leteren	2008	The Netherlands Hungary	Multiple	Ecology	-	Biocontrol	-	Intercrop	CC (living)	-	-
71	Trinchera et al.	2016a	Italy	Exp	Ecology	Agronomy	Biofertilization	Production	CC (living)	Intercrop	-	-
72	Trinchera et al.	2016b	Italy	Exp	Ecology	Agronomy	Biofertilization	Production	CC (living)	Intercrop	-	-
73	Umeh & Onukwu	2006	Nigeria	Exp	Agronomy	Ecology	Biocontrol	-	Intercrop	-	-	-
74	Umeh et al.	2002	Nigeria	Field	Ecology	Sociology	Biocontrol	-	Intercrop	-	-	-
75	Wang et al.	2008	USA	Exp	Ecology	Agronomy	Biocontrol	Biofertilization	CC (living)	CC (mulch)	-	-

† Farm type: Experimental site (Exp), Large-size farm (Field), Microfarm, Large-size or micro-farm (Multiple).

‡ Practices that were studied or intervened in studies: Cover crops incorporated, living or as mulch (CC incorp, living, mulch), Organic amendment (Amendment), Intercropping (Intercrop), Raised bed, Rotation, Tillage.

Table S3. Ecosystem services and Practices as 'context' matrices in the co-inertia analysis on the 75 references. Blanks were replaced by '0'. ID: Identification number papers. Cover crop includes mulch, living crop and incorporated crops.

	Ecosystem Services				Practices					
ID	Biocontrol	Biodiversity	Biofertilization	Production	Organic Amendment	Cover crop	Intercropping	Raise Bed	Rotation	Tillage
1		1							1	1
2		1				1			1	
3	1			1		1				
4	1					1				1
5	1				1	1				1
6	1						1			
7	1					1				
8		1			1	1			1	1
9			1		1	1				
10	1			1		1				1
11			1		1	1				
12	1			1	1				1	
13	1			1	1	1				
14		1			1				1	1
15		1					1			
16	1					1				1
17	1			1		1	1			
18	1	1				1				1
19			1	1	1	1			1	
20	1					1				
21	1	1				1	1			
22	1					1	1			
23	1					1	1			
24	1					1	1		1	
25	1				1				1	
26	1						1			
27	1						1			
28	1			1	1				1	
29	1			1		1				
30	1					1	1		1	1
31	1			1	1	1			1	1
32		1					1			
33			1	1	1	1				1
34		1				1		1		1
35		1			1					1
36	1		1		1		1			
37		1			1					

Table S3. *(continued)*

| | | |

Table S4. Crops† as 'context' matrix in the co-inertia analysis on the 75 references. Blanks were replaced by '0'. ID: Identification number papers.

ID	Amaranth	Amaryllid	Api	Aster	Brassic	Convolvul	Cucurbit	Dioscor	Euphorb	Fab	Lami	Malv	Po	Solan
1										1			1	
2							1							
3										1				1
4			1											
5			1											1
6			1											
7										1				1
8										1			1	1
9														1
10										1				
11				**1**										
12		1											1	
13							1						1	1
14			1	**1**	1					1				1
15					1									
16							1							
17					1									
18							1							
19				**1**	1		1							
20		1			1								1	
21							1							
22								1						
23					1									
24	1		1				1						1	1
25					1								1	1
26					1									
27					1									1
28							1							1
29					1									
30							1						1	1
31							1						1	1
32										1			1	
33														1
34										1				1
35					1									
36										1				
37				**1**									1	1
38					1									
39					1		1							
40							1							
41							1							1

Table S4. (continued)

| | | |

Table S5. Organisms† as 'species' matrix in the co-inertia analysis on the 75 references. Blanks were replaced by '0'. ID: Identification number papers.

ID	Archaea	Bacteria	Fungi	Nematoda	Acari	Collembola	Lumbricidae	Isopoda	Araneae	Opiliones	Myriapoda	Coleo. Carabidae	Coleo. Coccinellidae	Coleo. Chrysomelidae	Coleo. Staphylinidae	Coleo. other	Di. Syrphidae	Di. other	Hemi. Aleyrodidae	Hemi. Anthocoridae	Hemi. Aphididae	Hemi. Cicadellidae	Hemi. other	Dermaptera	Neuroptera	Orthoptera	Hy. Formicidae	Hy. other	Lepido. Noctuidae	Lepido. other	Mantodea	Odonates	Psocoptera	Thysanoptera	Virus	Weeds
1					1	1			1			1						1					1					1									
2		1																																		
3																																				1
4				1																																1
5				1	1	1	1	1	1		1																									
6																																				1
7																																				1
8											1																									
9		1	1																																	
10									1				1							1	1	1					1						1			1
11		1	1																																	
12		1																															1	1		
13		1	1																																	
14						1		1	1	1	1	1			1																					
15					1	1			1								1					1	1		1		1		1				1			
16																																				1
17																																				1
18																																				1
19						1		1	1	1	1	1			1																					
20																																				1
21																																				1
22				1																																
23						1		1	1	1	1	1			1															1	1					
24				1																																
25																																				1
26																				1									1							
27														1																						
28																																				1
29									1			1				1		1	1	1													1			
30									1		1				1																					
31																				1		1							1				1			
32											1																									
33		1																																		1
34		1	1																																	
35		1	1																																	
36					1	1																			1						1				
37		1																																		
38						1		1	1	1	1	1			1																					
39						1		1	1	1	1	1			1																					
40																				1																
41												1																									
42		1	1						1										1				1					1		1						
43		1																																		
44	1	1	1																																	
45																																				1
46					1				1			1	1		1		1		1			1	1							1	1					1
47																		1																		
48				1																																
49																																				1
50					1									1				1																1		
51		1	1																																	
52																	1																			
53					1	1								1		1		1	1		1					1							1			
54		1										1	1				1																			
55													1										1													
56		1	1			1	1		1		1	1			1								1			1									
57				1																																
58																											1						1		1	
59						1			1			1	1		1	1			1	1		1			1		1								1	
60									1										1				1					1		1						
61									1			1	1			1		1	1	1		1		1										1		
62		1	1	1																																
63				1																																
64									1			1	1	1	1	1			1	1	1	1	1			1	1						1			
65									1				1	1		1	1	1	1	1	1	1		1				1					1		1	
66													1		1		1		1		1			1			1			1						
67		1																																		
68																																				1
69																																	1			
70											1																									
71			1																																	
72			1																																	
73									1									1		1								1								
74																		1		1					1			1								
75				1																																1

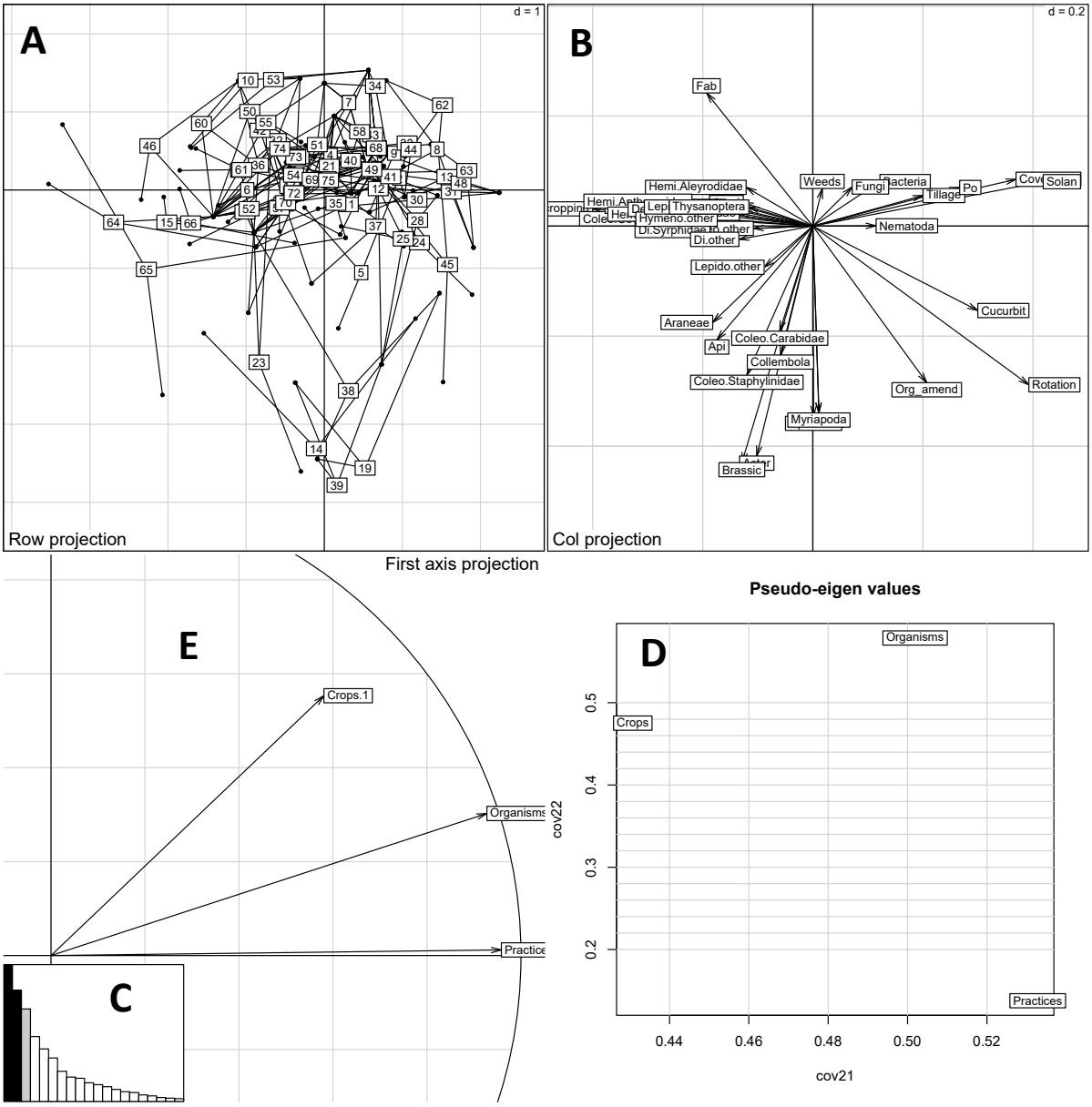

Fig. S1. Multiple co-inertia analyses (mCOA) performed on practices, crops and organisms extracted (presence/absence) from 73 papers. The overall ordination of each dataset is represented (dots) together with their ordination on the compromise plan (squares) (A), as well as the projection of all variables (B). Eigenvalues of all axes (C) are presented, as well as the projection of pseudo-eigenvalues of the three groups onto axes 1 and 2 (D) and their projection on the first axis (E).

Table S6. Pseudo-eigenvalues (cov2) of each dataset of multiple co-inertia analysis.

	Axis 1	Axis 2	Axis 3
Practices	0.53	0.14	0.12
Crops	0.43	0.48	0.81
Organisms	0.50	0.58	0.07

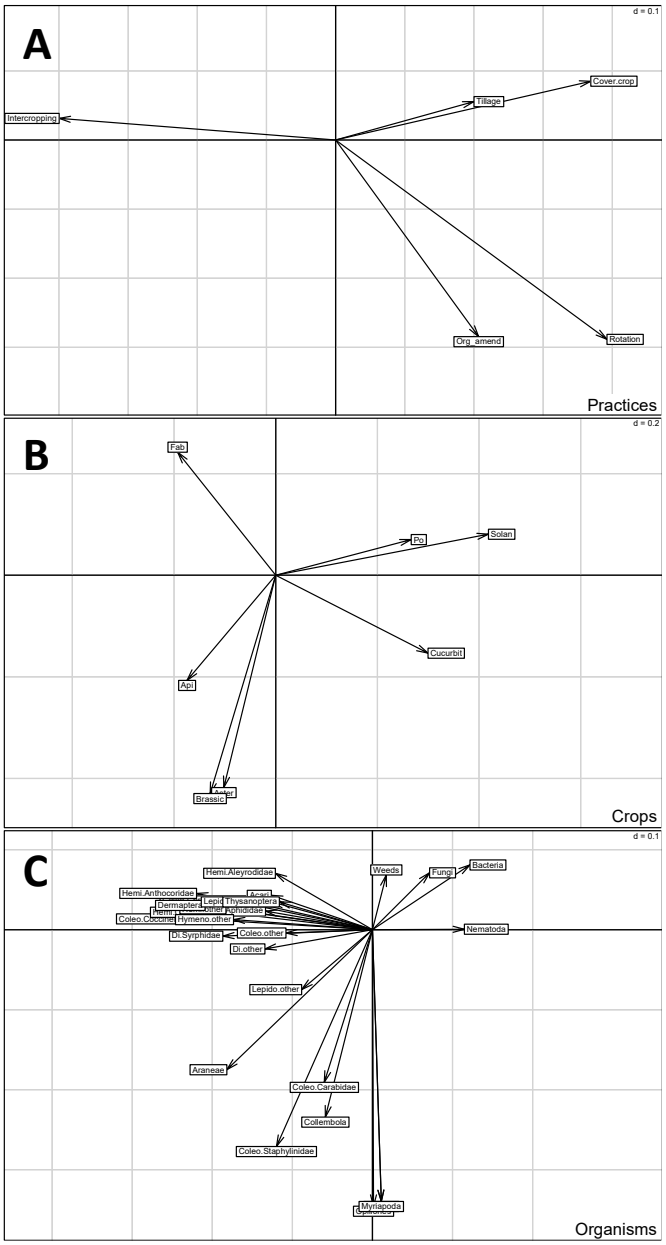

Fig. S2. Each set of variables is projected on the compromise plan of the multiple co-inertia analysis: (A) practices; (B) crops and (D) studied/sampled organisms.

Chapitre 1 - Impact of intercropping and raised beds on tomato yield and growth in vegetable farming

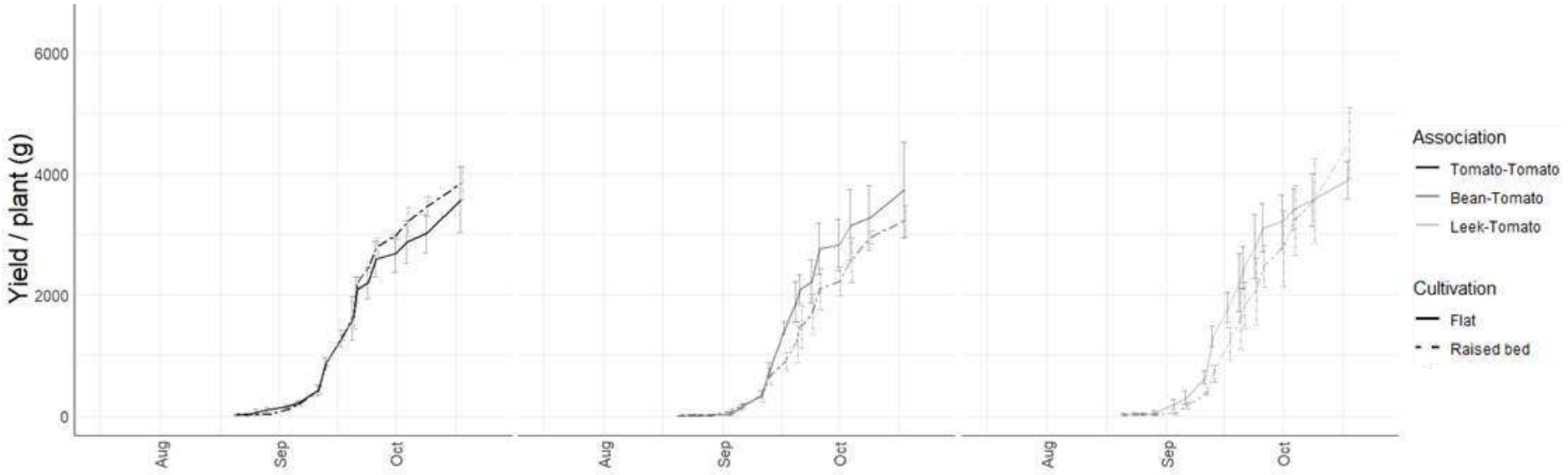

Fig. A.1: Cumulative yield of red tomatoes for each crop association and soil management during cultivation in 2018 At Pontenx-les-Forges at Pontenx-les-Forges (PF). Dark grey: Tomato monoculture (TT), medium grey: Bean-Tomato (BT) and light grey: Leek-Tomato (LT), full line: Flat cultivation (F) and hatched line: raised beds (Rb).

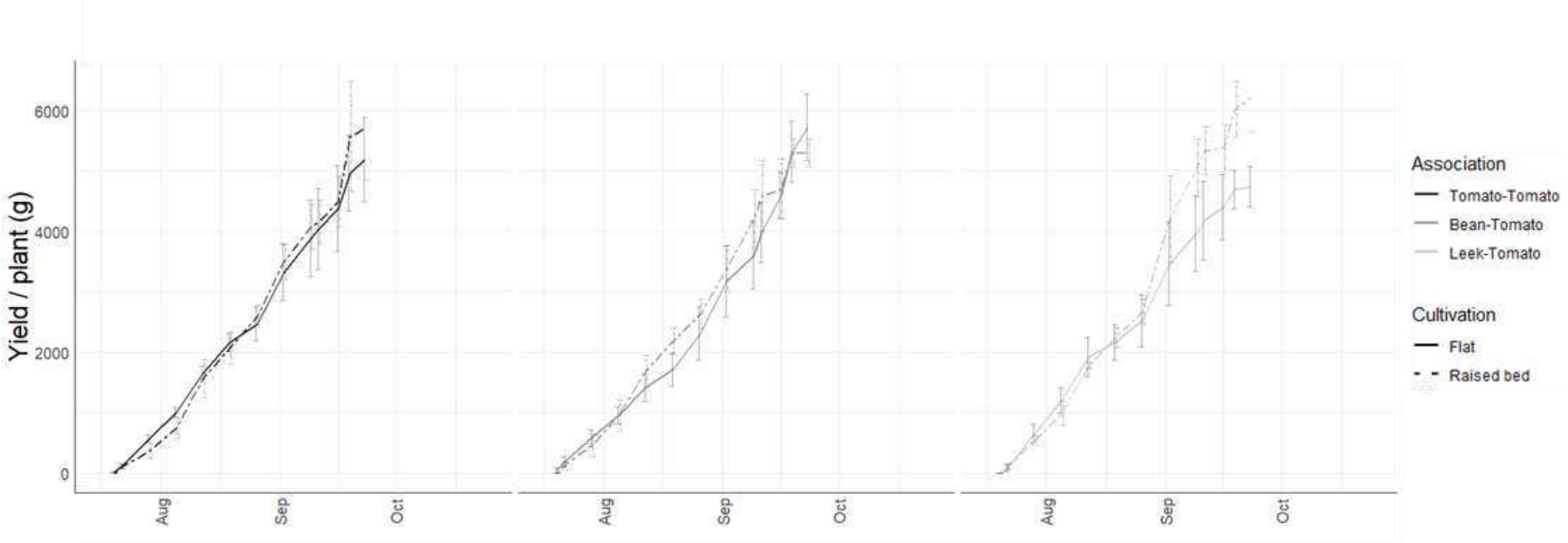

Fig. A.2: Cumulative yield of red tomatoes for each crop association and soil management during cultivation in 2019 At Pontenx-les-Forges at Pontenx-les-Forges (PF). Dark grey: Tomato monoculture (TT), medium grey: Bean-Tomato (BT) and light grey: Leek-Tomato (LT), full line: Flat cultivation (F) and hatched line: raised beds (Rb).

Table A.1: Soil nutrients dynamics (Mean % ± se) in the three crop associations (Tomato monoculture (TT), Bean-Tomato (BT) and Leek-Tomato (LT) associations) and the two soil managements (Flat ground (F) and Raised bed (Rb)), at ADriers (AD) and Pontenx-les-Forges (PF) for the two years of experimentation.

	AD					
	2018			**2019**		
	F			**F**		
	TT	**BT**	**LT**	**TT**	**BT**	**LT**
ΔTotal N (g/kg)	0.29 ± 0.08	0.05 ± 0.03	0.25 ± 0.03	0.14 ± 0.04	0.18 ± 0.07	-0.02 ± 0.03
ΔOrganic C (g/kg)	3.78 ± 1.06	0.58 ± 0.34	3.18 ± 0.38	2.62 ± 0.49	2.12 ± 0.82	0.73 ± 0.38
ΔP (mg/kg)	17.55 ± 7.74	-13.19 ± 1.85	7.85 ± 2.67	21.80 ± 4.35	4.25 ± 6.11	15.04 ± 1.89
ΔNH_4^+ (mg/kg)	-	-	-	-5.60 ± 0.18	-5.22 ± 0.22	-5.70 ± 0.12
ΔNO_3^- (mg/kg)	-	-	-	-2.10 ± 0.32	-0.40 ± 0.26	-3.70 ± 1.10
ΔK^+ (mmol/kg)	-0.89 ± 0.11	-1.39 ± 0.24	-0.17 ± 0.07	-1.53 ± 0.27	-1.89 ± 0.32	-0.47 ± 0.10
ΔCa^{2+} (mmol/kg)	6.74 ± 2.90	-3.79 ± 1.11	8.11 ± 0.73	6.86 ± 1.26	5.65 ± 3.96	13.85 ± 1.76
ΔMg^{2+} (mmol/kg)	2.49 ± 1.21	-1.62 ± 0.39	3.59 ± 0.45	3.81 ± 0.50	3.61 ± 1.79	7.01 ± 0.66
ΔNa^+ (mmol/kg)	0.52 ± 0.08	0.15 ± 0.06	0.37 ± 0.06	-0.26 ± 0.07	-0.62 ± 0.11	0.00 ± 0.09
ΔCu (mg/kg)	1.26 ± 0.31	-0.19 ± 0.06	0.71 ± 0.06	-	-	-
ΔZn (mg/kg)	4.54 ± 1.15	-0.74 ± 0.15	1.88 ± 0.32	-	-	-
ΔMn (mg/kg)	1.48 ± 2.92	6.53 ± 1.26	7.66 ± 1.06	-	-	-
ΔFe (mg/kg)	-15.18 ± 10.51	-12.43 ± 4.24	9.47 ± 3.50	-	-	-

Table A.1. (*continued*)

	PF					
	2018					
	F			**Rb**		
	TT	**BT**	**LT**	**TT**	**BT**	**LT**
ΔTotal N (g/kg)	0.03 ± 0.03	0.14 ± 0.02	-0.05 ± 0.02	0.26 ± 0.09	0.08 ± 0.08	0.50 ± 0.11
ΔOrganic C (g/kg)	0.50 ± 0.66	2.25 ± 0.27	-1.22 ± 0.47	3.45 ± 1.09	1.02 ± 0.87	5.73 ± 1.17
ΔP (mg/kg)	-0.54 ± 1.28	1.31 ± 1.56	1.09 ± 1.62	-1.53 ± 2.07	2.62 ± 0.89	6.87 ± 2.74
ΔNH_4^+ (mg/kg)	-	-	-	-	-	-
ΔNO_3^- (mg/kg)	-	-	-	-	-	-
ΔK^+ (mmol/kg)	-0.22 ± 0.17	-0.21 ± 0.12	-0.56 ± 0.08	0.95 ± 0.42	0.18 ± 0.20	0.57 ± 0.40
ΔCa^{2+} (mmol/kg)	0.51 ± 0.21	0.97 ± 0.29	0.98 ± 0.30	2.43 ± 0.97	2.34 ± 1.21	5.03 ± 0.95
ΔMg^{2+} (mmol/kg)	0.12 ± 0.10	0.26 ± 0.12	0.35 ± 0.12	0.83 ± 0.29	0.84 ± 0.27	1.23 ± 0.22
ΔNa^+ (mmol/kg)	0.39 ± 0.03	0.90 ± 0.11	0.38 ± 0.09	0.86 ± 0.12	1.41 ± 0.17	0.83 ± 0.15
ΔCu (mg/kg)	0.54 ± 0.09	0.16 ± 0.77	2.73 ± 0.37	1.06 ± 0.33	1.09 ± 0.29	0.00 ± 0.40
ΔZn (mg/kg)	0.14 ± 0.07	0.28 ± 0.09	0.27 ± 0.08	0.27 ± 1.05	2.30 ± 0.97	4.28 ± 0.96
ΔMn (mg/kg)	1.60 ± 0.56	-1.16 ± 0.98	1.27 ± 0.39	5.45 ± 0.78	3.44 ± 0.99	2.61 ± 0.61
ΔFe (mg/kg)	14.24 ± 0.53	-12.68 ± 14.50	44.08 ± 5.45	-2.45 ± 10.69	16.55 ± 2.48	13.69 ± 3.60

Table A.1. (*continued*)

	PF					
	2019					
	F			**Rb**		
	TT	**BT**	**LT**	**TT**	**BT**	**LT**
ΔTotal N (g/kg)	-0.11 ± 0.09	-0.09 ± 0.08	-0.08 ± 0.05	-3.76 ± 0.41	-0.20 ± 0.30	-1.19 ± 0.25
ΔOrganic C (g/kg)	-2.65 ± 1.39	-1.18 ± 1.23	-1.07 ± 1.05	-52.00 ± 4.04	-4.35 ± 4.05	-16.50 ± 3.52
ΔP (mg/kg)	-23.87 ± 1.08	-20.27 ± 2.74	-7.19 ± 2.39	-98.64 ± 7.82	-23.43 ± 5.95	-48.51 ± 9.89
ΔNH_4^+ (mg/kg)	-4.03 ± 1.39	-7.62 ± 0.17	-4.10 ± 1.71	-13.82 ± 2.50	5.70 ± 9.53	-21.60 ± 2.19
ΔNO_3^- (mg/kg)	-3.22 ± 0.85	-2.10 ± 0.20	-4.28 ± 1.33	-2.35 ± 0.30	-3.42 ± 0.22	-3.65 ± 0.93
ΔK^+ (mmol/kg)	-1.27 ± 0.11	-1.24 ± 0.06	-0.79 ± 0.10	-34.08 ± 3.87	-7.02 ± 0.54	-15.91 ± 2.40
ΔCa^{2+} (mmol/kg)	-0.95 ± 1.09	0.80 ± 0.51	-0.27 ± 0.95	-51.73 ± 8.59	-15.68 ± 3.35	-29.40 ± 5.04
ΔMg^{2+} (mmol/kg)	0.24 ± 0.42	-0.04 ± 0.19	-0.20 ± 0.38	-14.58 ± 2.09	-3.26 ± 0.81	-7.33 ± 1.42
ΔNa^+ (mmol/kg)	1.95 ± 0.32	1.10 ± 0.11	1.04 ± 0.36	-7.07 ± 1.40	-0.53 ± 0.22	-4.45 ± 0.88
ΔCu (mg/kg)	-	-	-	-	-	-
ΔZn (mg/kg)	-	-	-	-	-	-
ΔMn (mg/kg)	-	-	-	-	-	-
ΔFe (mg/kg)	-	-	-	-	-	-

Chapitre 2 - Effect of intercropping and organic raised-bed gardening on soil nematode community structure and metabolic footprints in tomato small-scale farming

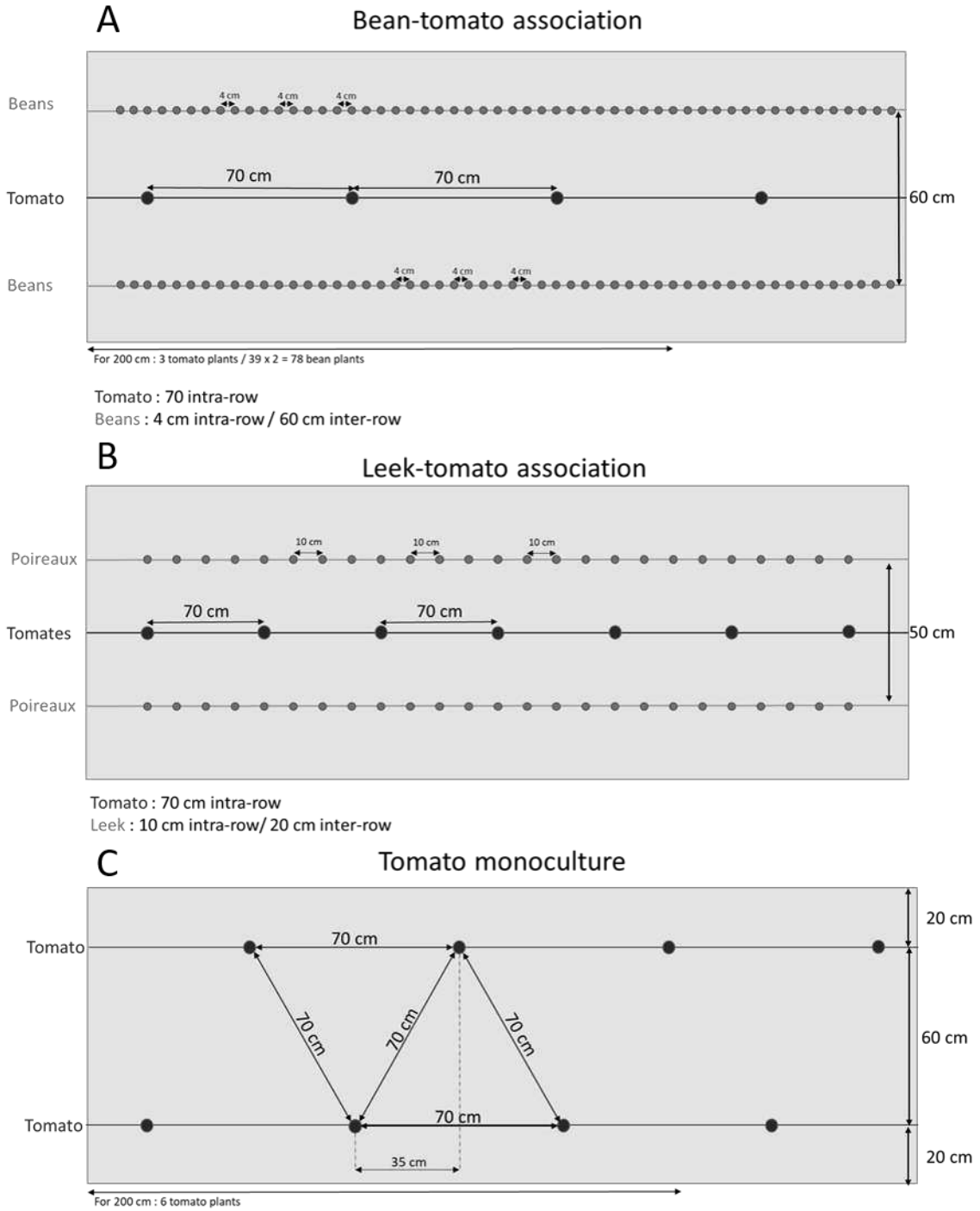

Fig. A.1. Planting/seeding set up of tomato plants, leeks and bean seeds within each crop association. A. Bean-Tomato (BT), B. Leek-tomato (LT), C. Tomato monoculture (TT).

Table B.1. Soil properties (Mean ± se) in the three crop associations (Tomato monoculture (TT), Bean-Tomato (BT) and Leek-Tomato (LT) associations) at Adriers (AD), and in the three crop associations and two soil managements (Flat ground (F) vs. Raised bed (Rb)), at Pontenx-le-Forges (PF) for the two years of experimentation.

Site	Year	Soil management	Crop association	Temperature (°C)	Humidity (%)	pH_{water}	Total N ($g.kg^{-1}$)	Organic Carbon ($g.kg^{-1}$)	Organic Matter ($g.kg^{-1}$)	P Olsen ($mg.kg^{-1}$)
AD	**2018**	**Flat ground**	**TT**	23.07 ± 0.13	9.53 ± 0.36	8.06 ± 0.06	1.45 ± 0.02	16.03 ± 0.32	29.93 ± 1.91	172.33 ± 11.40
			BT	23.37 ± 0.20	9.20 ± 0.37	8.04 ± 0.08	1.50 ± 0.10	16.77 ± 1.11	33.07 ± 3.09	203.33 ± 16.34
			LT	22.80 ± 0.20	8.77 ± 0.19	8.00 ± 0.09	1.65 ± 0.15	19.23 ± 1.98	29.00 ± 0.48	231.67 ± 16.06
	2019	**Flat ground**	**TT**	18.50 ± 0.15	6.60 ± 0.21	8.33 ± 0.05	1.63 ± 0.08	19.03 ± 0.95	32.47 ± 0.37	238.67 ± 15.88
			BT	18.67 ± 0.13	6.20 ± 0.22	8.27 ± 0.05	1.62 ± 0.02	18.27 ± 0.19	33.60 ± 2.51	226.33 ± 8.00
			LT	18.93 ± 0.34	5.63 ± 0.07	8.30 ± 0.06	1.68 ± 0.13	20.70 ± 2.07	32.60 ± 1.56	261.00 ± 10.69
PF	**2018**	**Flat ground**	**TT**	21.63 ± 0.17	6.67 ± 0.77	5.98 ± 0.06	0.84 ± 0.06	15.83 ± 1.05	17.60 ± 2.19	85.67 ± 5.40
			BT	21.17 ± 0.25	9.40 ± 1.14	5.40 ± 0.15	0.88 ± 0.11	15.07 ± 1.37	16.00 ± 1.14	98.00 ± 7.54
			LT	21.40 ± 0.15	7.90 ± 0.30	5.67 ± 0.09	0.80 ± 0.06	14.83 ± 1.19	16.80 ± 1.23	75.33 ± 8.64
		Raised bed	**TT**	22.73 ± 0.02	6.13 ± 0.40	7.08 ± 0.12	5.83 ± 0.53	80.30 ± 6.01	51.40 ± 6.14	326.67 ± 29.03
			BT	21.80 ± 0.12	11.77 ± 0.87	6.87 ± 0.03	2.57 ± 0.31	39.83 ± 4.09	68.27 ± 7.54	213.67 ± 25.90
			LT	21.77 ± 0.04	10.73 ± 0.40	6.88 ± 0.09	3.41 ± 0.38	50.90 ± 5.26	116.60 ± 10.60	255.33 ± 39.76
	2019	**Flat ground**	**TT**	20.90 ± 0.38	3.70 ± 0.85	6.73 ± 0.11	0.59 ± 0.03	11.00 ± 0.48	14.80 ± 0.40	27.00 ± 3.28
			BT	20.10 ± 0.29	8.37 ± 1.32	6.07 ± 0.17	0.74 ± 0.02	13.10 ± 0.57	15.20 ± 1.22	48.67 ± 3.75
			LT	20.37 ± 0.33	6.40 ± 0.80	6.25 ± 0.31	0.76 ± 0.06	14.57 ± 1.02	11.73 ± 0.57	64.00 ± 6.43
		Raised bed	**TT**	20.67 ± 0.21	3.53 ± 0.25	6.12 ± 0.09	1.46 ± 0.12	23.37 ± 1.30	44.93 ± 5.45	105.67 ± 9.11
			BT	20.70 ± 0.20	5.90 ± 1.60	6.53 ± 0.12	2.25 ± 0.27	33.33 ± 3.74	38.47 ± 2.84	150.00 ± 6.69
			LT	20.10 ± 0.17	3.83 ± 0.50	6.21 ± 0.06	1.92 ± 0.14	30.10 ± 1.68	29.13 ± 2.47	135.67 ± 3.36

Table B.1. (*continued*)

Site	Year	Soil management	Crop association	CEC Metson (mg 100 g)	K^+ ($mg.kg^{-1}$)	Ca^{2+} ($mg.kg^{-1}$)	Mg^{2+} ($mg.kg^{-1}$)	Na^+ ($mg.kg^{-1}$)	NO_3^- (ppm dry soil)	NH_4^+ (ppm dry soil)
AD	**2018**	**Flat ground**	**TT**	7.84 ± 0.53	146.67 ± 18.67	2197.67 ± 54.41	675.67 ± 14.30	35.33 ± 2.78	8.40 ± 0.49	7.80 ± 0.24
			BT	7.62 ± 0.39	205.00 ± 22.59	2015.00 ± 237.03	646.00 ± 73.49	41.67 ± 6.77	6.83 ± 0.22	7.43 ± 0.43
			LT	8.70 ± 0.51	113.67 ± 7.38	1778.00 ± 118.20	548.00 ± 30.34	25.00 ± 1.53	9.20 ± 1.05	7.77 ± 0.13
	2019	**Flat ground**	**TT**	8.78 ± 0.41	83.33 ± 4.44	2462.33 ± 103.97	794.67 ± 27.88	23.67 ± 3.91	6.03 ± 0.13	2.50 ± 0.12
			BT	9.37 ± 0.12	112.00 ± 6.66	2407.67 ± 125.45	815.00 ± 44.79	20.00 ± 2.52	6.10 ± 0.35	2.30 ± 0.17
			LT	9.59 ± 0.38	96.67 ± 3.47	2724.00 ± 89.47	870.33 ± 27.78	29.67 ± 4.34	4.17 ± 0.41	1.90 ± 0.03
PF	**2018**	**Flat ground**	**TT**	3.06 ± 0.07	90.67 ± 3.85	608.67 ± 15.49	152.33 ± 7.41	49.00 ± 4.91	5.80 ± 1.18	8.83 ± 0.47
			BT	4.18 ± 0.22	91.67 ± 2.69	516.67 ± 35.48	148.00 ± 14.01	81.33 ± 11.11	4.53 ± 0.32	14.37 ± 1.80
			LT	3.77 ± 0.29	73.67 ± 6.26	586.67 ± 53.72	167.67 ± 15.36	94.67 ± 13.09	7.67 ± 1.65	9.17 ± 2.35
		Raised bed	**TT**	19.27 ± 1.52	1839.33 ± 297.01	4940.33 ± 534.40	926.00 ± 106.50	386.00 ± 65.33	5.03 ± 0.55	24.40 ± 6.92
			BT	11.49 ± 1.55	877.33 ± 93.65	2893.67 ± 358.71	516.33 ± 57.64	217.33 ± 23.25	4.83 ± 0.54	30.57 ± 7.06
			LT	12.54 ± 1.61	1139.33 ± 144.45	3321.33 ± 491.40	596.33 ± 97.30	290.67 ± 40.49	5.07 ± 0.57	29.37 ± 3.04
	2019	**Flat ground**	**TT**	2.77 ± 0.07	20.33 ± 2.14	481.67 ± 74.36	149.67 ± 21.79	91.00 ± 10.33	3.50 ± 0.65	7.10 ± 1.07
			BT	3.49 ± 0.04	30.33 ± 2.41	582.67 ± 41.93	143.33 ± 12.08	110.33 ± 9.97	2.17 ± 0.20	6.93 ± 1.98
			LT	3.47 ± 0.42	30.00 ± 1.20	535.67 ± 102.91	152.33 ± 33.16	126.33 ± 20.39	1.97 ± 0.45	2.97 ± 0.34
		Raised bed	**TT**	5.82 ± 0.14	282.33 ± 35.00	1307.00 ± 132.71	223.00 ± 18.67	133.33 ± 6.08	2.37 ± 0.13	11.27 ± 3.16
			BT	8.18 ± 0.34	526.33 ± 59.46	1828.00 ± 100.24	354.67 ± 12.32	203.00 ± 13.74	1.70 ± 0.26	42.37 ± 14.76
			LT	7.42 ± 0.37	384.00 ± 42.53	1569.00 ± 90.02	296.67 ± 25.87	153.67 ± 20.73	2.90 ± 0.50	7.97 ± 1.15

Chapitre 3 - Growth and root-knot nematode infection of tomato are influenced by mycorrhizal fungi and earthworms in intercropping cultivation system with leeks

Table S1 Effect of the tomato monoculture or leek-tomato association and soil organisms on tomato plant growth and development parameters (mean ± se).

Association	Soil organisms[1]	Height increase (cm)		Shoot biomass[2] (g)		Root biomass (g)		Number of flowers		First flowering day (nb days)	
Tomato - tomato											
	Control	68.5 ± 3.7		7.8 ± 0.7		1.1 ± 0.1		11 ± 0.7		31.6 ± 3.5	
	RKN	70.9 ± 3.2		7.7 ± 0.7		1.4 ± 0.2		9.4 ± 1.5		25.6 ± 3.2	
	RKN/AMF	65.5 ± 5.6		7.0 ± 0.6		1.4 ± 0.1		6.8 ± 1.0		40.4 ± 2.7	
	RKN/EW	59.2 ± 2.4		6.9 ± 0.5		1.4 ± 0.3		7.8 ± 0.6		30.2 ± 2.7	
	RKN/EW/AMF	72.9 ± 4.2		7.4 ± 0.8		1.4 ± 0.2		8.0 ± 1.4		36.0 ± 4.6	
	Grand mean[3]	*67.4 ± 1.9*	*A*	*7.3 ± 0.3*	*A*	*1.3 ± 0.1*	*A*	*8.6 ± 0.5*	*A*	*32.8 ± 1.7*	*A*
Leek - tomato											
	Control	98.0 ± 5.8	b	14.6 ± 0.5	b	1.7 ± 0.1		16.4 ± 2.3		22.2 ± 1.8	
	RKN	80.8 ± 3.2	a	12.9 ± 0.5	ab	2.3 ± 0.3		14.4 ± 2.1		22.8 ± 1.9	
	RKN/AMF	86.7 ± 4.9	ab	12.2 ± 0.5	a	2.3 ± 0.2		11.0 ± 2.5		31.0 ± 3.4	
	RKN/EW	76.4 ± 2.7	a	13.3 ± 0.5	ab	2.4 ± 0.1		17.0 ± 3.7		25.0 ± 2.4	
	RKN/EW/AMF	91.4 ± 2.6	ab	13.4 ± 0.3	ab	2.3 ± 0.2		15.4 ± 1.9		27.8 ± 4.4	
	Grand mean[3]	*86.7 ± 2.3*	*B*	*13.3 ± 0.2*	*B*	*2.2 ± 0.1*	*B*	*14.8 ± 1.1*	*B*	*25.8 ± 1.4*	*B*
	MANOVA[3]	*F = 42.52 P < 0.001*		*F = 250.86 P < 0.001*		*F = 57.49 P < 0.001*		*F = 24.40 P < 0.001*		*F = 9.90 P = 0.003*	

[1]Control: without soil organisms, RKN: with nematodes *Meloidogyne incognita*, RKN/AMF: with *M. incognita* and arbuscular mycorrhizal fungi (AMF) *Rhizophagus irregularis*, RKN/EW: with *M. incognita*, and earthworm (EW) *Eisenia andrei*, RKN/EW/AMF: with *M. incognita, E. andrei* and *R. irregularis*.

[2]For each treatment within each association, means ± standard error followed by different lowercase letters are significantly different (ANOVA, df = 4 followed by a Tukey HSD test, $P < 0.05$).

[3]For each association, grand means ± standard error followed by different capital letters are significantly different (MANOVA, df = 1).

Table S2 Effect intensity of adding earthworms and mycorrhizal fungi alone or in combination in presence of RKN Meloidogyne incognita on tomato plant growth and development parameters, compared to the treatment with only RKN, within the tomato monoculture and the leek-tomato association (mean ± se).

Association	Soil organisms[1]	LnRR[2] Height increase	LnRR[2] Shoot biomass	LnRR[2] Root biomass	LnRR[2] Number of flowers	LnRR[2] First flowering day
Tomato - Tomato						
	RKN/AMF	-0.09 ± 0.09	-0.11 ± 0.09	-0.01 ± 0.09	-0.37 ± 0.16	0.45 ± 0.07 **
	RKN/EW	-0.18 ± 0.04 *	-0.11 ± 0.07	-0.11 ± 0.17	-0.20 ± 0.08	0.15 ± 0.09
	RKN/EW/AMF	0.02 ± 0.06	-0.06 ± 0.10	-0.06 ± 0.13	-0.22 ± 0.17	0.31 ± 0.13 *
Leek - tomato						
	RKN/AMF	0.06 ± 0.06	-0.06 ± 0.04	-0.01 ± 0.07	-0.38 ± 0.24	0.28 ± 0.13
	RKN/EW	-0.06 ± 0.03	0.03 ± 0.04	0.01 ± 0.04	0.04 ± 0.26	0.07 ± 0.10
	RKN/EW/AMF	0.12 ± 0.03 *	0.04 ± 0.02	-0.01 ± 0.07	0.04 ± 0.12	0.15 ± 0.15

[1]RKN/AMF: with *M. incognita* and arbuscular mycorrhizal fungi (AMF) *Rhizophagus irregularis*, RKN/EW: with *M. incognita*, and earthworm (EW) *Eisenia andrei*, RKN/EW/AMF: *M. incognita*, *E. andrei* and *R. irregularis*.

[2]The Log Response-Ratio LnRR #2 was calculated for each treatment (LnRR(variable$_i$=ln(variable$_i$ / mean(RKN)). Negative values mean negative effect; positive values mean positive effect. The deviation from 0 was tested with a one-sample t-tests and significant effects were indicated with asterisks (* $P < 0.05$, ** $P < 0.01$).

Table S3 Effect intensity of using the leek-tomato association on the tomato plant growth and development parameters compared to the tomato monoculture, for each of the five treatments (mean ± se).

Soil organisms[1]	LnRR[2] Height increase	LnRR[2] Shoot biomass	LnRR[2] Root biomass	LnRR[2] Number of flowers	LnRR[2] First flowering day
Control	0.35 ± 0.06 **	0.63 ± 0.03 ***	0.47 ± 0.07 **	0.36 ± 0.14	-0.37 ± 0.08 *
RKN	0.13 ± 0.04 *	0.51 ± 0.04 ***	0.46 ± 0.15 *	0.38 ± 0.14	-0.13 ± 0.08
RKN/AMF	0.27 ± 0.06 *	0.56 ± 0.04 ***	0.48 ± 0.07 **	0.37 ± 0.24	-0.29 ± 0.13
RKN/EW	0.25 ± 0.03 **	0.65 ± 0.04 ***	0.56 ± 0.04 **	0.66 ± 0.26	-0.21 ± 0.10
RKN/EW/AMF	0.22 ± 0.03 **	0.59 ± 0.02 ***	0.51 ± 0.07 **	0.63 ± 0.12 **	-0.31 ± 0.15

[1]Control: without soil organisms, RKN: with nematodes *Meloidogyne incognita*, RKN/AMF: with *M. incognita* and arbuscular mycorrhizal fungi (AMF) *Rhizophagus irregularis*, RKN/EW: with *M. incognita*, and earthworm (EW) *Eisenia andrei*, RKN/EW/AMF: with *M. incognita, E. andrei* and *R. irregularis*.

[2]The Log Response-Ratio LnRR #3 was calculated for each treatment (LnRR(variable$_i$ = ln(variable$_i$ / mean(TT)). Negative values mean negative effect; positive values mean positive effect. The deviation from 0 was tested with a one-sample t-tests and significant effects were indicated with asterisks (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$).

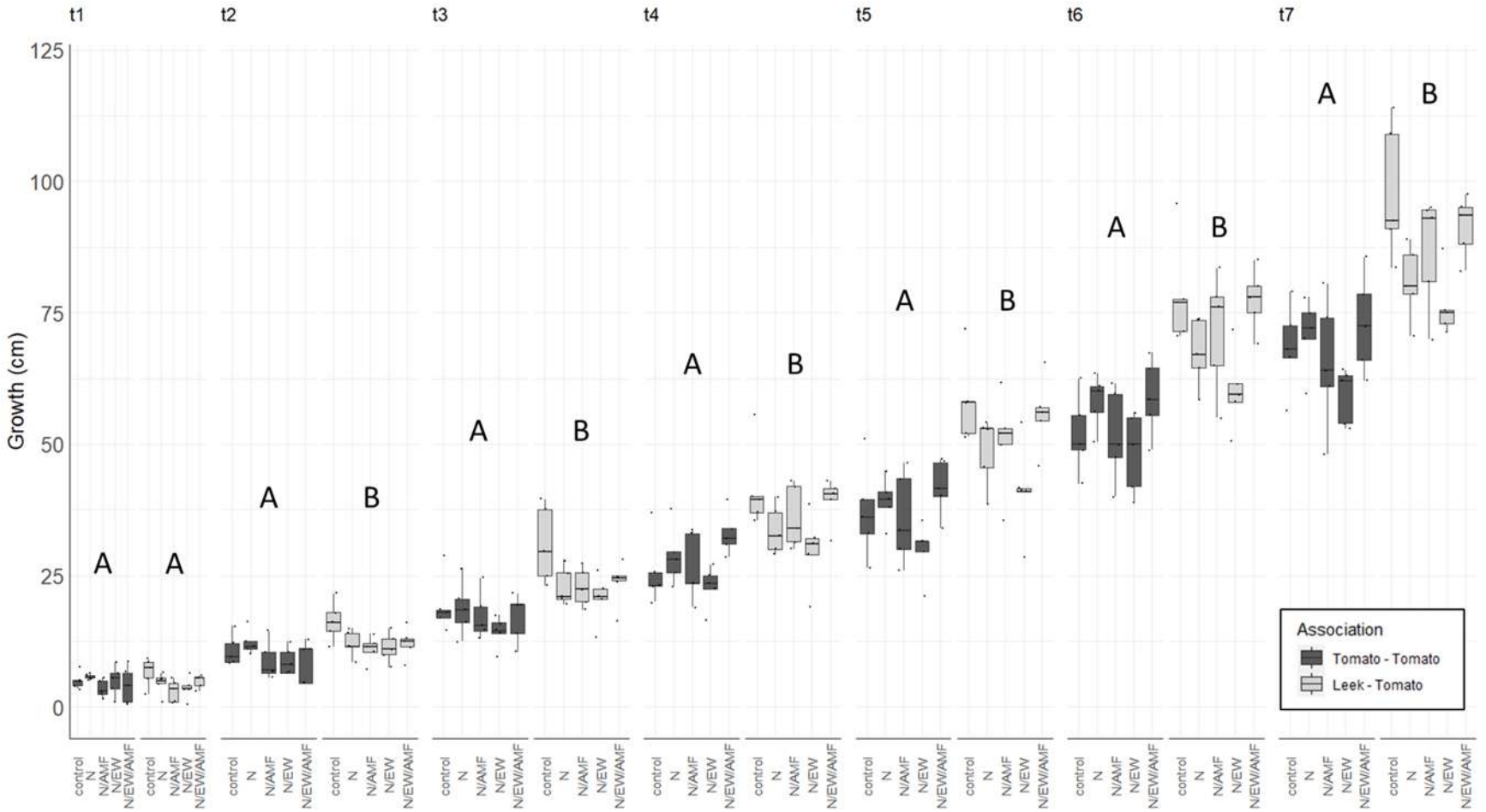

Fig. S1 Height increase of tomato plants (final height – initial height) over time for each of the five treatments within two plant associations: Tomato monoculture (dark grey) and Leek-Tomato association (light grey). Control: without soil organisms, RKN: with *Meloidogyne incognita*, RKN/AMF: with *M. incognita* and arbuscular mycorrhizal fungus (AMF) *Rhizophagus irregularis*, RKN/EW: with *M. incognita*, and earthworm (EW) *Eisenia andrei*, RKN/EW/AMF: *M. incognita, E. andrei* and *R. irregularis*. t_1 to t_7: week 1 to week 7 after the start of the experiment (= end). Different capital letters indicate significant differences between plant associations, when all treatments are combined within each association, tested by MANOVA test.

Table S4 Effect intensity of adding earthworms and mycorrhizal fungi alone or in combination in presence of RKN Meloidogyne incognita on the tomato root infestation by RKN, compared to the treatment with only RKN, within the tomato monoculture and the leek-tomato association (mean ± se).

		Total root system			Per gram of tomato root		
Association	Soil organisms	LnRR Total number of galls	LnRR Number of egg masses	LnRR Number of galls with multiple egg masses	LnRR Total number of galls/g root	LnRR Number of egg masses/g root	LnRR Number of galls with multiple egg masses/g root
Tomato - tomato							
	RKN/AMF	0.16 ± 0.11	0.13 ± 0.18	0.34 ± 0.36	0.13 ± 0.05	0.14 ± 0.2	0.36 ± 0.37
	RKN/EW	-0.08 ± 0.15	-0.51 ± 0.16 *	-0.54 ± 0.27	-0.01 ± 0.17	-0.40 ± 0.22	-0.42 ± 0.36
	RKN/EW/AMF	-0.01 ± 0.16	0.00 ± 0.26	0.19 ± 0.42	0.01 ± 0.10	0.06 ± 0.28	0.26 ± 0.39
Leek - tomato							
	RKN/AMF	0.11 ± 0.16	0.24 ± 0.05 **	0.71 ± 0.11 **	0.06 ± 0.18	0.02 ± 0.1	0.44 ± 0.12 *
	RKN/EW	-0.05 ± 0.07	0.21 ± 0.14	0.12 ± 0.24	-0.13 ± 0.08	-0.04 ± 0.16	-0.18 ± 0.26
	RKN/EW/AMF	0.10 ± 0.09	0.43 ± 0.23	0.57 ± 0.33	0.04 ± 0.08	0.21 ± 0.25	0.30 ± 0.35

[1]RKN/AMF: with *M. incognita* and arbuscular mycorrhizal fungi (AMF) *Rhizophagus irregularis*, RKN/EW: with *M. incognita*, and earthworm (EW) *Eisenia andrei*, RKN/EW/AMF: *M. incognita*, *E. andrei* and *R. irregularis*.

[2]The Log Response-Ratio LnRR #2 was calculated for each treatment ($LnRR(variable_i)=ln(variable_i / mean(RKN))$). Negative values mean negative effect; positive values mean positive effect. The deviation from 0 was tested with a one-sample t-tests and significant effects were indicated with asterisks (* $P < 0.05$, ** $P < 0.01$).

Table S5 Effect intensity of using the leek-tomato association on the tomato root infestation by RKN, compared to the tomato monoculture, for each of the five treatments (mean ± se).

	Total root system			Per gram of tomato root		
Soil organisms[1]	LnRR[2] Total number of galls	LnRR[2] Number of egg masses	LnRR[2] Number of galls with multiple egg masses	LnRR[2] Total number of galls/g root	LnRR[2] Number of egg masses/g root	LnRR[2] Number of galls with multiple egg masses/g root
RKN	0.42 ± 0.09 **	-0.05 ± 0.32	-0.11 ± 0.55	-0.08 ± 0.15	-0.51 ± 0.42	-0.55 ± 0.63
RKN/AMF	0.36 ± 0.16	0.18 ± 0.05 *	0.44 ± 0.11 *	-0.11 ± 0.18	-0.33 ± 0.10 *	-0.06 ± 0.12
RKN/EW	0.42 ± 0.07 **	0.79 ± 0.14 **	0.83 ± 0.24 *	-0.22 ± 0.08	0.12 ± 0.16	0.08 ± 0.26
RKN/EW/AMF	0.49 ± 0.09 **	0.43 ± 0.23	0.34 ± 0.33	-0.02 ± 0.08	-0.13 ± 0.25	-0.15 ± 0.35

[1]RKN: with nematodes *Meloidogyne incognita*, RKN/AMF: with *M. incognita* and arbuscular mycorrhizal fungi (AMF) *Rhizophagus irregularis*, RKN/EW: with *M. incognita*, and earthworm (EW) *Eisenia andrei*, RKN/EW/AMF: with *M. incognita, E. andrei* and *R. irregularis*.

[2]The Log Response-Ratio LnRR #3 was calculated for each treatment ($LnRR(variable_i = \ln(variable_i / mean(TT))$). Negative values mean negative effect; positive values mean positive effect. The deviation from 0 was tested with a one-sample t-tests and significant effects were indicated with asterisks (* $P < 0.05$, ** $P < 0.01$).

Table S6 Effect of the tomato monoculture or the leek-tomato association and soil organisms on tomato root infestation by RKN Meloidogyne incognita (mean ± se).

		Total root system					Per gram of tomato root					
Association	Soil organisms[1]	Total number of galls		Number of egg masses		Number of galls with multiple egg masses	Total number of galls/g root		Number of egg masses/g root		Number of galls with multiple egg masses/g root	
Tomato - tomato												
	RKN	3912.0 ± 429.0		2156.0 ± 595.1		168.0 ± 99.3	2861.9 ± 330.6		1517.0 ± 356.1		117.0 ± 61.5	
	RKN/AMF	4704.0 ± 543.0		2608.0 ± 402.4		300.0 ± 99.6	3264.6 ± 151.3		1865.4 ± 281.0		214.1 ± 72.6	
	RKN/EW	3768.0 ± 609.0		1360.0 ± 198.5		112.0 ± 27.3	3010.2 ± 529.1		1122.9 ± 244.1		100.6 ± 38.8	
	RKN/EW/AMF	4064.0 ± 602.9		2448.0 ± 590.1		288.0 ± 118.8	2942.6 ± 314.4		1846.7 ± 446.4		202.3 ± 70.4	
	Grand mean[3]	*205.6 ± 13.3*	*A*	*107.2 ± 12.2*	*A*	*10.8 ± 2.3*	*A*	*151.0 ± 8.4*	*A*	*79.4 ± 8.6*	*A*	*7.9 ± 1.5*	*A*
Leek - tomato												
	RKN	6020.0 ± 562.6		2436.0 ± 643.4		228.0 ± 80.1	2759.7 ± 414.1		1315.9 ± 608.3		129.4 ± 71.0	
	RKN/AMF	7092.0 ± 1095.4		3124.0 ± 153.4		476.0 ± 54.2	3087.1 ± 450.6		1373.9 ± 136.4		206.5 ± 25.0	
	RKN/EW	5788.0 ± 394.0		3108.0 ± 403.8		284.0 ± 56.4	2456.3 ± 203.1		1328.7 ± 204.0		121.9 ± 26.4	
	RKN/EW/AMF	6768.0 ± 579.2		4140.0 ± 884.1		500.0 ± 160.9	2919.2 ± 235.4		1828.2 ± 427.3		221.1 ± 76.1	
	Grand mean[3]	*320.9 ± 17.4*	*B*	*160.1 ± 15.2*	*B*	*18.6 ± 2.6*	*B*	*140.3 ± 8.3*	*A*	*73.1 ± 9.3*	*A*	*8.5 ± 1.4*	*A*
	MANOVA[3]	*F = 27.80* *P < 0.001*		*F = 7.38* *P < 0.01*		*F = 4.89* *P = 0.03*	*F = 0.82* *P = 0.37*		*F= 0.05* *P = 0.83*		*F=0.07* *P=0.79*	

[1]Control: without soil organisms, RKN: with nematodes *Meloidogyne incognita*, RKN/AMF: with *M. incognita* and arbuscular mycorrhizal fungi (AMF) *Rhizophagus irregularis*, RKN/EW: with *M. incognita*, and earthworm (EW) *Eisenia andrei*, RKN/EW/AMF: with *M. incognita, E. andrei* and *R. irregularis*.

[2]For each treatment within each association, means ± standard error followed by different lowercase letters are significantly different (ANOVA, df = 4 followed by a Tukey HSD test, $P < 0.05$).

[3]For each association, grand means ± standard error followed by different capital letters are significantly different (MANOVA, df = 1).

Table S7 Total inertia and first eigenvalues of the between-within class Principal Component Analysis (PCA) to test for an explanatory effect of the plant association and soil organisms on plant performances and nematode infestation variables.

	Total inertia	**First eigenvalue**	**Inertia ratio (%)**	**Interpretation**
General PCA	8			
Between Association	2.41	2.41	30.15 ***	Percentage of total variation explained by differences between associations
Within Association	5.59	0.29	69.48	Percentage of total variation explained by soil organisms within associations
Between Soil organisms	0.77	0.19	9.56	Percentage of total variation explained by differences between soil organisms
Within Soil organisms	7.23	3.21	90.43	Percentage of the total variation explained by associations within soil organisms
Residuals			60.28	Percentage of total variation explained neither by differences between associations nor between soil organisms

Table S8 Correlation results of the most correlated variables with the Axes 1 to 3 of the Principal Component Analysis (PCA).

Axes	Variables	r	*P* value
Dim 1	root_biomass	**0.8908557**	1.364994e-14
	shoot_biomass	**0.8508103**	3.599307e-12
	flower_nb	**0.7415708**	4.394604e-08
	growth	**0.6219237**	1.837416e-05
	P	0.4124629	8.173288e-03
	galls_multi_masses_ratio	-0.3217326	4.292144e-02
	first_flowering_day	-0.4941582	1.191803e-03
	egg_masses_ratio	-0.4999731	1.019874e-03
	galls_ratio	-0.5379084	3.438839e-04
Dim 2	galls_multi_masses_ratio	**0.8752828**	1.495045e-13
	egg_masses_ratio	**0.7773518**	3.649037e-09
	growth	0.5219004	5.525564e-04
	galls_ratio	0.3719773	1.810312e-02
	shoot_biomass	0.3390808	3.232291e-02
	C.N	-0.3470049	2.825499e-02
Dim 3	first_flowering_day	**0.7625990**	1.072690e-08
	F	0.4344294	5.094013e-03
	M	0.4200916	6.959641e-03
	galls_ratio	0.4076166	9.035208e-03

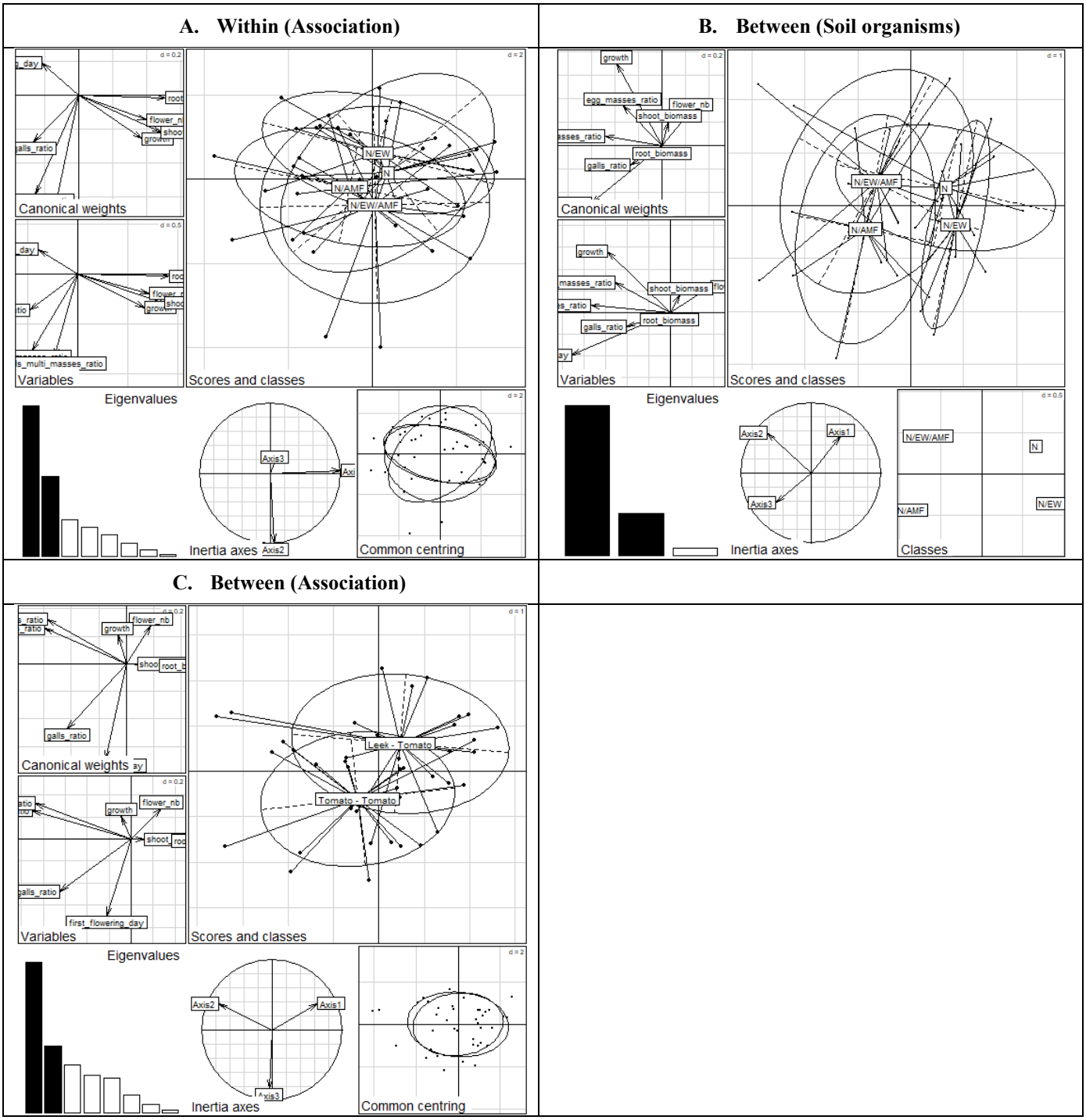

Figure S2 Within-Between Principal Component Analyses (PCA) of the 8 nematode and plant variables showing A. differences explained by different soil organisms within the association factor, B. overall differences explained by different soil organisms, and C. differences explained by different associations within soil organisms factor. Canonical weights, variables explaining axes, eigenvalues and the strength of the three first axes in explaining the representation are shown. RKN: with *Meloidogyne incognita*, RKN/AMF: with *M. incognita* and arbuscular mycorrhizal fungus (AMF) *Rhizophagus irregularis*, RKN/EW: with *M. incognita*, and earthworm (EW) *Eisenia andrei*, RKN/EW/AMF: *M. incognita, E. andrei* and *R. irregularis.*

Table S9 Soil properties in all treatments at the end of the experiment (mean + se).

Association	Soil organisms	P Olsen (mg/kg)	N-NH4 (mg/kg)	N-NO3 (mg/kg)	N tot (g/kg)	C org (g/kg)	pH
Tomato - tomato							
	Control	15.87 ± 0.27	6.10 ± 0.20	0.12 ± 0.01	1.12 ± 0.02	11.64 ± 0.20	7.04 ± 0.03
	RKN	17.70 ± 0.18	6.36 ± 0.17	0.17 ± 0.02	1.11 ± 0.02	11.64 ± 0.15	7.09 ± 0.03
	RKN/AMF	17.79 ± 0.24	8.33 ± 0.36	0.13 ± 0.01	1.15 ± 0.02	12.00 ± 0.21	7.16 ± 0.03
	RKN/EW	17.09 ± 0.46	5.01 ± 0.19	0.21 ± 0.02	1.24 ± 0.02	13.08 ± 0.24	7.17 ± 0.01
	RKN/EW/AMF	18.31 ± 0.25	6.36 ± 0.28	0.25 ± 0.02	1.15 ± 0.02	11.96 ± 0.19	7.10 ± 0.03
Leek - tomato							
	Control	17.00 ± 0.16	5.94 ± 0.14	0.10 ± 0.01	1.08 ± 0.03	11.28 ± 0.28	7.08 ± 0.05
	RKN	19.88 ± 0.28	6.52 ± 0.13	0.09 ± 0.01	1.13 ± 0.01	11.72 ± 0.11	7.10 ± 0.03
	RKN/AMF	19.79 ± 0.55	7.74 ± 0.49	0.17 ± 0.03	1.18 ± 0.02	12.14 ± 0.24	7.02 ± 0.05
	RKN/EW	19.79 ± 0.50	6.61 ± 0.24	0.06 ± 0.01	1.21 ± 0.03	12.62 ± 0.28	7.16 ± 0.04
	RKN/EW/AMF	18.05 ± 0.29	6.86 ± 0.32	0.19 ± 0.02	1.16 ± 0.03	11.90 ± 0.28	7.06 ± 0.03

Association	Soil organisms	CEC (Metson meq/100 g)	K (mmol/kg)	Mg (mmol/kg)	K/Mg	Na (mmol/kg)	Ca (mmol/kg)
Tomato - tomato							
	Control	4.22 ± 0.05	0.73 ± 0.04	5.01 ± 0.08	0.15 ± 0.01	2.28 ± 0.07	19.42 ± 0.21
	RKN	4.51 ± 0.06	0.88 ± 0.02	4.84 ± 0.04	0.18 ± 0.00	1.86 ± 0.04	19.45 ± 0.24
	RKN/AMF	4.56 ± 0.04	1.07 ± 0.03	4.92 ± 0.06	0.22 ± 0.01	1.67 ± 0.05	20.28 ± 0.28
	RKN/EW	4.90 ± 0.11	0.77 ± 0.05	4.81 ± 0.05	0.16 ± 0.01	1.91 ± 0.07	20.61 ± 0.27
	RKN/EW/AMF	4.58 ± 0.05	0.91 ± 0.02	4.92 ± 0.06	0.19 ± 0.01	1.83 ± 0.05	19.76 ± 0.29
Leek - tomato							
	Control	4.57 ± 0.08	0.72 ± 0.02	4.98 ± 0.12	0.15 ± 0.00	2.15 ± 0.11	19.26 ± 0.63
	RKN	4.57 ± 0.10	0.92 ± 0.03	4.92 ± 0.08	0.19 ± 0.01	1.78 ± 0.04	20.16 ± 0.29
	RKN/AMF	4.45 ± 0.07	1.17 ± 0.06	4.94 ± 0.08	0.24 ± 0.01	1.69 ± 0.07	19.84 ± 0.28
	RKN/EW	4.40 ± 0.06	1.04 ± 0.06	4.54 ± 0.14	0.23 ± 0.01	1.68 ± 0.04	19.63 ± 0.63
	RKN/EW/AMF	5.04 ± 0.05	0.86 ± 0.04	5.04 ± 0.06	0.17 ± 0.01	2.07 ± 0.09	20.98 ± 0.27

Table S10 Number of earthworms remaining and the AMF colonization on tomato roots at the end of the experiment (mean + se).

Association	Soil organisms[1]	Earthworm abundance	F[2] (%)	M[2] (%)	m[2] (%)
Tomato - Tomato					
	Control	-	7.3 ± 2.5	0.2 ± 0.1	2.0 ± 0.8
	RKN	-	10 ± 2.8	0.2 ± 0.1	1.2 ± 0.4
	RKN/AMF	-	84.8 ± 2.7	26.1 ± 10.2	30.2 ± 11.1
	RKN/EW	3.8 ± 0.9	5.3 ± 2.5	0.1 ± 0.1	1.2 ± 0.6
	RKN/EW/AMF	9.6 ± 0.7	66.7 ± 5.8	6.8 ± 2.3	9.6 ± 2.7
Leek - tomato					
	Control	-	18.7 ± 6.0	1.0 ± 0.5	8.4 ± 5.5
	RKN	-	11.3 ± 4.3	0.1 ± 0.1	0.9 ± 0.2
	RKN/AMF	-	74.0 ± 11.7	18.7 ± 8.4	23.0 ± 8.7
	RKN/EW	7.0 ± 0.9	16.7 ± 9.2	0.8 ± 0.7	2.4 ± 1.1
	RKN/EW/AMF	9.4 ± 1.0	75.3 ± 6.5	10.4 ± 2.5	13.5 ± 2.6

[1] Control: without soil organisms, RKN: with nematodes *Meloidogyne incognita*, RKN/AMF: with *M. incognita* and arbuscular mycorrhizal fungi (AMF) *Rhizophagus irregularis*, RKN/EW: with *M. incognita*, and earthworm (EW) *Eisenia andrei*, RKN/EW/AMF: with *M. incognita, E. andrei* and *R. irregularis*.

[2] F: frequency of the mycorrhizal colonization over the 30 fragments; M: i intensity of the root colonization by the arbuscular mycorrhizal fungi over the 30 root fragments; m: intensity of the root colonization by the arbuscular mycorrhizal fungi in mycorrhized root fragments only.