



**Influencia de diferentes técnicas de manejo en agricultura  
intensiva bajo plástico sobre las comunidades microbianas  
del suelo**

**Influence of different management techniques in intensive  
greenhouse on soil microbial communities**

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- Cierra ojos. Confía. Concentra. Piensa solo árbol. Haz imagen perfecta hasta última hoja. Borra de mente todo excepto árbol. Nada existe mundo entero. Solo árbol. Ya está. Abre ojos. ¿Recuerdas imagen?

- Sí

- Haz como imagen. Confía en imagen.

- Pero ¿cómo sé que mi imagen es la buena?

- Si vista dentro de ti, siempre la buena

*Enseñanza de la poda del bonsái*

*Señor Miyagi a Daniel LaRusso*

*The karate kid (1984)*



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**RESUMEN**

En esta tesis se pretende evaluar el efecto que tienen varias técnicas de manejo del suelo de los invernaderos de Almería sobre las comunidades microbianas del mismo, y qué efectos pueden tener estas comunidades sobre el crecimiento y la producción de la planta. El estudio se ha enfocado en (i) el manejo de la materia orgánica aplicada al suelo, y (ii) la desinfección del suelo en el periodo entre cultivos. Para evaluar el efecto de ambas técnicas se han planteado una serie de experimentos, tanto en invernaderos comerciales como experimentales, para obtener una visión de la estructura de las comunidades microbianas asociadas a las distintas técnicas de manejo, y el efecto de estas comunidades sobre el crecimiento y la producción del cultivo.

El primer experimento se planteó en invernaderos comerciales durante un ciclo de cultivo de tomate. Se consideraron tres opciones de manejo de la materia orgánica, muy comunes en los invernaderos de Almería: i) la no aplicación de materia orgánica, completando los requerimientos nutricionales del cultivo sólo con fertilización química; ii) la aplicación de materia orgánica a la vez que se realiza una fertilización química, y iii) la aplicación exclusivamente de materia orgánica certificada (invernaderos ecológicos). Se llevó a cabo un seguimiento de la actividad de los microorganismos mediante medidas periódicas de respiración del suelo y se analizaron los nutrientes en el suelo, sus comunidades microbianas y la producción final de tomate. Como resultado de este experimento, se observó que la aplicación de materia orgánica conlleva una mayor actividad de las comunidades microbianas del suelo, así como una disminución de la presencia de microorganismos

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potencialmente patógenos. Además, la combinación de materia orgánica y fertilización química incrementó la disponibilidad de nitrógeno para la planta, lo que se tradujo en una mayor producción de tomate.

En el segundo experimento se evaluó el efecto que tenían las comunidades microbianas asociadas a los diferentes manejos de la materia orgánica estudiados en el experimento anterior sobre el crecimiento de las plantas en ausencia de variabilidad en el suelo. Para ello, se extrajeron las comunidades microbianas de los suelos utilizados en el anterior experimento y se inocularon en macetas con un sustrato homogéneo y esterilizado previamente a la inoculación. Se sembraron semillas desinfectadas de tomate y se dejaron crecer en un invernadero experimental con la única aplicación de agua. Previo a la cosecha de las plantas, se midió la tasa fotosintética máxima, se realizaron análisis nutricionales y moleculares del sustrato y se obtuvieron medidas de biomasa de raíz y parte aérea. Los resultados mostraron que las plantas que habían crecido en presencia de comunidades microbianas asociadas a cultivos ecológicos tenían una mayor tasa de intercambio gaseoso, así como una mayor biomasa en comparación con las que habían sido inoculadas con comunidades microbianas procedentes de cultivos a los que no se les aplicaba materia orgánica. Estos resultados nos dan una idea muy clara del importante efecto que tiene la aplicación de materia orgánica sobre las comunidades microbianas, y cómo un manejo adecuado de la materia orgánica determina la composición de las comunidades microbianas del suelo, influyendo de forma positiva en el crecimiento de las plantas y en su producción.

En el tercer experimento se estudió la desinfección del suelo, técnica muy común en los invernaderos de Almería. Esta técnica se aplica de forma puntual generalmente en verano, en el periodo entre cultivos, cuando el suelo está desnudo,

y su duración es de unos 30 días. Sin embargo, tiene un efecto muy importante sobre la comunidad microbiana, y de grandes consecuencias para mantener la sostenibilidad económica de la agricultura intensiva al eliminar patógenos que puedan mermar la producción. Para comprobar el efecto que tienen los tres tipos de desinfección del suelo más comúnmente utilizados en Almería sobre las comunidades microbianas, y cómo éstas comunidades influyen en la producción, se analizaron las comunidades de microorganismos supervivientes tras la realización de tres tipos de desinfección: i) química, mediante la aplicación de 1,3-dicloropropeno, de uso común en la zona; ii) térmica, mediante solarización, colocando un plástico sobre el suelo para incrementar la temperatura durante un mes, y iii) pasiva, dejando el invernadero estanco y sin cultivo durante un mes, sin colocación de plástico ni aplicación de desinfectantes químicos. Tras estas desinfecciones, se extrajeron los microorganismos supervivientes de dos profundidades del suelo (0-10 cm y 10-20 cm) y se inocularon en macetas con un sustrato homogéneo y esterilizado; se sembraron semillas de tomate desinfectadas y se dejaron crecer en un invernadero experimental con la única aplicación de agua. Al final del ciclo, se midió la tasa fotosintética máxima, así como la biomasa aérea y subterránea y la producción obtenida. Se observó que las plantas inoculadas con microorganismos de los suelos que habían sufrido desinfección química o térmica crecieron más y obtuvieron una mayor producción que las plantas inoculadas con microorganismos provenientes de suelos con desinfección pasiva. La solarización se mostró equivalente a la desinfección química en sus efectos sobre las plantas y la producción. Frente a los problemas medioambientales y de salud que lleva aparejada la aplicación de desinfectantes químicos, y que se ha traducido en una reducción drástica de los productos autorizados para tal fin, estos resultados muestran que la solarización es

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una alternativa viable a la desinfección química siendo, además, más respetuosa con el medio ambiente y con la salud humana y más económica en su aplicación, como han indicado múltiples autores.

La relevancia de esta tesis se basa en la falta de información --en el contexto de la horticultura bajo invernadero de Almería-- sobre las consecuencias del manejo del suelo en relación a los aportes de materia orgánica y a la desinfección sobre las comunidades microbianas del suelo, que juegan un papel primordial en el crecimiento de las plantas y en la producción hortícola. Comprender estos efectos es, por tanto, clave para la sostenibilidad económica y medioambiental de la agricultura intensiva en un mundo con una población creciente. Los resultados obtenidos marcan pautas para estudios futuros, en los que el análisis del manejo del suelo sobre las comunidades microbianas y las interacciones de éstas con las plantas incrementarán nuestro conocimiento de los agrosistemas, buscando la sostenibilidad medioambiental y económica de los mismos.

**ABSTRACT**

This thesis assesses the effect of different soil management techniques in greenhouses of the Almería Province on soil microbial communities, as well as the effect of these communities on plant growth and production. This study focused on (i) the management of the organic matter, and (ii) soil disinfection between crop cycles. Different experiments were carried out to assess the effect of these two techniques, being in commercial and experimental greenhouses, to gain a wide knowledge about the structure of soil microbial communities associated to the different management techniques, and the effect of such communities on plant growth and fruit production.

The first experiment was conducted in commercial greenhouses during a tomato crop cycle. Three common organic matter managements were selected: i) no application of organic matter, covering plant nutritional needs with synthetic fertilizers; ii) application of organic matter combined with synthetic fertilizers to cover nutritional needs; and iii) application of organic matter in certified organic greenhouses, with no application of synthetic fertilizers. We measured soil microbial activity with periodic measurements of soil respiration rates and analyzed nutrient contents in soils and final production. Our results showed that organic matter application led to higher microbial activity in soils, as well as less potential pathogens. Furthermore, the combination of organic matter and synthetic fertilizers increased nitrogen availability in the soil and tomato production.

In the second experiment, we evaluated the effect of microbial communities associated to different organic matter managements. To assess this, we extracted

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microbial communities from soils of the previous experiment and inoculated pots with a homogenized, sterilized substrate. We sowed disinfected tomato seeds and plants grew in an experimental greenhouse with only water application (i.e., without fertilizers). Before harvest, we measured maximum photosynthetic rate and took substrate samples for nutritional and genetic analyses. The results showed that plants inoculated with microbial communities from organic certified greenhouses had higher maximum photosynthetic rate as well as higher biomass than plants inoculated with microbial communities from greenhouses without organic matter application. These data evidence the important effect of organic matter application on microbial communities, and how a proper organic matter management can have a positive influence on plant growth and fruit production.

In the third experiment, we evaluated soil disinfection techniques, a common soil management procedure applied in Almería. This technique is applied during summer, between two crop cycles on uncropped soil for about 30 days. This procedure has important effects on microbial communities, with major consequences for sustainability, as it controls potential plant pathogen infections. To assess the effect of different disinfection techniques on microbial communities, we analyzed the surviving microbial communities after three disinfection techniques: i) chemical with 1,3-dichloropropene, commonly used in the region; ii) thermal (solarization), using a plastic cover to increase soil temperature for one month; and iii) passive, closing the greenhouse and leaving soil with no plants during one month. After disinfection, surviving microbial communities were extracted from two different depths (0-10 cm and 10-20 cm), and they were inoculated on pots with homogenized, sterilized substrate. We sowed disinfected tomato seeds and plants were grown in an experimental greenhouse supplied with water but not fertilizers. Before harvest, we



measured maximum photosynthetic rate, and after harvest, we measured shoot and root biomass as well as fruit production. Plants inoculated with microbial communities from chemical or thermally disinfected soils grew more and had higher production than plants inoculated with microbial communities from passively disinfected soils. Thermal disinfection (solarization) showed results similar to chemical disinfection in plant growth and production. Due to the environmental and health problems associated to chemical disinfection, we show that solarization is a viable alternative, more environmental-friendly and with less health hazards, more economically sustainable as well.

In the context of intensive greenhouse horticulture in the Almería Province, the relevance of this thesis is based on the lack of information on the consequences of soil management techniques on soil microbial communities, especially organic matter application and soil disinfection. Microbial communities have a key role on plant growth and production. Knowledge in this topic is essential in the search of an economically and environmentally sustainable agriculture in a world with a growing population. Our results set guidelines for new experiments, in which the effects of soil management on microbial communities and their interactions with plants will increase our understanding of agrosystems, seeking their environmental and economic sustainability.



# CAPÍTULO I

## Introducción y objetivos generales





## 1. INTRODUCCIÓN GENERAL

### *1.1 La intensificación de la agricultura a nivel mundial*

La intensificación de la agricultura a nivel mundial ha sido un fenómeno gradual y constante asociado al incremento de la población, que podría llegar a 9700 millones de personas en 2050 (United Nations, 2019). En este contexto, la intensificación ha conllevado cambios muy importantes a nivel agronómico (Altieri, 1999; Philpott, 2013) como: i) cambios en el uso del suelo, convirtiendo hábitats naturales en sistemas de producción, provocando fragmentación del terreno natural, destrucción del ecosistema, simplificación del paisaje y necesitando la adecuación de infraestructuras (construcción de caminos, adecuación eléctrica, acceso a puntos de agua...); ii) cambios en los cultivos, minimizando el número de especies cultivadas (monocultivos), uso de híbridos comerciales, limitación de altura y forma de árboles, entutorado de plantas de porte rastrojero y eliminación de malas hierbas; y iii) aplicación de insumos, como fertilizantes inorgánicos y orgánicos, uso de agua de riego, uso de fumigantes y agroquímicos para combatir plagas y enfermedades, uso de microorganismos exógenos e insectos de polinización o de control biológico y uso de maquinaria para realizar las labores.

Sin embargo, y ante los problemas medioambientales que ha conllevado una intensificación descontrolada, la tendencia es la búsqueda de la sostenibilidad, minimizando el impacto sobre el medio ambiente y maximizando la seguridad alimentaria (Vásquez et al., 2018). Cabe mencionar como problemas medioambientales una mayor cantidad de emisiones de CO<sub>2</sub> y NO<sub>x</sub> (Stoate et al., 2001), contaminación (Padilla et al., 2018; Tsoraeva et al., 2020) y agotamiento de

acuíferos (Custodio et al., 2016), uso de pesticidas persistentes perjudiciales para la salud humana (Cozma et al., 2018; Silva et al., 2019), degradación del suelo (Bakker et al., 2008; Baude et al., 2019; Shah et al., 2017) y acumulación y aparición de patógenos, debido al incremento del monocultivo (Li et al., 2014; Santini et al., 2018; Yan et al., 2017).

### ***1.2. El caso particular de la agricultura intensiva en Almería***

Dentro de la intensificación de la agricultura destaca el caso de la provincia de Almería. La intensificación de la región ha sido muy llamativa desde los años 70 (Mendoza-Fernández et al., 2021), concentrando a día de hoy más de 32,000 ha de cultivo intensivo bajo plástico en los que se producen todo tipo de hortalizas (Cajamar Caja Rural, 2019). La intensificación resultó en un importante incremento de la producción y de rendimientos de los cultivos, llegando a día de hoy a los 2,6 millones de toneladas al año (Cajamar Caja Rural, 2019). Demográficamente, la provincia de Almería pasó de poco más de 360,000 habitantes en 1950 hasta más de 720,000 en 2020 (Instituto Nacional de Estadística, 2021). En cuanto al crecimiento económico, destaca la gran importancia que ha conllevado el incremento de las exportaciones hortícolas, que a día de hoy son más del 80% de lo que se produce, y que se traduce en unos ingresos superiores a los 2,000 millones de euros (Cajamar Caja Rural, 2019).

Este caso tan particular de la provincia de Almería ha sido posible debido a múltiples mejoras agronómicas, que han incrementado la producción y los rendimientos de los cultivos, incluyendo el riego localizado (García-Caparrós et al., 2017), el uso del enarenado para romper la capilaridad y amortiguar las oscilaciones

térmicas (Tout, 1990); el uso generalizado de fertilizantes químicos (Egea et al., 2018), la utilización del polinizadores (Dag, 2008) y el control biológico (Chiurciu et al., 2020). Más recientemente, el desarrollo de preparados microbiológicos para el control de microorganismos patógenos de suelo y la mejora en los rendimientos de los cultivos, usando tanto base fúngica (Diáñez et al., 2016) como bacteriana (Plant Growth-Promoting Bacteria o PGPB; Mota et al., 2017). Igualmente importante han sido la comercialización de variedades con resistencia a enfermedades (Almeida et al., 2020) y las mejoras técnicas de los invernaderos (Valera et al., 2016).

Por otro lado, hay que destacar los problemas medioambientales que supone esta intensificación agrícola. Más allá de los mencionados a nivel global, en Almería destacan la sobreexplotación y contaminación de los acuíferos (García-Caparrós et al., 2017; Pulido-Bosch et al., 2020), la pérdida de hábitats singulares (Mendoza-Fernández et al., 2015; Mota et al., 1996) y el incremento de residuos plásticos y biológicos que se generan (Sayadi-Gmada et al., 2019), y que son, a día de hoy, uno de los retos a los que se está enfrentando el sector.

### ***1.3. El cultivo del tomate***

El cultivo del tomate es uno de los más importantes económicamente a nivel mundial, con más de 180 millones de toneladas producidas y 5 millones de hectáreas cultivadas en 2019 (FAOSTAT, 2020). España es el principal productor de tomate para consumo en fresco a nivel mundial, con casi 2 millones de toneladas en 2019 (MAPA, 2019). Gran parte de esta producción se realiza en la provincia de Almería, hasta casi 900,000 toneladas, siendo prácticamente la totalidad producida de manera intensiva en invernaderos.

En el sistema intensivo de invernadero de Almería, el cultivo del tomate es uno de los más importantes en cuanto a manejo de planta (Salas, 2002) y mano de obra, ya que conlleva gran cantidad de labores y una atención continua. Cabe destacar, además, el largo periodo de recolección, que requiere un importante mantenimiento de la estructura para mantener el microclima tanto en periodos de alta como de baja temperatura (Arellano et al., 2006). Es importante indicar que no hay una gran expansión del cultivo sin suelo en la región de Almería (Urrestarazu, 2015), y que por tanto las técnicas de manejo de suelo son esenciales para mantener la fertilidad de los mismos, y mantener una producción que conlleve sostenibilidad económica para el agricultor. Por ello destaca el aporte de materia orgánica, la desinfección del suelo, el subsolado, etc. (Argote et al., 2015).

Estas técnicas de manejo de suelo tan intensas y constantes hacen que entren en juego gran cantidad de factores a tener en cuenta, como el efecto de todas ellas sobre la macro- y microbiota (Song et al., 2018; Zhong et al., 2010), así como sobre los nutrientes del suelo (Luan et al., 2019; Ma et al., 2018). Sin embargo, los estudios que engloban el efecto de las técnicas de manejo de suelo realizadas sobre los microorganismos del suelo y cómo estos microorganismos pueden interactuar con las plantas y con los nutrientes del suelo son escasos.

### ***1.4. Efectos de las técnicas de manejo del suelo sobre las comunidades microbianas.***

Las comunidades microbianas del suelo juegan un papel fundamental en los ecosistemas a nivel mundial, influyendo directa e indirectamente sobre los ciclos de nutrientes (Pugnaire et al., 2019), la respiración del suelo (Mbuthia et al., 2015), el



crecimiento (Bever et al., 2010) y salud de las plantas (Mendes et al., 2011) y en la composición de la vegetación adventicia (Bennett et al., 2017). La intensificación y el monocultivo han favorecido la degradación del suelo, así como la pérdida de capacidad productiva (Fried et al., 2017), atribuida principalmente a pérdidas en la diversidad microbiana del suelo (Nielsen et al., 2015) y la acumulación de patógenos (Savary et al., 2012). El manejo sostenible de los suelos se ha convertido en una necesidad, mostrándose como única alternativa para mantener comunidades microbianas que favorezcan el crecimiento de la planta y la producción. La salud del suelo ha sido definida por diferentes indicadores, como la abundancia y diversidad de las comunidades microbianas, disponibilidad y absorción de nutrientes, contenido de materia orgánica, incidencia de patógenos, respiración del suelo o actividad metabólica (Bender et al., 2016; Bünemann et al., 2018; Curiel-Yuste et al., 2007). Ante esta coyuntura, el manejo de suelo se ha vuelto una práctica común e indispensable para asegurar las producciones. Dentro del manejo del suelo en sistemas intensivos destacan tanto el aporte de materia orgánica como la desinfección pre-cultivo.

### ***1.5. El aporte de materia orgánica en la agricultura intensiva***

El aporte de materia orgánica está considerada como una técnica positiva, que mejora la estructura del suelo (Hartmann et al., 2015) e incrementa la diversidad y biomasa microbianas (Bengtsson et al., 2005). Sin embargo, la intensificación de la agricultura ha disminuido la periodicidad de esta práctica en favor de un mayor uso de fertilizantes químicos (Ferraro and Aznar, 2008). Esta disminución del contenido de materia orgánica en el suelo tiene un efecto negativo sobre las

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comunidades microbianas, incrementando la incidencia de patógenos en detrimento de microorganismos positivos (Blok et al., 2000), y disminuyendo la diversidad microbiana (Stoate et al., 2001). Las comunidades microbianas tienen un papel clave sobre la salud de los suelos agrícolas, siendo responsables de la mineralización de la materia orgánica (Postma-Blaauw et al., 2010), la respiración del suelo (Mbuthia et al., 2015) o el control de patógenos (Senechkin et al., 2010; van Bruggen et al., 2015), y tienen un importante efecto sobre la resiliencia del suelo (Lehman et al., 2015), pudiendo mejorar la salud de las plantas en casos de salinidad o estrés (Yadav, 2021). El aporte de materia orgánica incrementa la diversidad y actividad microbiana, ayudando al crecimiento de las plantas e incrementando su producción (Bever et al., 2010; Finney and Kaye, 2017; Kardol et al., 2013; Mendes et al., 2011).

En Almería, la aplicación de materia orgánica varía enormemente entre invernaderos, y va desde no aplicarla y completar la totalidad de la demanda nutricional con fertilizantes químicos (un 32% de los casos según Thompson et al. (2007)), hasta un aporte anual de la misma sin fertilizantes químicos. Esta aplicación se realiza en bandas, líneas, a todo el invernadero o por pulsos (aplicándose únicamente en el punto de plantación de cada plántula). La procedencia de la materia orgánica aplicada es difícil de saber en muchos casos, y según Alonso et al. (2014) en el 60% de los casos no hay asociado ningún análisis químico por parte de la empresa comercializadora. La materia orgánica más usada en la región suele ser estiércol de origen animal (principalmente vaca y oveja; Thompson et al. (2007)). Como alternativas encontramos la aplicación de pellets de crucíferas (Lacasa et al., 2015) o vermicompost (Aznar-Sánchez et al., 2020).

### ***1.6. La desinfección del suelo en la agricultura intensiva***

Ante el incremento de la incidencia de patógenos, la desinfección de los suelos se ha convertido en una práctica habitual y necesaria en los invernaderos de todo el mundo, siendo la técnica más común el uso de productos químicos. Sin embargo, múltiples estudios han demostrado el efecto negativo de estos productos sobre el medio ambiente (Ruzo, 2006; Yates and Ashworth, 2018) y la salud pública (Beauvais, 2015), por lo que existe un movimiento que ha desembocado en la desautorización a nivel europeo del uso de numerosos desinfectantes químicos (EC-Regulation 1107/2009). La desinfección química de los suelos tiene un importante efecto sobre las comunidades microbianas (Dangi et al., 2017), disminuyendo la presencia de patógenos, pero también de microorganismos positivos (Cheng et al., 2020), como las bacterias que intervienen en el ciclo del nitrógeno (Fang et al., 2019; Yan et al., 2013) o en diversos procesos enzimáticos (Hussain et al., 2009), disminuyendo la diversidad bacteriana (Hoshino and Matsumoto, 2007). Como alternativa a la desinfección química está la desinfección térmica, en la que se reducen los microorganismos del suelo mediante la aplicación de calor con la colocación de un plástico (Katan, 2014). Se trata tanto de la solarización como de la biosolarización. En la biosolarización, además de la colocación de plástico se realiza un aporte de materia orgánica fresca, combinando el efecto de la temperatura con los volátiles de la descomposición de la materia orgánica. Ambas alternativas han mostrado resultados positivos, siendo la solarización más común debido a que es más económica (Lombardo et al., 2012).

En Almería, la desinfección del suelo es una técnica generalizada que se realiza anualmente, particularmente desde la desautorización del bromuro de metilo. La tendencia actual es hacia una desinfección libre de productos químicos, por lo

que las distintas alternativas de desinfección están bajo estudio. Si bien la biosolarización ha obtenido buenos resultados (Flores et al., 2008), la solarización parece más aceptada por el agricultor debido a su menor precio (Bach et al., 2016; Rowlings et al., 2019), obteniendo resultados positivos y equiparables a la desinfección química (Rubin et al., 2007).

Estas técnicas de manejo (aporte de materia orgánica y desinfección de suelo) tienen un efecto muy importante sobre las comunidades microbianas del suelo. Además, conocer los efectos que tienen en la microbiota del suelo, el crecimiento de las plantas y la producción es clave para una agricultura sostenible capaz de alimentar a la humanidad a la vez que minimice su efecto negativo sobre el medio ambiente. Por eso, objeto de esta tesis es conocer el efecto de las diferentes técnicas de manejo de la materia orgánica y de la desinfección del suelo sobre las comunidades microbianas edáficas, y cómo éstas influyen en el crecimiento de las plantas y la producción. Focalizamos los experimentos en el monocultivo intensivo bajo plástico del tomate, uno de los más importantes en la provincia de Almería y a nivel mundial.

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## **2. OBJETIVOS GENERALES**

Ante la falta de información sobre el efecto de los aportes de materia orgánica y la desinfección sobre las comunidades microbianas del suelo en invernaderos del sureste de España, así como el efecto que ejercen estas comunidades sobre la producción del cultivo, los objetivos de esta tesis son:

1. Estimar el efecto de las diferentes técnicas de aporte de materia orgánica sobre las características químicas del suelo, la actividad microbiana y la estructura de las comunidades microbianas del suelo a lo largo de un ciclo productivo, así como evaluar el efecto sobre la producción.
2. Evaluar el efecto sobre el crecimiento de las plantas que ejercen las comunidades microbianas asociadas a distintos sistemas de aplicación de materia orgánica en los invernaderos.
3. Cuantificar el efecto de los diferentes métodos de desinfección del suelo de los invernaderos sobre las comunidades microbianas, y cómo éstas afectan a su vez al crecimiento de las plantas y la producción.



## CAPÍTULO II

### **Influence of organic matter management on the activity and structure of soil microbial community in intensive greenhouse farming**





**INFLUENCE OF ORGANIC MATTER MANAGEMENT ON THE  
ACTIVITY AND STRUCTURE OF SOIL MICROBIAL COMMUNITY IN  
INTENSIVE GREENHOUSE FARMING**

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*(En revisión en Applied Soil Ecology)*

**Abstract**

Intensive agriculture impacts physical, chemical, and biological characteristics of soil and thus, the addition to soil of organic matter (OM) can have important consequences for crop production. We examined how three crop management systems differing in the use of OM and synthetic chemical fertilizers influenced (i) tomato production in intensive greenhouse farming, and (ii) the structure and activity of soil microbial communities. We selected three crop management systems including (1) conventional management, using synthetic chemical fertilizers with no OM application (CM); (2) conventional management using synthetic chemical fertilizers that had at least one OM application in the last three years (CMOM); and (3) fully organic management with yearly OM applications and no addition of synthetic chemical fertilizers (ORG). OM addition led to higher soil  $\text{NO}_3^-$  and  $\text{NH}_4^+$  content, influencing nitrogen (N) availability, increasing soil respiration, and modifying the composition of prokaryotic and fungal soil communities. Compared to CM soils, the addition of OM reduced the presence and abundance of potential fungal pathogenic organisms, increased soil respiration and, consequently, microbial

activity. Production results suggest that OM addition to conventionally managed greenhouses (CMOM) was associated with higher crop production than in CM (without OM addition) greenhouses. With organic management (ORG), production was lower and may have been affected by nutrient and pest management practices. Knowledge of how soil organic matter management affects soil microbial community structure and activity, and their influence on crop production, will contribute to the development of more sustainable intensive greenhouse systems.

**Keywords:** amplicon sequencing, intensive agriculture, manure, tomato crop production, respiration.

## 1. INTRODUCTION

There are approximately 170,000 ha of intensively farmed greenhouses in the Mediterranean Basin (Pardossi et al., 2004); the largest concentration of approximately 32,000 is in the province of Almería in southeast Spain (Cajamar Caja Rural, 2019). The different management techniques used in this intensive production system can affect the physical, chemical, and microbiological characteristics of soils. One of the major impacts of crop production on soil properties is how organic matter (OM) addition affects soil organic matter (SOM) (Scotti et al., 2015). Many aspects of how organic matter management influences crop production, in intensive agriculture, are well understood (De Ponti et al., 2012; Kalam et al., 2017; Sacco et al., 2015; Seufert et al., 2012; Stanhill, 1990), particularly nutritional aspects (Ewulo et al., 2008). However, the effects of OM management on soil microbial community structure and function, and its relation to nutrient availability and plant production in these crop systems are largely unknown.

Traditionally, the soil in SE Spain greenhouses is covered with a sand mulch to maintain soil moisture and reduce diel temperature fluctuations (Pardossi et al., 2004; Thompson et al., 2007; Tout, 1990). The sand mulch makes it difficult to add OM because of the cost of pushing sand aside (Valera et al., 2017). Consequently, in many greenhouses in SE Spain, OM is applied every 3-4 years instead of annually. Reduced OM application can increase the requirement for synthetic chemical fertilizers to ensure that crop nutrient requirements are met (Barberis et al., 1995). This can result in excess N being applied which can cause environmental problems (Soto et al., 2015), such as nitrate leaching into groundwater (Gallardo et al., 2006).

Indirectly, low levels of organic matter in soil can contribute to an increased incidence of plant pathogens (Savary et al., 2012), and a decrease of soil microbial

(Wu et al., 2013) and mesofauna abundance and diversity (Battigelli et al., 2004). Soil chemical disinfectants are now banned, which increases the possibility of higher populations of soil-borne plant pathogens (Stapleton and DeVay, 1986). Therefore, knowledge concerning microbial population dynamics and activity in greenhouse soils is a pressing need.

The diversity of soil microbial communities is directly linked to the amount of SOM (Bausenwein et al., 2008; Lee et al., 2019). Soil microbial community composition and structure have a key role in soil function (Hortal et al., 2015; Rodríguez-Echeverría et al., 2013) and crop production. This is because they (1) are the major drivers of SOM mineralization (Duchicela et al., 2012; Postma-Blaauw et al., 2010); (ii) are responsible of soil respiration and function (Mbutia et al., 2015); (iii) are involved in plant health by controlling soil-borne pathogens (Senechkin et al., 2010; van Bruggen et al., 2015), and (iv) affect soil resilience after disturbance (Lehman et al., 2015). Diverse soil microbial communities may also contribute to alleviating soil salinity and other stressful conditions (Delgado-Baquerizo et al., 2020). Generally, when OM is applied regularly, being added to conventional inorganic fertilization, soil microbial communities are more diverse, and crops are healthier and more productive (Bever et al., 2010; Finney and Kaye, 2017; Kardol et al., 2013; Mendes et al., 2011).

Soil respiration is linked to organic matter decomposition and depends on environmental conditions, particularly soil temperature and water availability. Soil respiration is a consequence of soil microbial activity, particularly of three components; roots, mesofauna, and the soil microbial community (Estruch et al., 2020). The interactions between soil organisms are also important drivers of soil respiration as well. For example, high soil respiration is commonly related to high

plant photosynthesis and the release of root exudates, which can lead to higher microbial diversity and activity (Baldocchi et al., 2006). Soil respiration can be used as a biological indicator of soil quality (Bünemann et al., 2018), reflecting soil metabolic activity (Curiel-Yuste et al., 2007), and it can be indirectly related to crop production (Lampthey et al., 2019). These relationships show the importance of soil respiration, which fluctuates seasonally and differs between agroecosystems (Benbi et al., 2019), and requires frequent measurement to understand its dynamics (Curiel-Yuste et al., 2007).

In this study, we address how three different greenhouse management systems, differing in soil OM and synthetic chemical fertilizer application, influence soil microbial community structure, composition, and activity, and how these microbial communities have an effect on crop production in the intensive greenhouse agricultural system of SE Spain. We hypothesized that OM addition will influence microbial community composition, structure, and activity, and that higher OM additions might result in more diverse and active soil microbial communities, which may translate into increased crop production.

## **2. MATERIAL AND METHODS**

### ***Study area and greenhouse selection***

The study was carried out in the province of Almeria, where there are currently more than 32,000 hectares of greenhouses. This greenhouse system is the main producer of fresh market tomato in Spain. The annual cropped surface is approximately 10,000 hectares, and annual production is 890,000 tonnes (MAPA, 2019). In this area, we selected 15 different commercial greenhouses of 1-2 hectares,

growing tomato, with three different soil management systems, having five different greenhouses per management. The three management systems were: (1) conventional management (CM), with no addition of organic matter in the previous ten years, and use of synthetic chemical fertilizers. Synthetic chemical fertilizers met crop nutrient requirements, with a total average input of 370 kg N ha<sup>-1</sup>, 50 kg P ha<sup>-1</sup>, 680 kg K ha<sup>-1</sup>, 290 kg Mg ha<sup>-1</sup> and 45 kg Ca ha<sup>-1</sup> (Papadopoulos, 1991). The applied fertilizers were Ca(NO<sub>3</sub>)<sub>2</sub>, Mg(NO<sub>3</sub>)<sub>2</sub>, KH<sub>2</sub>PO<sub>4</sub>, K<sub>2</sub>SO<sub>4</sub> and a combination of micronutrients, including Fe, Cu, B, Mn, Mo and Zn. They were applied in nutrient solution that was applied every 1-4 days through the drip irrigation system; (2) a conventional management with organic matter addition (CMOM), where there had been at least one addition of organic matter in the previous three years but where synthetic chemical fertilizers were routinely used (as in CM), and (3) organic management (ORG) with organic matter addition every year and without synthetic chemical fertilizer addition. The crop growth cycle was from April (seedling transplant) to July (harvest). Organic matter additions were 18,000 kg ha<sup>-1</sup> per application (recommended dose) of fresh manure. Typically, the applied manure had 65% dry matter, 2.2% of N and 30% of C, and was a mix of 60% goat, 30% sheep, and 10% poultry. In the ORG management, the manure applied was certified as organic. Measurements and sampling within the greenhouses were conducted from April 2017 to July 2017.

### *Soil analyses*

Immediately prior to harvest, 100 ml of soil volume was sampled in each of 10 points randomly distributed in each greenhouse, after removing the sand mulch, to a depth of 10 cm (total soil sampled per greenhouse: 10 X 100 ml). Samples in



each greenhouse were mixed to produce a combined soil sample of 1 L per greenhouse (15 soil samples, 5 per management, 3 managements). Shovels and all material used for sampling were sterilized between different greenhouse samples with 96% ethanol.

Soil nutrients were determined at the CEBAS-CSIC ionomics lab (Murcia, Spain), including total C and N content using a C/N analyzer (LECO Truspec, St. Joseph, MI, USA) and organic C after removal of inorganic carbon with HCl 2N (Schumacher, 2002); anion phosphate ( $\text{PO}_4^{3-}$ ) and sulphate ( $\text{SO}_4^{2-}$ ) concentrations in water extract (1:5 soil:water, w:v) were analyzed by HPLC (Metrohm, HE, Switzerland). Soil nitrate ( $\text{NO}_3^-$ ) and ammonium ( $\text{NH}_4^+$ ) were extracted with potassium chloride (KCl 2M) and their contents were determined with an automatic continuous segmented flow analyzer (model SAN++, Skalar Analytical B.V., Breda, The Netherlands). Other elements were determined after acid digestion with an inductively coupled plasma (ICP) emission spectrometer (ICAP 6500 DUO Thermo; Thermo Scientific, Wilmington, DE, USA) pH was measured in an aqueous solution of 1:2.5 (w:v), with a pH-meter (Crison, Spain).

### ***Soil respiration and crop production***

In the soil of every greenhouse, we randomly established 6 PVC collars 10 cm in diameter to measure soil respiration. Collars were inserted 5 cm into the soil, maintaining the sand mulch above the soil, at mid distance between two adjacent drip emitters and two tomato plants in the same line of drippers/plants. Soil respiration was measured monthly, for four months, during the cropping cycle using a portable infrared gas analyzer (EGM-4) connected to an SRC-1 chamber (PPSystems, Amesbury, MA, USA). For each monthly measurement, measurements

in the different greenhouses were made during a period of five consecutive days, with measurements being made in three greenhouses, selected randomly, per day. Measurements were made when daily air temperatures were highest, between 12:00 and 16:00 GMT each day. Within this time period, respiration measurements were steady.

For each soil respiration measurement, soil temperature and volumetric soil water content (v:v) were measured next to each soil respiration collar, using a thermocouple and a TDR-300 FieldScout soil moisture meter (Spectrum Technologies, Inc., Aurora, IL, USA), respectively. For each soil respiration measurement, three soil temperature readings and three soil moisture measurements were taken; the mean values were used as covariates for the soil respiration analyses.

At the end of the cropping season, the grower's co-operative provided data of total crop production for each greenhouse in the study (Table 1).

**Table 1.** Tomato crop production in greenhouses, provided by co-operative. CM: conventional soil management with no OM application; CMOM: conventional management with OM application, and ORG: fully organic management with yearly OM application and no chemicals added.

| ID    | Management | Production (kg m <sup>-2</sup> ) |
|-------|------------|----------------------------------|
| CM1   | CM         | 9.38                             |
| CM2   | CM         | 8.90                             |
| CM3   | CM         | 9.50                             |
| CM4   | CM         | 12.25                            |
| CM5   | CM         | 7.00                             |
| CMOM1 | CMOM       | 10.88                            |
| CMOM2 | CMOM       | 11.00                            |
| CMOM3 | CMOM       | 9.00                             |
| CMOM4 | CMOM       | 12.00                            |
| CMOM5 | CMOM       | 8.50                             |
| ORG1  | ORG        | 8.50                             |
| ORG2  | ORG        | 8.50                             |
| ORG3  | ORG        | 7.00                             |
| ORG4  | ORG        | 7.50                             |
| ORG5  | ORG        | 7.50                             |

***DNA extraction and quantitative PCR***

DNA was extracted from 250 mg soil samples using the DNeasy Powersoil<sup>®</sup> Kit (Qiagen, Inc., Venlo, Netherlands), following manufacturers protocol. DNA concentration was estimated using a Qubit Fluorometric Quantification (Thermo Scientific, USA) and samples were stored at -80°C.

Quantitative PCR (qPCR) analyses were performed in soil DNA extracts in order to determine the abundance of microbial marker genes for bacteria and fungi. The primer pairs used for the qPCR analyses were 515f (5'-GTGYCAGCMGCCGCGGTAA-3') and 806r (5'-GGACTACNVGGGTWTCTAAT-3') for prokaryote (Walters et al., 2015), and ITS1 (5'-TCCGTAGGTGAACCTGCGG-3'; (Gardes and Bruns, 1993)) and ITS5.8S (5'-CGC TGC GTT CTT CAT CG-3'; (Vilgalys and Hester, 1990)) for fungi, respectively. Amplifications were performed by using a SYBR<sup>®</sup> Green (Sigma-Aldrich, USA) based qPCR method in a CFX96<sup>™</sup> Real-Time PCR Detection System (BioRad Laboratories, USA). Standard curves were prepared in every assay using 10-fold serial dilutions of stock solutions containing the target DNA molecules. The reaction mixture contained 10 µl of 2X PowerUp<sup>™</sup> SYBR<sup>™</sup> Green Master Mix (Applied Biosystems, USA), 1 µl of each primer (20 µM), 10-100ng of template DNA and nuclease free water (Ambion Thermofisher) up to 20 µl of final volume. Amplification conditions were as follows: 95°C for 10 min, bacteria: 35 cycles of 10 s at 95°C, 30 s at 57°C and 30 s at 72°C, fungi: 40 cycles of 15 s at 95°C, 30 s at 53°C and 1 min at 72°C, followed by melt curve from 60°C to 95°C at 0.5 °C increment. Triplicate reactions were performed for each DNA extract, standard curve, and negative control. PCR efficiency for different assays ranged

between 75% and 95% with  $R^2 > 0.9$ . The specificity of amplified products was verified by melting curves and agarose gel electrophoresis analysis.

### *Amplicon sequencing and bioinformatics*

Amplicon sequencing was performed using Earth Microbiome Project (EMP) standard protocols (Thompson et al., 2017) at the facilities of Genyo (Granada, Spain). PCR was done in triplicate on the V4 region of the 16S rRNA gene using the primer pair 515f-806r and on the ITS1 region with the primer pair ITS1f-ITS2 (Walters et al., 2015). Barcoded PCR products were quantified using a Qubit dsDNA (Thermo Fisher Scientific) instrument and pooled in equal concentrations. The multiplexed DNA library was purified using Agencourt AMPure XP beads (Beckman Coulter). DNA quality and size were checked with a High Sensivity DNA Assay (Bioanalyzer 2100, Agilent) and sequenced in an Illumina MiSeq sequencing platform using the Illumina reagent kit V3 (600 cycles) generating 300 bp pair-end reads.

Demultiplexed pair-end Illumina reads were processed using QIIME 2 pipeline v.2019.4 (Bolyen et al., 2019). The cutadapt plugin (Martin, 2011) was used to trim primers. Data was denoised with the q2-dada2 plugin (Callahan et al., 2016) which included: performing sequence quality control, truncation of the reads, stitching R1 and R2 reads, generation of Amplicon Sequence Variants (ASV) and screening out potentially chimeric sequences. PCR negative controls, DNA extraction controls and a commercial mock community sample (ZymoBIOMICS Microbial Community Standard, Zymo Research) were also sequenced. After checking the very weak amplification of the negative and extraction controls and the correct classification at genus level of the 8 bacterial and 2 fungal strains included in

the mock sample (data not shown), control samples were excluded from the analysis. In the case of ITS data, and after a round of analysis, we only used the R1 reads, as the taxonomic classification of the mock community at genus level was less accurate combining R1 and R2 reads. The sequenced dataset has been deposited in the NCBI Biosample Dataset PRJNA629769.

Taxonomy was assigned using the QIIME2 q2-feature-classifier Naïve Bayes machine-learning classifier (Bokulich et al., 2018). The databases SILVA v.132 (Quast et al., 2013) and UNITE v8 dynamic (Kõljalg et al., 2005) were used to train the classifiers for 16S and ITS data, respectively. ASVs assigned to chloroplasts and mitochondria (16S data), and eukaryotic non-fungal lineages (ITS) were removed, as also ASVs not classified at phylum level. Diversity indices such as  $\alpha$ -diversity (observed ASVs and Shannon's diversity index) and  $\beta$ -diversity (Bray-Curtis and Jaccard index) were estimated using q2-diversity plugin after samples were rarified (subsampling without replacement).

We performed a predictive functional profiling of bacterial communities using the PICRUSt software (Langille et al., 2013), that predicts the functional gene content based on KEGG database annotation for reference genomes (Kanehisa et al., 2014). We applied the latest version PICRUSt2 (Douglas et al., 2019), following its GitHub Wiki Manual (<https://github.com/picrust/picrust2/wiki>). These metagenomic predictions are neutral to whether the input sequences are within a taxonomic reference or not, as PICRUSt2 allows the use of ASV sequences as input data instead of ASV taxonomic assignments. ASVs with nearest sequenced taxon index (NSTI)  $>2$  were excluded. Functional predictions were shown as Enzyme Classification numbers (EC numbers) (Kanehisa et al., 2017).

We performed a predictive functional guild analysis of soil fungi ASVs using FUNGuild version v1.0 (Nguyen et al., 2016), a program that parses ASVs into guilds based on taxonomic assignments. We only considered ASVs with either “probable” or “highly probable” confidence, as stated in FUNGuild, which bases guild assignments on a database curated by experts in fungal lineages with >13.000 fungal taxa included (<https://github.com/UMNFuN/FUNGuild/blob/master/README.md>). We note that many fungal ITS sequences were not assignable to any guild, probably as a consequence of no relative sequenced isolates included yet in the database.

### *Statistical analysis*

The effects of OM management on crop production, soil respiration, soil chemical properties, and abundance of bacteria and fungi (qPCR) were analyzed using linear mixed-effects models (LMM), with management practice as the fixed factor. For respiration, when we had multiple measurements per greenhouse, greenhouse ID was included as a random factor. In LMM of soil respiration, OM management, time and their interaction were included as fixed factors, and the PVC-collar was considered the repeated measurement unit. Soil temperature and soil water content were included as covariates in soil respiration analysis. As their effect was not significant, these covariates were not included in the final respiration analysis. When necessary, we selected a variance function structure to avoid heteroscedasticity. Logarithmic transformations of respiration and qPCR results were also needed to meet normality assumptions. The restricted maximum likelihood estimator (REML) was used to run the models. Post-hoc comparisons were performed using Fischer’s LSD test for each factor. The combined effects of biotic

and abiotic factors on respiration were analyzed using a partial least squares regression (PLS) model, where soil chemical properties and prokaryotic and fungal DNA abundance (qPCR results) were included as predictors and respiration was the dependent variable.

Unless otherwise specified, all analyses were done with R 3.5.2 version (R Core Team<sup>®</sup>, 2018) using the interface implemented in InfoStat<sup>®</sup> 2018 statistical software (Di Rienzo et al., 2019). Significance of differences between treatments were set at  $p < 0.05$ . Results throughout the text, figures, and tables are mean  $\pm$  1 SE.

Finally, Calypso software (Zakrzewski et al., 2017) was used to calculate  $\alpha$ -diversity indices on normalized 16S rRNA and ITS datasets, to produce multivariate diagrams and to perform statistical tests on the microbiome data, using the ASV matrix and the taxonomic assignments generated by QIIME2 as input data. We then performed analyses of  $\alpha$ -diversity using a Kuskal-Wallis test at a 95% confident level and  $\beta$ -diversity using PERMANOVAs and calculated a linear discriminant analysis (LDA) effect size (LEfSe) algorithm (Segata et al., 2011) to identify specific features (ASVs, taxa and predicted functions) in soils with significant associations to OM managements ( $p < 0.05$ ).

### 3. RESULTS

#### *Soil nutrients*

Soil chemical properties and nutrient content varied with greenhouse soil management technique, and showed high variability. The most notable differences were in SOM, pH and N forms (Table 2). There were significant differences in total SOM, with CM soils having the lowest levels and the other two greenhouse soils

types having similar contents. There were also significant differences in pH, which was higher in CM soils compared to CMOM and ORG. Total N was higher in CMOM than in CM soils, with ORG being intermediate. N forms showed clear differences, with ammonium content being higher in ORG than in CM soils, and with CMOM being intermediate; Nitrate content tended to be higher in CMOM soils than in the other two treatments, although the differences were not significant (Table 2).

**Table 2.** Soil chemical properties for the three different OM managements. Values represent mean  $\pm$ 1 SE. Different letters indicate significant differences ( $p < 0.05$ ) among greenhouse management treatments (Fischer LSD post-hoc comparisons; in such cases the variable and mean values are highlighted in bold). Legend of greenhouse managements as in Table 1.

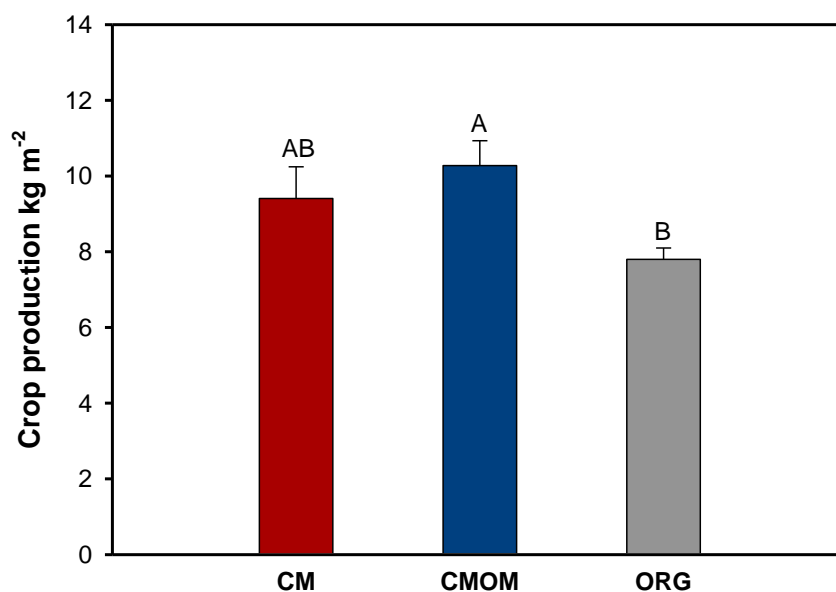
| Variable                          | Unit          | Treatment                         |                                    |                                    | p-value     |
|-----------------------------------|---------------|-----------------------------------|------------------------------------|------------------------------------|-------------|
|                                   |               | CM                                | CMOM                               | ORG                                |             |
| <b>pH</b>                         |               | <b>8.47<math>\pm</math>0.09 A</b> | <b>7.62<math>\pm</math>0.22 B</b>  | <b>8.05<math>\pm</math>0.14 B</b>  | <b>0.01</b> |
| <b>Total N</b>                    | <b>g/100g</b> | <b>0.08<math>\pm</math>0.01 B</b> | <b>0.13<math>\pm</math>0.02 A</b>  | <b>0.15<math>\pm</math>0.04 AB</b> | <b>0.05</b> |
| Total C                           | g/100g        | 1.82 $\pm$ 0.43 A                 | 2.00 $\pm$ 0.32 A                  | 2.22 $\pm$ 0.99 A                  | 0.91        |
| <b>Organic C</b>                  | <b>g/100g</b> | <b>0.54<math>\pm</math>0.12 B</b> | <b>1.01<math>\pm</math>0.15 A</b>  | <b>1.24<math>\pm</math>0.46 A</b>  | <b>0.05</b> |
| <b>Total SOM</b>                  | <b>g/100g</b> | <b>0.93<math>\pm</math>0.20 B</b> | <b>1.75<math>\pm</math>0.25 A</b>  | <b>2.13<math>\pm</math>0.79 A</b>  | <b>0.05</b> |
| CaCO <sub>3</sub>                 | g/100g        | 10.66 $\pm$ 3.73 A                | 8.22 $\pm$ 1.64 A                  | 8.20 $\pm$ 4.43 A                  | 0.84        |
| Al                                | g/kg          | 62.67 $\pm$ 10.81 A               | 42.94 $\pm$ 18.11 A                | 62.16 $\pm$ 21.45 A                | 0.64        |
| Ca                                | g/100g        | 5.69 $\pm$ 2.96 A                 | 3.10 $\pm$ 0.61 A                  | 3.56 $\pm$ 0.87 A                  | 0.66        |
| Cu                                | mg/kg         | 31.45 $\pm$ 8.64 A                | 35.94 $\pm$ 11.70 A                | 28.65 $\pm$ 4.34 A                 | 0.83        |
| Fe                                | g/kg          | 26.70 $\pm$ 2.72 A                | 20.29 $\pm$ 3.68 A                 | 21.63 $\pm$ 3.33 A                 | 0.33        |
| K                                 | g/100g        | 0.89 $\pm$ 0.37 A                 | 0.69 $\pm$ 0.16 A                  | 0.71 $\pm$ 0.13 A                  | 0.89        |
| Mg                                | g/100g        | 0.73 $\pm$ 0.23 A                 | 0.50 $\pm$ 0.10 A                  | 0.76 $\pm$ 0.14 A                  | 0.30        |
| Mn                                | mg/kg         | 465.09 $\pm$ 75.87 A              | 360.15 $\pm$ 70.43 A               | 350.74 $\pm$ 57.28 A               | 0.48        |
| Na                                | g/100g        | 0.16 $\pm$ 0.06 A                 | 0.09 $\pm$ 0.02 A                  | 0.18 $\pm$ 0.06 A                  | 0.32        |
| Pb                                | mg/kg         | 24.88 $\pm$ 6.79 A                | 29.32 $\pm$ 11.92 A                | 20.10 $\pm$ 4.35 A                 | 0.70        |
| P                                 | g/100g        | 0.1 $\pm$ 0.02 A                  | 0.19 $\pm$ 0.06 A                  | 0.20 $\pm$ 0.06 A                  | 0.16        |
| S                                 | g/100g        | 0.05 $\pm$ 0.01 A                 | 0.10 $\pm$ 0.05 A                  | 0.21 $\pm$ 0.15 A                  | 0.36        |
| Zn                                | mg/kg         | 51.59 $\pm$ 5.74 A                | 71.72 $\pm$ 20.56 A                | 56.91 $\pm$ 14.75 A                | 0.63        |
| Cl                                | mg/L          | 13.07 $\pm$ 2.45 A                | 12.07 $\pm$ 2.07 A                 | 11.51 $\pm$ 2.57 A                 | 0.91        |
| NO <sub>3</sub> <sup>-</sup>      | mg/L          | 5.84 $\pm$ 0.71 B                 | 20.09 $\pm$ 7.96 A                 | 5.05 $\pm$ 1.92 B                  | 0.08        |
| <b>NH<sub>4</sub><sup>+</sup></b> | <b>mg/L</b>   | <b>0.90<math>\pm</math>0.13 B</b> | <b>1.19<math>\pm</math>0.04 AB</b> | <b>1.38<math>\pm</math>0.12 A</b>  | <b>0.05</b> |
| SO <sub>4</sub> <sup>2-</sup>     | mg/L          | 45.06 $\pm$ 24.32 A               | 156 $\pm$ 124.98 A                 | 343.32 $\pm$ 303.87 A              | 0.45        |

### *Crop production*

There were differences between CMOM and ORG regarding tomato production, being CM in between (Figure 1). Data suggested that in conventionally managed greenhouses, OM addition contributed to higher production, although



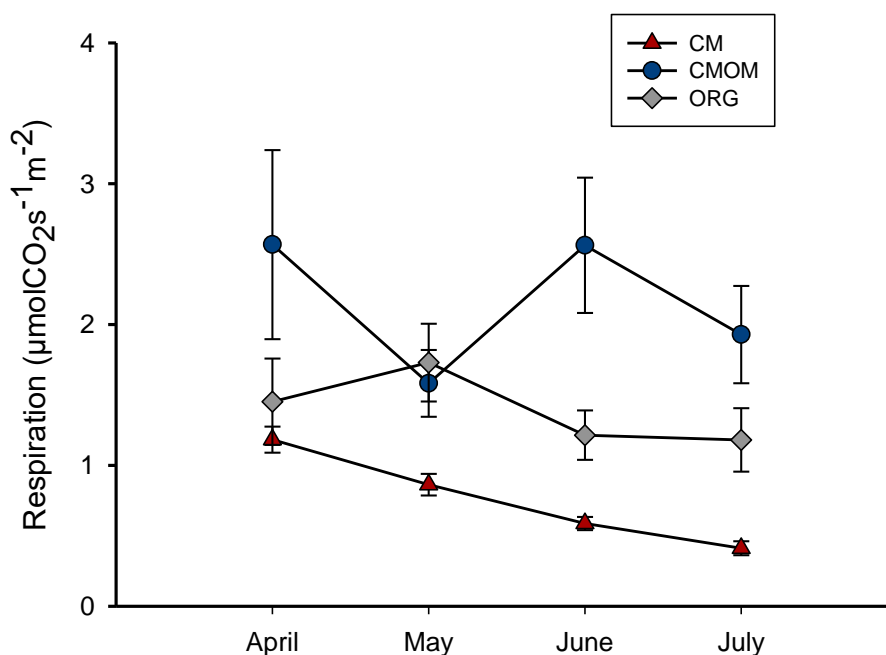
differences may not be significant due to the low number of replicates. This low number was due to availability of greenhouses using the same crop and cycle. Overall, production tended to be higher in CMOM than in CM, being ORG the less productive. Several factors likely affected ORG greenhouses, like limited nutrient supply or pest management, which could have had a negative effect in crop production.



**Figure 1.** Tomato crop production (n=5). Bars are mean value  $\pm 1$  SE. Different letters across bars indicate significant differences ( $p < 0.05$ ) among treatments after Fischer LSD post-hoc tests. Legend of greenhouse managements as in Fig. 1. CM: conventional soil management with no OM application; CMOM: conventional management with OM application, and ORG: fully organic management with yearly OM application and no chemicals added.

### *Soil respiration and microbial communities*

Considering all soils, respiration declined every month during the growing season (Figure 2), with significant differences between months. Overall, CMOM greenhouse soils had the highest respiration rates followed by ORG and then by CM soils, with no significant differences between the latter two (Table 3).



**Figure 2.** Soil respiration rates throughout the crop cycle for different soil greenhouse managements (A). Symbols are means  $\pm 1$  SE ( $n=5$ ). Different letters across symbols indicate significant differences ( $p < 0.05$ ) among treatments after Fischer LSD post-hoc test. Legend of greenhouse managements as in Fig. 1.

**Table 3.** Results of the linear models analyzing the effects of management, month, and their interaction on soil respiration rate ( $\log_{10}$  transformed). Soil humidity and soil temperature (covariates) were not significant, so they were not included in the final model. Tables 3.2 and 3.3 show mean and SE respiration values ( $\log_{10}$  transformed) across greenhouse managements or months; different letters indicate significant differences ( $p < 0.05$ ) among treatment levels after Fischer LSD post-hoc tests. Legend of greenhouse managements as in Table 1.

| (3.1)               |    |         |         |
|---------------------|----|---------|---------|
| Factor <sup>a</sup> | DF | F-value | p-value |
| Management          | 2  | 7.28    | 0.0008  |
| Month               | 3  | 15.39   | <0.0001 |
| Management:Month    | 6  | 0.83    | 0.5460  |

<sup>a</sup>Effects of factors were assessed by repeated measures LMM analysis. Values represent: degrees of freedom (DF), univariate F statistic (F-value) and p-values.

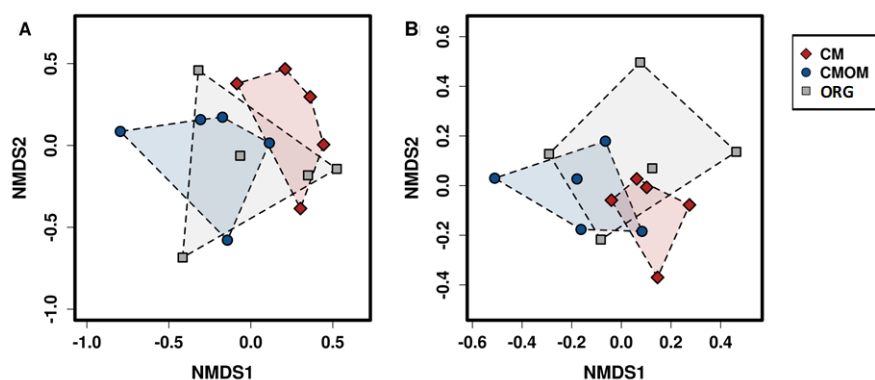
| (3.2)      |      |      |   |
|------------|------|------|---|
| Management | Mean | S.E. |   |
| CM         | 0.42 | 0.01 | B |
| CMOM       | 1.53 | 0.10 | A |
| ORG        | 0.93 | 0.05 | B |

| (3.3) |      |      |   |
|-------|------|------|---|
| Month | Mean | S.E. |   |
| April | 1.71 | 0.25 | A |
| May   | 1.20 | 0.14 | B |
| June  | 1.00 | 0.13 | C |
| July  | 0.94 | 0.15 | D |

Microbial abundance analysis, estimated by qPCR, showed that prokaryotic and fungal abundances and the fungi:prokaryota ratio were similar in soils of the three OM management types (Table S1).

The bioinformatics analysis of the 16SrRNA and ITS gene libraries yielded a total of 21,528 and 829 prokaryotic and fungal ASVs, respectively. Diversity of soil prokaryotic and fungal communities displayed distinctive patterns. While  $\alpha$ -diversity (richness and Shannon-index) did not differ among greenhouse managements (Figs. S1, S2 and Table S2),  $\beta$ -diversity did, revealing a similar pattern for both, prokaryotic and fungal communities (Figure 3). Thus,  $\beta$ -diversity NMDS plots based on Bray-Curtis distance showed a divergence between CM and CMOM, suggesting an effect of the addition of OM on the structure and composition of microbial communities. By contrast, ORG soils displayed a more disperse  $\beta$ -diversity pattern, overlapping CM and CMOM communities. Due to the high variability within managements, particularly in ORG soils, PERMANOVA analyses did not show significant differences concerning  $\beta$ -diversity at the community level (Table S3).



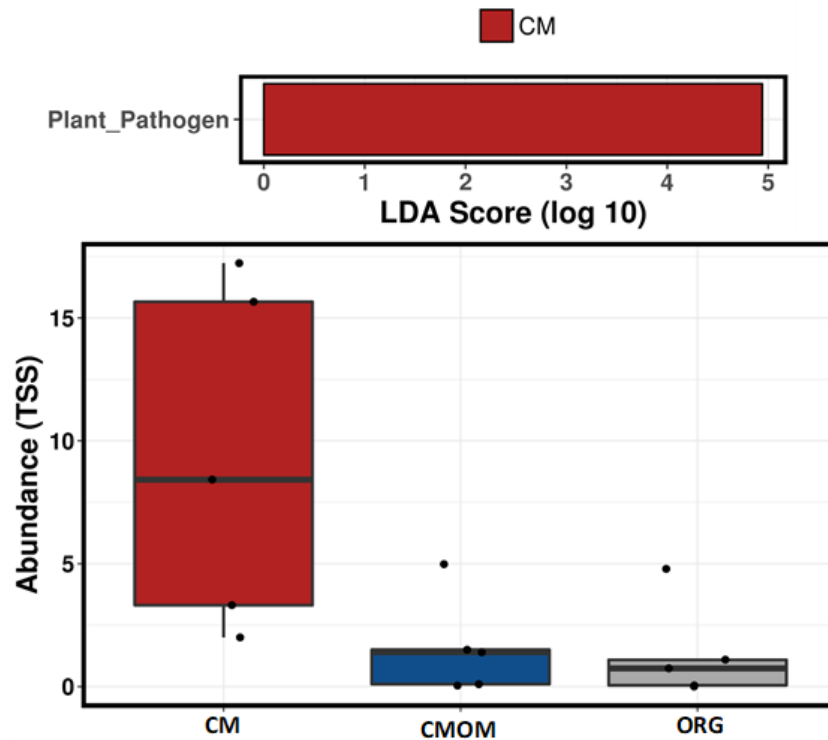
**Figure 3.** Non-metric multidimensional scaling (NMDS) based on Bray-Curtis distance matrices of prokaryotic (A; stress value 0.113) and fungal communities (B; stress value 0.119), n=5. Legend of greenhouse managements as in Fig. 1.

Overall, prokaryotic ASVs were assigned to 47 phyla (4 archaeal and 43 bacterial), but the 10 most abundant phyla accounted for more than 90% of the total number of reads. Predominant phyla were Proteobacteria, Bacteroidetes, Chloroflexi, Acidobacteria, and Firmicutes (Figure S1A). A detailed description of the different taxonomic families and genera of the prokaryotic dataset associated to each soil management is included in Appendices (Appendix 1).

Fungal ASVs were assigned to 10 phyla but, similarly, the three most abundant phyla, Olpidiomycota, Ascomycota and Basidiomycota, did account for more than 90% of fungal ASVs (Figure S1B). A detailed description of the different taxonomic families, genera and ASVs of the fungal dataset associated to each soil management is included in Appendices (Appendix 1). FUNGuild predicted high relative abundances of saprotrophic, parasitic, and pathogenic fungi in all measured soils. Interestingly, results showed only one guild, “plant pathogens”, markedly associated to CM (Figure 4). In total, 21 fungal ASVs were predicted to contribute to this guild, being taxonomically affiliated to different genera of well-known fungal pathogens. Some of these taxa, like *Sclerotinia* or *Plectosphaerella*, were found in high abundance in some CM greenhouse soils and have been reported as infective agents in tomato crops in this region (Table 4). Differences in prokaryotic functional profiles between management systems, as predicted by PICRUSt, are shown in Figure S5.

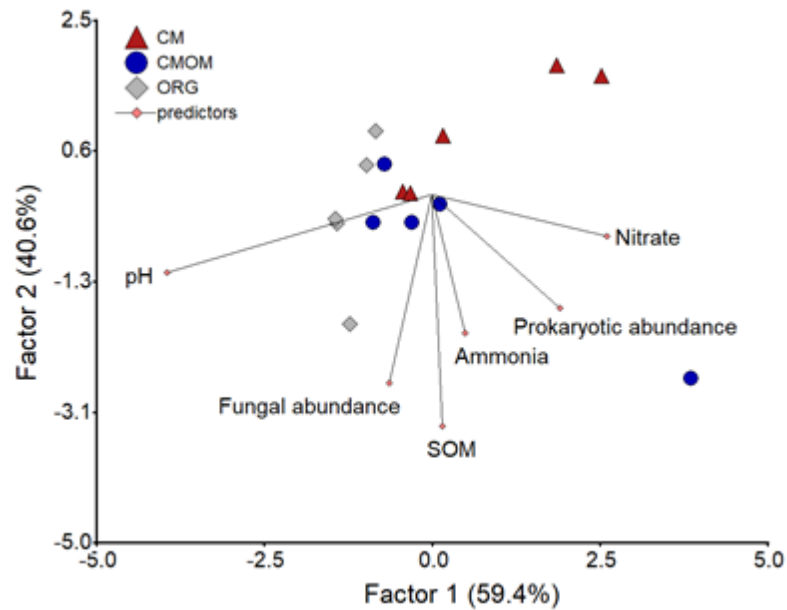
**Table 4.** Plant pathogen guilds, taxonomical association and reports as tomato pathogens. All these ASVs were associated with “probable” confidence. Legend of greenhouse managements as in Table 1. The color pattern represents the percentage of presence of each ASV ID, from green (no presence) to red (maximum percentage of presence).

| ASV ID                           | CM   |      |     |      |      | CMOM |     |     |      |     | ORG |     |     |     |     | Taxonomy | Reported as tomato pathogen |         |
|----------------------------------|------|------|-----|------|------|------|-----|-----|------|-----|-----|-----|-----|-----|-----|----------|-----------------------------|---------|
| da2dca82efc26b0bb7e2ffca27104cba | 0.0  | 12.1 | 0.0 | 0.0  | 0.0  | 0.0  | 0.0 | 0.7 | 0.0  | 0.0 | 0.0 | 1.0 | 0.0 | 0.0 | 0.0 | 0.4      | Plectosphaerella cucumerina | [84-86] |
| a934a70ad3fffaad69f037880a972ed  | 0.0  | 0.0  | 0.7 | 33.1 | 0.0  | 0.0  | 0.0 | 0.0 | 1.3  | 1.5 | 0.0 | 5.7 | 2.6 | 0.0 | 0.0 | 2.5      | Sclerotinia sp.             | [83,84] |
| afc75baa127916aabfb9b668fefbb833 | 13.1 | 5.5  | 1.2 | 0.0  | 0.0  | 0.0  | 0.0 | 8.1 | 0.0  | 6.5 | 2.8 | 0.9 | 0.0 | 0.0 | 0.0 | 0.4      | Plectosphaerella cucumerina | [84-86] |
| 1020e88dac96e318259720cee266b4eb | 14.1 | 1.4  | 0.3 | 0.0  | 0.0  | 0.0  | 0.0 | 0.0 | 0.0  | 6.2 | 0.0 | 0.6 | 0.0 | 0.0 | 0.0 | 0.0      | Plectosphaerella cucumerina | [84-86] |
| 6fc67c653263abec7ea7e48ea7302479 | 0.0  | 0.0  | 0.0 | 1.0  | 20.5 | 0.0  | 0.0 | 0.0 | 0.0  | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0      | Thyostroma sp.              |         |
| b007fa791b38e5ab6fd39b60ae5b4cf4 | 0.0  | 0.0  | 0.0 | 0.0  | 0.0  | 0.0  | 0.0 | 0.0 | 0.0  | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0      | Sclerotinia sp.             | [83,84] |
| 35e37a753885e1303bfd993657140624 | 0.0  | 0.0  | 0.1 | 0.0  | 0.0  | 0.0  | 0.0 | 0.0 | 0.0  | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0      | Monosporascus cannonballus  |         |
| e62e168b81e71ca27eee68415d92d5f2 | 3.3  | 0.0  | 0.0 | 0.0  | 0.0  | 0.0  | 0.0 | 0.0 | 0.0  | 0.0 | 0.0 | 0.0 | 0.6 | 0.0 | 0.0 | 0.0      | Ramularia eucalypti         |         |
| 7f727114b5dce2313cb9e95a98881f1e | 0.0  | 0.0  | 0.0 | 0.0  | 0.0  | 0.0  | 0.0 | 0.0 | 0.0  | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.4      | Plectosphaerella cucumerina | [84-86] |
| 265f89519fe4bfe4c565831029830bf4 | 0.0  | 0.0  | 0.1 | 0.0  | 0.0  | 0.0  | 0.0 | 0.0 | 0.0  | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0      | Mycosphaerella tassiana     |         |
| 374e75b12461a8589201ea354c6c849f | 0.0  | 0.0  | 0.0 | 0.0  | 0.0  | 0.0  | 0.0 | 0.0 | 0.0  | 1.8 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0      | Lectera colletotrichoides   |         |
| ce77650c312e855968a1c8f8037cb90d | 0.0  | 0.0  | 0.0 | 0.0  | 0.0  | 0.0  | 0.0 | 0.0 | 0.0  | 0.2 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0      | Macrophomina phaseolina     |         |
| b7a81aeca8f6c24594fa4020c7c60214 | 0.0  | 0.0  | 0.0 | 0.2  | 0.0  | 0.0  | 0.0 | 0.0 | 0.0  | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0      | Stagonospora sp.            |         |
| beea654f57db872fa891f91a5c10357d | 0.0  | 0.0  | 0.0 | 0.0  | 0.0  | 0.0  | 0.0 | 0.0 | 0.0  | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.1      | Veronaea sp.                |         |
| 21430b009a3fa43df27639697c657361 | 0.0  | 0.0  | 0.0 | 0.0  | 0.0  | 0.0  | 0.0 | 0.1 | 0.0  | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0      | Podosphaera astericola      |         |
| d079226fa51c93f00f538a52aa70abfe | 0.0  | 0.0  | 0.0 | 0.0  | 0.0  | 0.0  | 0.0 | 0.0 | 0.0  | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.7 | 0.0      | Sclerotinia sp.             | [83,84] |
| 08146d1e3ce889d4f96b6b10418c0803 | 0.0  | 0.0  | 0.0 | 0.0  | 0.0  | 0.0  | 0.0 | 0.0 | 0.0  | 0.0 | 0.0 | 0.0 | 0.2 | 0.0 | 0.0 | 0.0      | Devriesia pseudoamericana   |         |
| cf7a81c2a8505f4199d36d62c52d17f5 | 0.0  | 0.0  | 0.0 | 0.0  | 0.0  | 0.0  | 0.0 | 0.0 | 0.0  | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.1      | Podosphaera astericola      |         |
| e138850dbbcf24b5e29319574ec7963c | 0.0  | 0.0  | 0.0 | 0.0  | 0.0  | 0.0  | 0.0 | 0.0 | 0.0  | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0      | Volutella sp.               |         |
| c30dd7e27a93fc5ef1fb938543fd646b | 0.0  | 0.0  | 0.0 | 0.0  | 0.0  | 0.0  | 0.0 | 0.1 | 0.0  | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0      | Stagonosporopsis sp.        |         |
| ff96986abc4e40611d332e74e05ceddc | 0.0  | 0.0  | 0.0 | 0.0  | 0.0  | 0.0  | 0.0 | 0.0 | 0.0  | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.3 | 0.0      | Plectosphaerella cucumerina | [84-86] |
| Plant pathogens ASVs (%)         | 30.5 | 19.0 | 2.4 | 34.3 | 20.5 | 0.0  | 8.9 | 1.4 | 16.0 | 3.1 | 8.2 | 3.4 | 0.0 | 1.0 | 3.9 |          |                             |         |



**Figure 4.** Linear discriminant analysis (LDA) effect size (LEfSe) performed on fungal guilds, showing the only feature significantly associated with a management system (logarithmic LDA score  $\geq 2$ ,  $p < 0.05$ ) (A). Boxplot showing the relative abundance of the guild “Plant pathogen” in each greenhouse soil management. TSS = Total Sum Scaling (relative abundance of sequences). (B)  $n=5$ . Legend of greenhouse managements as in Fig. 1.

We analyzed the effects of microbial abundance, nutrient content, and pH on soil respiration rate using PLS regression analysis, where prokaryote and fungal abundance and soil variables such as ammonium, nitrate, total SOM and pH were included as predictors and soil respiration as the response variable. CM and CMOM managements clearly separated, with ORG in between. Nitrate, pH, and prokaryote abundance were negatively linked to soil respiration rates (Figure 5).



**Figure 5.** Regression diagram (Partial least squares - PLS) showing the effects of soil microbial abundance (qPCR), pH and nutrients (predictor variables) on soil respiration among three different greenhouse OM management practices (n=5). Legend of greenhouse managements as in Fig. 1.

#### 4. DISCUSSION

Organic matter management in the different intensive greenhouse studied influenced soil microbial communities, affecting their structure and function. As a consequence, soils had different microbial activity, as indicated by soil respiration, and soil chemical properties. These data could help farmers to develop more sustainable intensive cropping practices. In our study, we selected 15 different commercial greenhouses, five per OM management type, which resulted in different soil properties and microbial communities across OM managements. The results demonstrated the strong influence of soil OM management on soil chemical properties and soil microbial community composition, structure, function and activity, and the consequence of this management on crop production.

We recorded overall higher respiration rates in CMOM greenhouses than in CM, with ORG being intermediate, which suggested a combined effect of organic and inorganic fertilization in CMOM (Song et al., 2018). The higher respiration rate in CMOM may have contributed through more turnover of root biomass, root exudation and possibly larger rhizosphere populations. The lack of differences in respiration between CM and ORG was probably mostly due to the high variability in soil respiration. As we did not use experimental greenhouses, but commercial ones, factors such as the type of greenhouse, climate control or soil texture could contribute to differences observed between systems. In the CM and ORG greenhouses, soil respiration decreased at the end of the crop cycle, probably due to SOM decrease.

Respiration rate was positively related to the combination of OM addition and inorganic fertilizer supply (Mbuthia et al., 2015), represented in CMOM greenhouses. This effect of OM application has been related to higher soil microbial activity (Song et al., 2018), likely because of the organic C content, as well as the total N and ammonium contents of the added OM. On one hand, organic C content, which was higher in CMOM and ORG than in CM, increased microbial respiration. On the other hand, total N content (and marginally nitrate) was higher in CMOM than in CM soils, the latter with only inorganic N addition, while in CMOM soils there was a combination of inorganic N addition and organic N addition from OM application. These combined N additions in CMOM might favor higher N uptake by plants, which increased soil respiration in this greenhouse management, an indicator of higher microbial activity. Besides, higher nitrate and ammonium content is related to higher respiration rates which had a consequence of higher microbial activity (Feng et al., 2015), higher N uptake and linked to avoiding N limitation (Zakrzewski



et al., 2017). In our results, only ammonium was positively related to soil respiration. This could be because nitrate content was more variable, with high variance in CMOM. Soil pH was basic in all cases but our results showed that lower pH (CMOM soils) also increased respiration, as reported by Blagodatskaya and Anderson (1998), relying on the fact that with pH above 8 nutrient availability decreases.

The addition of OM to conventionally managed soils was associated with higher crop production, which tended to be more productive than CM greenhouses. These results suggest beneficial effects of OM addition in intensive agriculture, as reported by Zink and Allen (1998). Furthermore, the combination of inorganic and organic fertilization has been reported to increase plant N uptake compared to just synthetic chemical fertilization (N'Dayegamiye et al., 2013). There was a link between soil respiration and production, being respiration generally higher in CMOM than in CM soils. Microbial richness was not affected by management practices, which contrasted other reports (Francioli et al., 2016; Hartmann et al., 2015; Lori et al., 2017) that reported higher bacterial richness in greenhouse soils when organic amendments were applied. By contrast, Bonanomi et al. (2016) found higher bacterial diversity in conventional than in organic greenhouses, suggesting it was a consequence of microbial community selection in response to synthetic chemical fertilizer addition.

The lack of a clear relationship between OM management and fungal diversity in intensive agriculture is surprising. Similarly, Hartmann et al. (2015) did not find changes in fungal diversity when OM was added, compared to a conventionally-managed soil. Our results showed high variability in microbial community composition between greenhouses under the same OM management system, which was probably related to diverse factors, such as manure type and

origin, and OM application frequency. In this sense, community coalescence, the process of mixing soil microbial communities from diverse origins, and the time needed to reach a new equilibrium (Wu et al., 2019), might have contributed to this variability. In ORG soils, with continuous addition of manure from different origins, and thus carrying different microbes, microbial communities might be farther from reaching an equilibrium status than in the other two management systems, where no exogenous organic matter is added (CM) or it is added but less often (CMOM).

Our data showed that several prokaryotic taxa were associated to specific OM management. For example, the genus *Thauera* was significantly linked to the ORG treatment. This genus has been reported to be associated with denitrification at pH of <8 (Shinoda et al., 2004; Song et al., 1998) and is involved in the N cycle when ammonium concentrations are high in aerobic conditions (Fang et al., 2020), as in our ORG greenhouses. *Actinomadura* was associated with the CMOM greenhouses; this genus is associated with composting manure, having a key role as a growth-promoting rhizobacteria (PGPR; (Wani and Gopalakrishnan 2013)). *Actinomadura* is one of the most studied Actinomycetes in soil agronomy because its potential application in agriculture due to its capacity to produce natural antibiotics against plant pathogens (Maskey et al., 2003; Nakamura et al., 1981; Patel et al., 1984). It is also involved in the N cycle in presence of high SOM content (Zeffa et al., 2020). *Pirellula* was associated to CM; it is an anaerobic  $\text{NH}_4^+$  oxidizing (Anammox) bacteria which uses  $\text{NO}_2^-$  to oxidize  $\text{NH}_4^+$  and to generate  $\text{N}_2$  under anaerobic conditions (Xia et al., 2019). In CM with no OM applications, soils might be less permeable (Zebarth et al., 1999) and  $\text{O}_2$  could be limiting, favoring *Pirellula*, which decreases when OM is applied (Cheng et al., 2019). There were also some fungal ASVs associated to ORG, including *Pseudallescheria*, *Stemphylium*, *Phaeotheca*

and *Wallemia*. To our knowledge, this is the first time that these genera have been linked to organic agriculture, a fact that deserves further research.

We found potential fungal pathogens associated to the CM management, whose presence is likely to be a consequence of the low SOM levels (Li et al., 2014); generally, OM applications enhance the control of fungal soil-borne diseases (Bonanomi et al., 2017; Jaiswal et al., 2017). In CM soils, we found various pathogenic genera like *Monosporascus*, *Mycosphaerella*, *Plectosphaerella*, *Ramularia*, *Sclerotinia*, *Stagonospora* and *Thyrostroma*. *Sclerotinia*, which has been reported as a specific tomato soil-borne pathogen, infecting roots and causing production loss (Adams and Ayers, 1979; Lobo Jnr et al., 2000); *Plectosphaerella* has also been reported as a tomato pathogen in Italy (Carlucci et al., 2012), Australia (Pascoe et al., 1984) and China (Xu et al., 2014), causing tomato wilt. Interestingly, and in relation to prokaryotes, the enzyme peroxiredoxin, a PICRUST-predicted prokaryotic functional pathway associated to CM, has been previously reported as a bioindicator of stress situations and plant pathogens in soils (Ghabooli et al., 2013). This enzyme plays a key role in reactive oxygen species when plant defenses are activated (Wang et al., 2019), perhaps due to the higher abundance of fungal pathogens in CM soils.

## 5. CONCLUSIONS

This study focused on developing a better understanding of the effects of OM management practices on the soil microbial community and on crop production to reach more sustainable intensive greenhouse systems. Our data show the influence that different OM management practices have on soil microbial community

composition, structure and function. Such differential effects led to higher microbial activity with OM addition, which decreased soil-borne pathogens and show a pattern positively influencing crop production.

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## 7. APPENDIX 1

### *Detailed description of the different taxonomic families and genera of the prokaryotic and fungal dataset.*

We calculated a linear discriminant analysis (LDA) effect size (LEfSe) algorithm to determine features (taxa and ASVs) significantly associated with a particular SOM management. In the prokaryotic dataset, LEfSe identified nine families and 25 genera (LDA score > 2 and  $p < 0.05$ ; Figures S2-3). Some of these microbial taxa included abundant lineages clearly associated to different SOM managements (LDA > 3,  $p < 0.05$ ), like the families *Rhodocyclaceae* (associated to ORG) and *Pedospaeraceae* (CM), and the genera *Thauera* (ORG), *Actinomadura* (CMOM), *Pirellula* (CM) and candidate MM2 (CM). In a closer look at ASV level, LEfSe identified 52 significant ASVs (LDA > 2,  $p < 0.05$ ; Figure S4A), covering a broad phylogenetic spectrum (10 phyla). Overall, three of the five phyla with higher effect size ASVs (LDA > 3,  $p < 0.05$ ), were Bacteroidetes, Proteobacteria and Acidobacteria, which were associated to ORG soils, and one (Gemmatimonadetes) to CM (Figure S4B), and the predicted functional enzymatic gene profiles of prokaryotic communities identified eight enzymatic types significantly associated to particular SOM managements (Figure S5). The LDA-LEfSe algorithm analysis on soil fungal communities identified did not identified families or genera associated to any management. In a closer look, four ASVs associated to ORG management (LDA > 3,  $p < 0.05$ ) belonging to the Ascomycota and Basidiomycota phyla (Figure S6).



## 8. SUPPLEMENTARY MATERIAL

**Table S1.** Microbial abundance and prokaryote:fungi ratio determined by qPCR. Values are mean  $\pm$ 1 SE. Different letters in a column show significant differences ( $p < 0.05$ ) between treatments (Fischer LSD post-hoc comparison). CM: conventional soil management with no OM application; CMOM: conventional management with OM application, and ORG: fully organic management with yearly OM application and no chemicals added.

| Management | Prokaryote<br>Log <sub>10</sub> (16S copies g <sup>-1</sup> ) | Fungi<br>Log <sub>10</sub> (ITS copies g <sup>-1</sup> ) | Prokaryote:Fungi        |
|------------|---|--|-------------------------|
| CM         | 8.39 $\pm$ 0.29 A   | 5.26 $\pm$ 1.19 A  | 7062.47 $\pm$ 3502.75 A |
| CMOM       | 8.91 $\pm$ 0.43 A   | 5.69 $\pm$ 0.60 A  | 3632.35 $\pm$ 1906.68 A |
| ORG        | 8.77 $\pm$ 0.61 A   | 5.69 $\pm$ 1.12 A  | 4103.12 $\pm$ 2352.98 A |

**Table S2.** Results of Kruskal-Wallis analysis of total ASV richness and Shannon index comparing the different SOM managements. Legend of greenhouse managements as in table S1.

| Factor <sup>a</sup>      | Prokaryota (16S) |         |               |         | Fungi (ITS) |         |               |         |
|--------------------------|------------------|---------|---------------|---------|-------------|---------|---------------|---------|
|                          | Shannon          |         | Observed ASVs |         | Shannon     |         | Observed ASVs |         |
|                          | H                | p-value | H             | p-value | H           | p-value | H             | p-value |
| Management               | 0.14             | 0.93    | 0.42          | 0.81    | 0.50        | 0.78    | 0.02          | 0.99    |
| Managements <sup>b</sup> | H                | p-value | H             | p-value | H           | p-value | H             | p-value |
| CM-CMOM                  | 0.10             | 0.75    | 0.10          | 0.75    | 0.88        | 0.35    | 0.04          | 0.83    |
| CM-ORG                   | 0.10             | 0.75    | 0.27          | 0.60    | 0.01        | 0.92    | 0.10          | 0.75    |
| CMOM-ORG                 | 0.01             | 0.92    | 0.27          | 0.60    | 0.01        | 0.92    | 0.01          | 0.92    |

<sup>a</sup>Effects of factor “Management” were assessed by Kruskal-Wallis analysis taking into account all groups. Values represent the univariate H statistic and the p-value at 95% confidence level.

<sup>b</sup>Pairwise comparisons between management systems. Values represent the univariate H statistic and the p-value at 95% confidence level assessed by Kruskal-Wallis analysis.

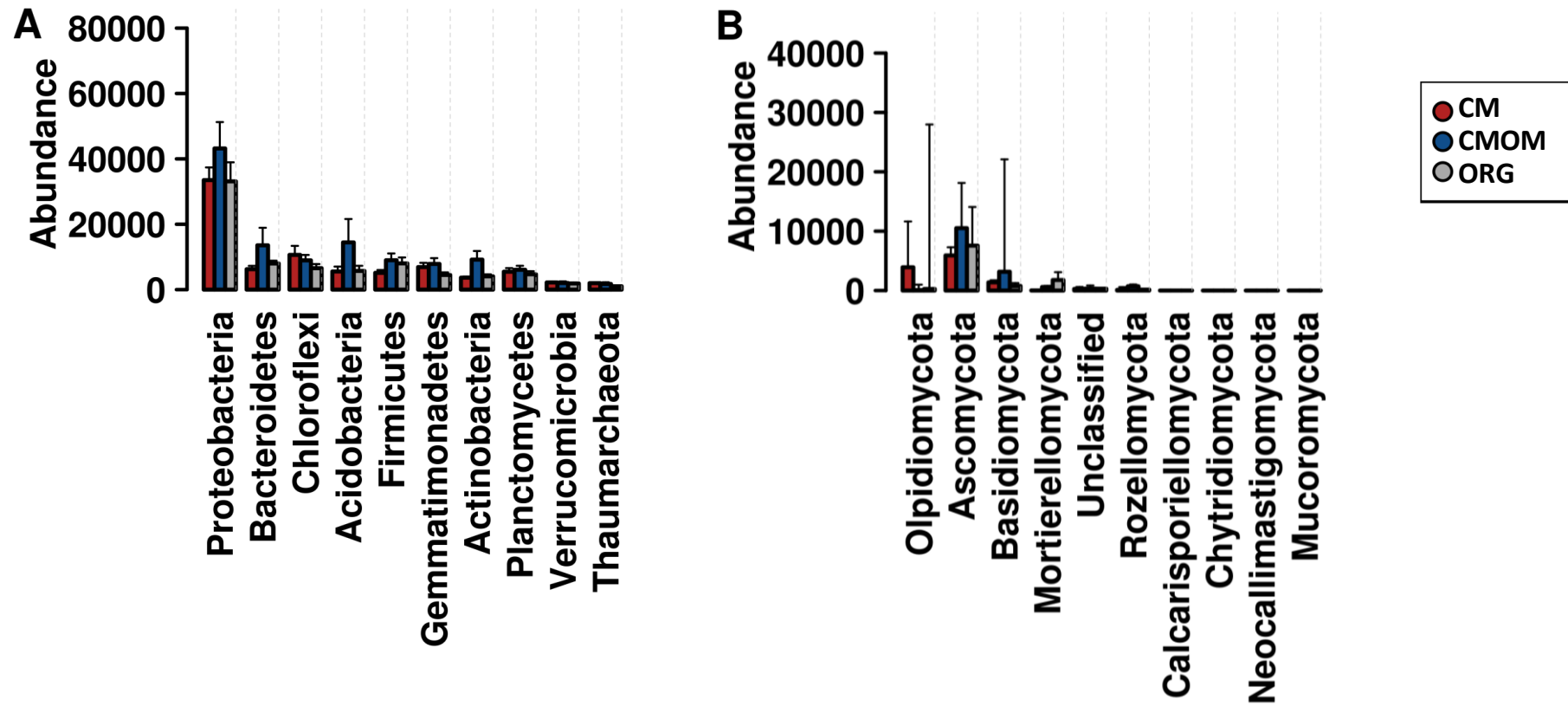
**Table S3.** PERMANOVA analysis of  $\beta$ -diversity based on Bray-Curtis and Jaccard distances comparing the three SOM management practices. Legend of greenhouse managements as in table S1.

| Factor <sup>a</sup>      | Prokaryota (16S) |         |          |         | Fungi (ITS) |         |          |         |
|--------------------------|------------------|---------|----------|---------|-------------|---------|----------|---------|
|                          | Bray-Curtis      |         | Jaccard  |         | Bray-Curtis |         | Jaccard  |         |
|                          | Pseudo-F         | p-value | Pseudo-F | p-value | Pseudo-F    | p-value | Pseudo-F | p-value |
| Management               | 0.97             | 0.57    | 1.00     | 0.47    | 1.00        | 0.46    | 1.00     | 0.50    |
| Managements <sup>b</sup> | Pseudo-F         | p-value | Pseudo-F | p-value | Pseudo-F    | p-value | Pseudo-F | p-value |
| CM-CMOM                  | 1.07             | 0.24    | 1.06     | 0.18    | 1.00        | 0.51    | 1.03     | 0.40    |
| CM-ORG                   | 1.01             | 0.36    | 1.00     | 0.40    | 0.85        | 0.67    | 0.94     | 0.74    |
| CMOM-ORG                 | 0.85             | 0.91    | 0.94     | 0.80    | 1.15        | 0.13    | 1.02     | 0.34    |

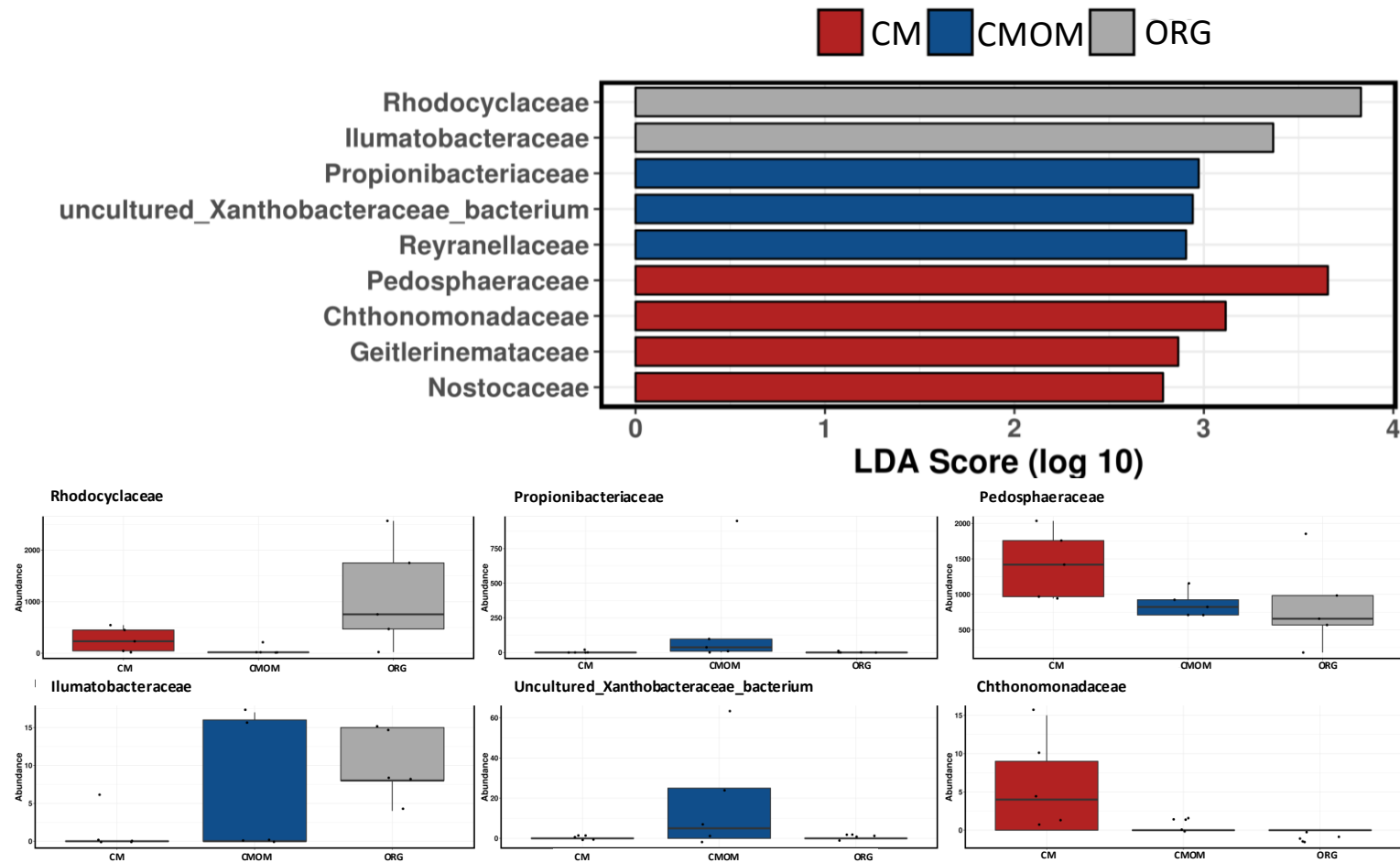
<sup>a</sup>Effects of factor “Management” were assessed by PERMANOVA analysis taking into account all groups. Values represent the univariate Pseudo-F and the p-value at 95% confidence level.

<sup>b</sup>Pairwise comparisons between management systems. Values represent the univariate Pseudo-F and the p-value at 95% confidence level assessed by PERMANOVA analysis.

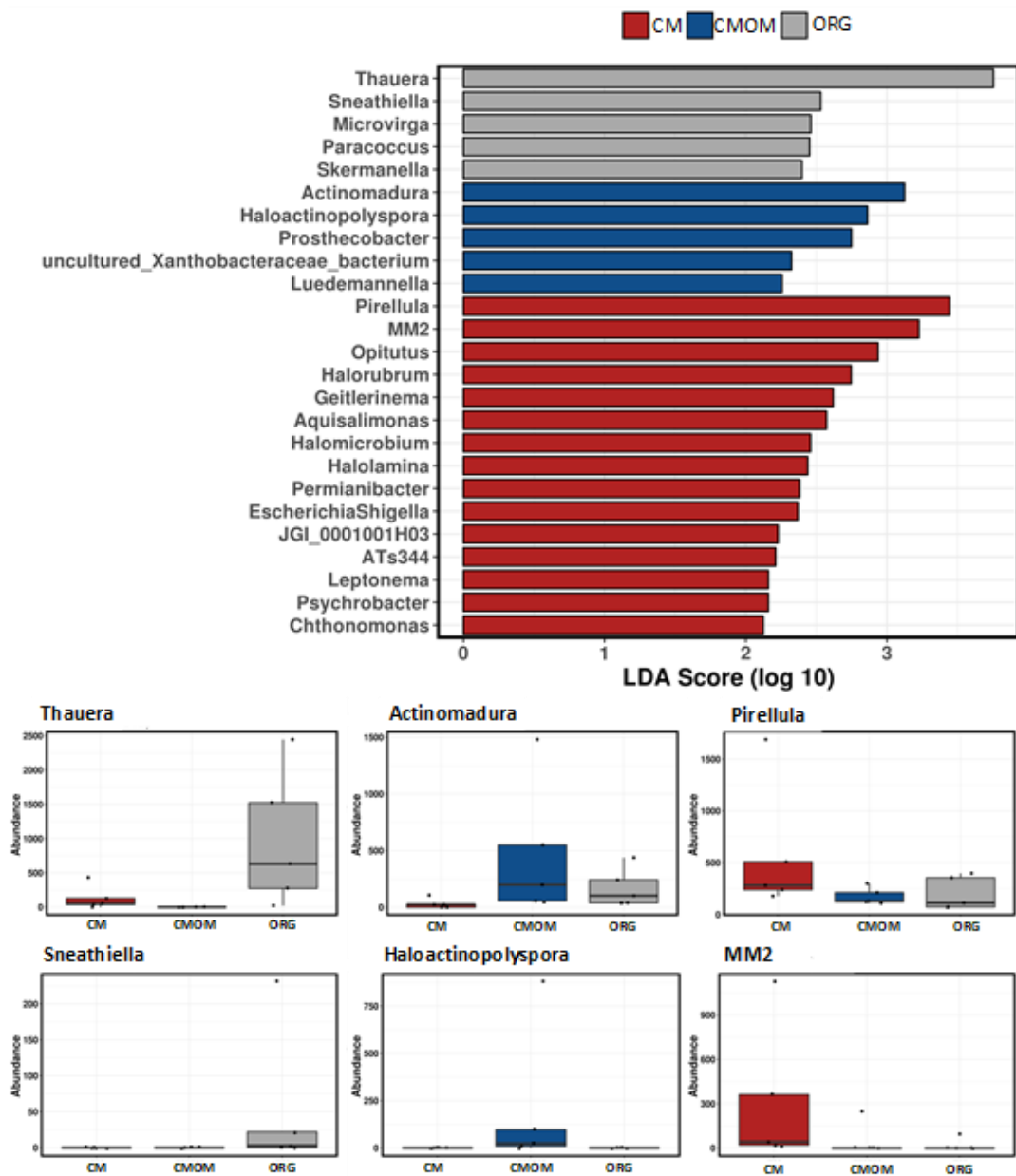
**Figure S1.** Relative abundance of the ten more frequent prokaryotic (A) and fungal (B) phyla. Bars represent mean  $\pm$ 1 SE. CM: conventional soil management with no OM application; CMOM: conventional management with OM application, and ORG: fully organic management with yearly OM application and no chemicals added.



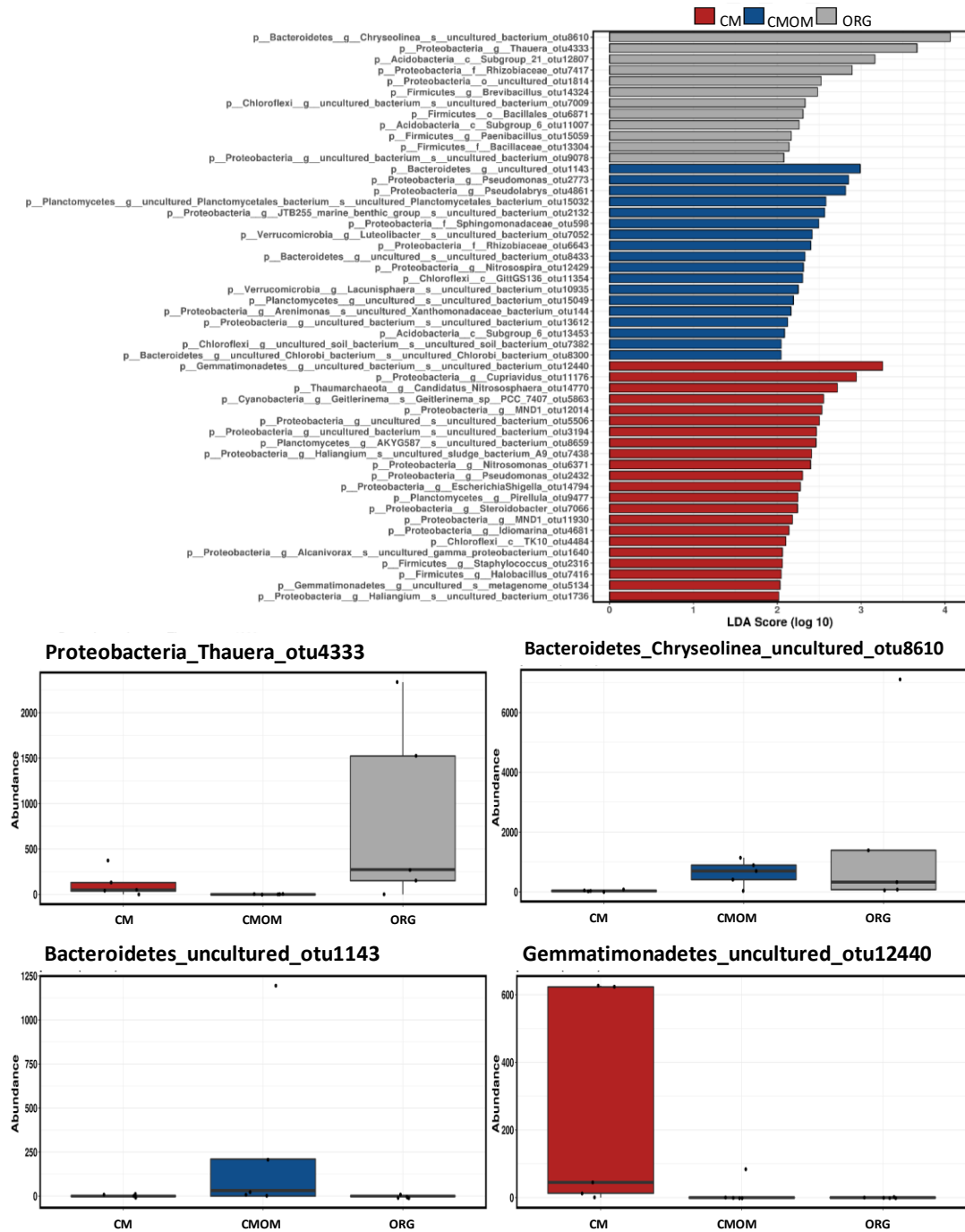
**Figure S2.** Prokaryotic families associated to particular OM management practices (LDA>2, p<0.05) (A). Boxplots representing relative abundance of the highly significant features (LDA>3, p<0.05) (B). Legend of greenhouse managements as in Fig. S1.



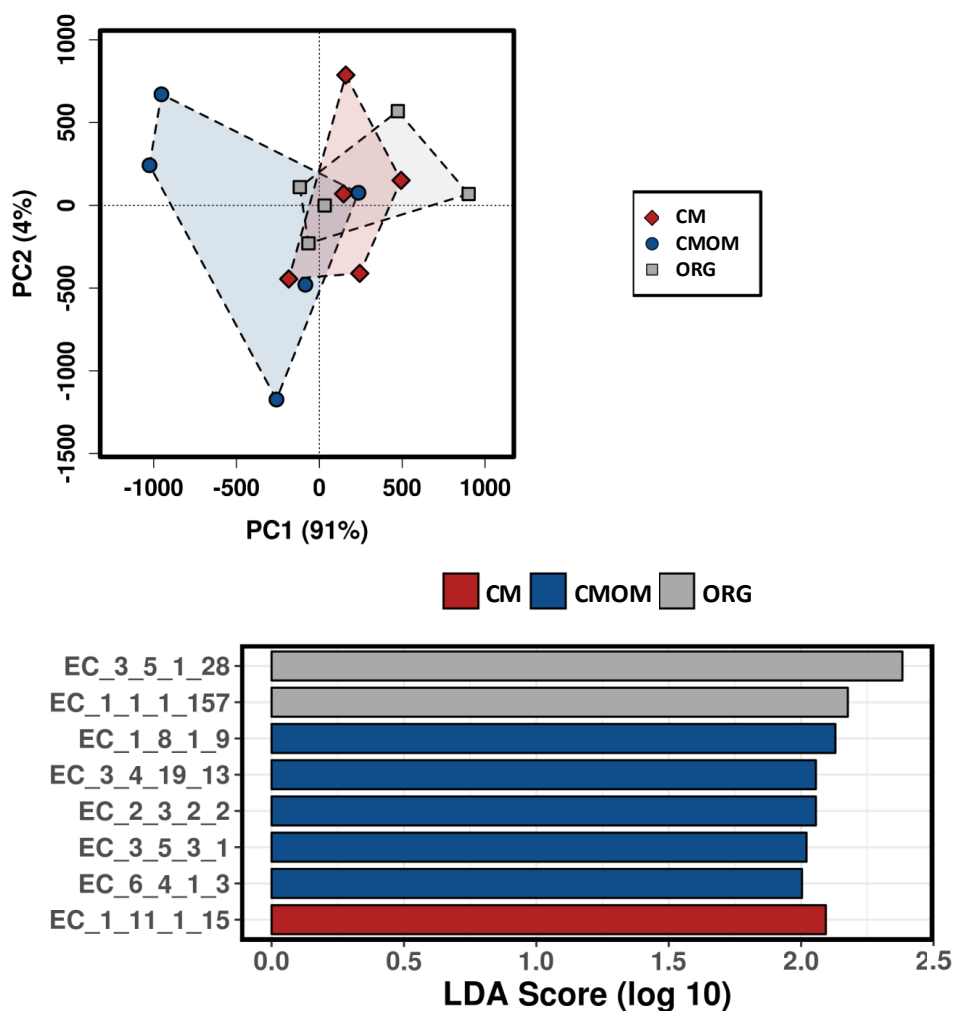
**Figure S3.** Prokaryotic genera associated to OM management practices (LDA>2, p<0.05) (A). Boxplots representing relative abundances of the highly significant features (LDA>3, p<0.05) (B). Legend of greenhouse managements as in Fig. S1.



**Figure S4.** Prokaryotic ASVs associated to OM management practices (LDA>2, p<0.05) (A). Boxplots representing relative abundances of the highly significant features (LDA>3, p<0.05) (B). Legend of greenhouse managements as in Fig. S1.



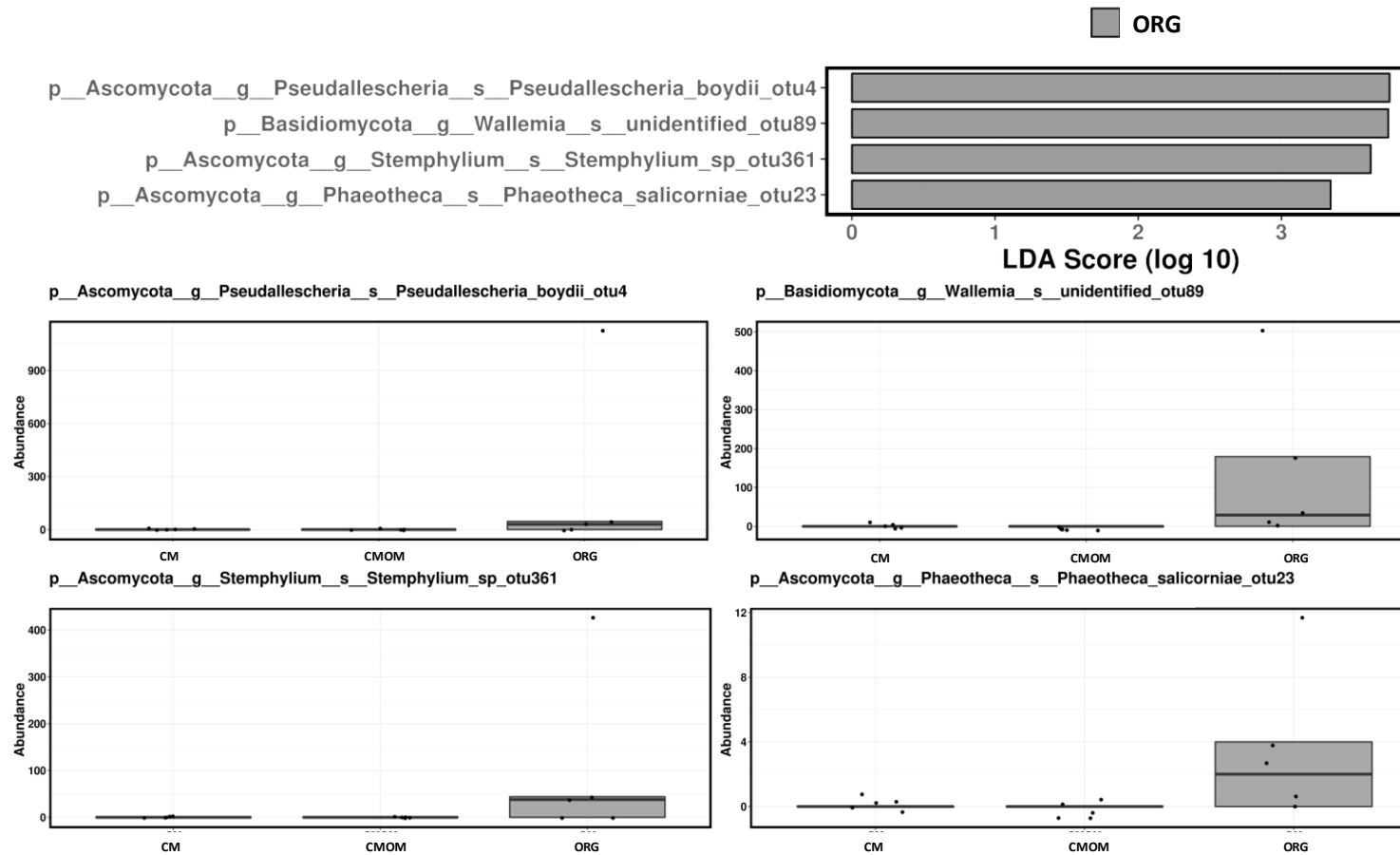
**Figure S5.** Principal coordinates analysis (PCoA) based on the Bray-Curtis distance of Enzymes Classification (EC) data inferred by Picrust2 (A). Results of linear discriminant analysis effect size (LDA-LEfSe) showing the EC numbers significantly associated to particular OM managements (LDA>2, p<0.05) (B). Description of EC numbers identified by LEfSe (C). Legend of greenhouse managements as in Fig. S1.



| Selected feature | Predicted functional pathway       | LDA Score | Associated Group |
|------------------|------------------------------------|-----------|------------------|
| EC_3_5_1_28      | N-acetylmuramoyl-L-alanine amidase | 2.3825781 | ORG              |
| EC_1_1_1_157     | 3-hydroxybutyryl-CoA dehydrogenase | 2.1763900 | ORG              |
| EC_1_8_1_9       | Thioredoxin-disulfide reductase    | 2.1294294 | CMOM             |
| EC_2_3_2_2       | Gamma-glutamyltransferase          | 2.0557693 | CMOM             |
| EC_3_4_19_13     | Pyroglutamyl-peptidase I           | 2.0557693 | CMOM             |
| EC_3_5_3_1       | Arginase                           | 2.0203345 | CMOM             |
| EC_6_4_1_3       | Propionyl-CoA carboxylase          | 2.0033495 | CMOM             |
| EC_1_11_1_15     | Peroxiredoxin                      | 2.0934232 | CM               |



**Figure S6:** Fungal ASVs associated to particular OM management practices (LDA>2, p<0.05) (A). Boxplots representing relative abundances of the highly significant features (LDA>3, p<0.05) (B). Legend of greenhouse managements as in Fig S1.





## **CAPÍTULO III**

### **Effects of soil microbial communities associated to different soil fertilization practices on tomato growth in intensive greenhouse agriculture**





**EFFECTS OF SOIL MICROBIAL COMMUNITIES ASSOCIATED TO DIFFERENT SOIL FERTILIZATION PRACTICES ON TOMATO GROWTH IN INTENSIVE GREENHOUSE AGRICULTURE**

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**ABSTRACT**

Intensive greenhouse vegetable production is one of the most important economic activities in south-east Spain. Agricultural intensification has limited the application of organic matter (OM) in favor of synthetic chemical fertilizers, leading to altered soil microbial communities and production loss. We addressed the effects of soil microbial communities on plant productivity depending on different soil management practices in greenhouse agriculture. Greenhouse managements were i) conventional (i.e., with addition of synthetic chemical fertilizers) without organic amendments (CM), ii) conventional with organic amendments (CMOM) and with addition of synthetic chemical fertilizers, and iii) organic management with annual organic amendments and with no synthetic chemical fertilizer addition (ORG). We extracted soil microbial communities from five greenhouses per management type, added these inocula to pots with sterile substrate (peat:sand), and seeded disinfected tomato seeds. Plants grew for two months without nutrient addition (only water irrigation). Immediately prior to the end of the study, we measured photosynthetic rate, plant growth, and leaf functional traits. At the end of study, pot substrates

inoculated with i) ORG soil communities had higher bacterial abundance (qPCR) compared to microbial communities inoculated with CM extracts; and ii) prokaryotic communities of CM and CMOM substrates differed in composition. Besides, substrates inoculated with CM inocula were significantly associated with the presence of a potential fungal pathogen. Plants inoculated with extracts from organic greenhouses grew more and had a higher photosynthetic rate than plants receiving soil microbial extracts from greenhouses with conventional management. There were differences in the  $\text{NO}_3^-$ , total N and organic matter contents of substrates between treatments at the end of the study, but not at the beginning of the study, suggesting differences in microbial activity between treatments. Although substrate N content differences did not translate into differences in leaf N, leaf  $\delta^{15}\text{N}$  differed between treatments, indicating that the source of the soil microbial inocula influenced the N compound used by the tomato plants. Overall, this study suggested that soil microbial communities from organic greenhouses had a positive effect on crop productivity in intensive greenhouse agriculture.

**KEYWORDS:** microorganisms; organic agriculture; organic matter; soil inoculum.

## 1. INTRODUCTION

Soil microbial communities play a key role in every ecosystem around the world, establishing feedback processes with plants that influence nutrient cycling (Pugnaire et al., 2019), soil respiration (Mbuthia et al., 2015), plant growth (Bever et al., 2010), plant health (Mendes et al., 2011), and plant community composition (Bennett et al., 2017) amongst others. High microbial diversity enables high resilience of the soil community to disturbance, and by enhancing soil fertility (van Elsas et al., 2012) which increases plant productivity in agrosystems (Finney and Kaye, 2017). For this reason, soil microbial diversity is an important factor in most agricultural soil monitoring studies (Entry et al., 2008), as well as in sustainability studies (Bender and van der Heijden, 2015). Many approaches are used to assess soil microbial diversity; these can be generally considered to assess three broad characteristics: genetic, functional, and structural diversity (Nielsen and Winding, 2002). Some reports have shown the importance of addressing all three approaches because they may not be correlated (Griffiths et al., 2001) nor have the same effects on soil fertility or agrosystem productivity (Strickland et al., 2009).

Changes in soil microbial communities over time are influenced by factors such as organic matter input, plant-microbe interactions and feedback mechanisms (Pugnaire et al., 2019), microbe-microbe competition (Hortal et al., 2015), soil properties such as pH, and C, N and P contents (Lozano et al., 2020), and land use history (Estruch et al., 2018). In agrosystems, plant-microbe interactions are critical and microbial diversity usually enhances plant productivity (Chen et al., 2020). However, increasing use of monoculture agriculture favors soil degradation and losses in soil microbial diversity (Nielsen et al., 2015), paralleled by losses in crop

productivity (Fried et al., 2017). Therefore, there is a pressing need to address the responses of soil bacterial and fungal communities to different soil management practices in agrosystems.

Soil microbial communities contain groups of organisms with positive or negative effects on plant productivity. On the positive side, plant growth-promoting bacteria can improve plant nitrogen and phosphorous uptake via root symbionts like *Rhizobacteria* and free-living nitrogen fixers (Dini-Andreote et al., 2016). Mycorrhizal communities can increase soil P mobilization and availability to plants (Zhu et al., 2018), and there is a well-known set of soil microorganisms that are antagonists to plant pathogens (Kwak et al., 2018). On the negative side, soils may host groups of pathogenic microorganisms that can accumulate in agrosystems, decreasing production (Savary et al., 2012).

Sustainable agrosystem management influences soil microbial communities and has a positive effect on plant growth (Bender et al., 2016). Increases in soil microbial abundance and diversity, as well as pathogen control or enhanced nutrient supply have been linked to techniques such as tillage (Beare et al., 1992), use of cover crops (Pittelkow et al., 2015), and the addition of compost teas (Marín et al., 2014), manure (Hestmark et al., 2019) or biochar (Güereña et al., 2015).

One of the most important factors influencing soil microbial community composition and functioning in agrosystems is the type and amount of organic amendments to the soil (Bünemann et al., 2018), which is a key soil management practice in agricultural production (Bausenwein et al., 2008). Soil organic matter (SOM) is managed through organic amendments with practices such as crop rotation, soil tillage techniques, application of organic wastes (manure, slurry) and green manure (e.g., cover crops) (Bausenwein et al., 2008). Organic matter addition to



agrosystems enhances SOM which can have an effect on soil structure (Hartmann et al., 2015) and change soil microbial community composition (Griffiths et al., 1999), usually by increasing microbial biodiversity and biomass (Bengtsson et al., 2005). However, agricultural intensification has generally reduced the periodicity of organic amendments, because of increased reliance on synthetic chemical fertilizers (Ferraro and Aznar, 2008). These fertilizers can be associated with an increase in soil pathogens that are usually countered by the application of biocides and the use of disease-resistant plant varieties (Hoitink and Boehm, 1999). An increase in soil pathogens may inhibit the positive effects of other organisms (Blok et al., 2000) and affect soil microbial biodiversity (Stoate et al., 2001). Although there is some knowledge of the effects of organic amendments and synthetic fertilizer application on soil microbial communities in agrosystems, these effects are poorly understood for intensive agriculture. Taking into account the increasing importance of intensive agriculture on human food supply, more knowledge on these effects may contribute to the design of more sustainable intensive agricultural systems.

The aim of this study was to assess the effects of microbial communities, associated to different soil fertilization practices, on plant growth, focusing on the use of organic amendment and synthetic fertilizers in intensive agriculture. We hypothesized that differences in soil community composition associated to different soil fertilization practices would lead to changes in plant growth and changes in the availability of different soil nutrients to plants. We further hypothesized that, when comparing substrates receiving inocula from greenhouse soils with or without regular organic amendments, treatments associated to organic amendments would have a positive influence on nutrient uptake and plant growth.

## 2. MATERIAL AND METHODS

### *Soil greenhouse management*

Fifteen commercial greenhouses with tomato crops were selected in Almeria province in southeast Spain that used three different types of fertilization practices. The three fertilization treatments applied to greenhouse soils were (1) conventional management in which synthetic chemical fertilizers, applied by fertirrigation dripping system, were regularly used. Synthetic fertilizers covered all plant requirements with a combination of soluble nitrogen ( $\text{HNO}_3$ ,  $\text{Ca}(\text{NO}_3)_2$ ,  $\text{Mg}(\text{NO}_3)_2$ ,  $\text{KNO}_3$ ), soluble phosphorus ( $\text{H}_3\text{PO}_4$ ,  $\text{KH}_2\text{PO}_4$ ,  $\text{K}_2\text{HPO}_4$ ), soluble potassium ( $\text{K}_2\text{SO}_4$ ) and a commercial combination of micronutrients (Fe, Cu, B, Mn, Mo, Zn), with no manure added for at least ten years. This treatment is called CM hereafter. (2) Conventional management, with manure addition ( $20,000\text{--}25,000 \text{ kg ha}^{-1} \text{ year}^{-1}$ ) in the last five years and with regular synthetic chemical fertilization (as CM) (CMOM hereafter). (3) Organic management, in which for at least the previous two years, manure was added annually ( $20,000 - 25,000 \text{ kg ha}^{-1} \text{ year}^{-1}$ ) and no synthetic chemical fertilizers had been applied (ORG hereafter). Five greenhouses were selected for each organic matter management approach that were growing tomato in a short spring cropping cycle.

Soil in each greenhouse was sampled at the end of the crop cycle which grew with above-ground drip irrigation, and just before crop residues were removed. All the greenhouses used the local “enarenado” artificial soil system in which an 8–10 cm layer of coarse sand mulch is placed over the soil (Thompson et al., 2007). Soil samples were collected from the first 5 cm of soil beneath the sand layer, between two adjacent plants along the same dripline. Ten such samples were randomly

collected in each greenhouse; the sampling areas were selected to be representative of the greenhouse. The ten samples were combined to form a composite sample for each greenhouse and were then rapidly transferred to the laboratory. The soil sampling equipment was sterilized with ethanol between samples.

### ***Preparation of soil microbial community inoculum***

Soil inoculum was prepared from each composite soil sample (giving 15 batches of soil inocula, one per greenhouse) by stirring 0.5 L of soil in 1 L of deionized, sterilized water and then filtered through a 0.5 mm sieve to remove soil particles while permitting passage of fungal spores and hyphae, and soil bacteria (Lozano et al., 2018).

### ***Experimental design***

To assess the effect of the different soil microbial inoculum on substrate-grown plants, 150 ml of inoculum was added to 3 L plastic (PE) pots filled with a peat and sand (2:1 v/v) substrate mix. Prior to adding the inocula, the substrate had been autoclaved three times at 121°C for 60 min. Ten replicate pots were prepared for each individual inoculum: There were 150 treatment pots (3 soil management systems x 5 greenhouses x 10 replicates); in addition, there were 10 additional pots that each received 150 ml of deionized sterilized water as a Control treatment. After application of the inocula in the treatment pots and water in the Control, three hybrid tomato seeds of a commercial variety (Hulk F1<sup>®</sup>, CapGen Seeds, Vicar, Spain) were sown in each pot. These seeds had been sequentially disinfected in 70% ethanol for 1 minute, cleaned with sterilized water, disinfected with 5% sodium hypochlorite

solution for 5 minutes, and cleaned with sterilized water. After seedling establishment, seedlings were thinned to one plant per pot.

The plants were grown in the pots for two months in a greenhouse during a short spring cycle. The pots were relocated randomly every 15 days (Figure S1). After sowing, two additional inoculations of 150 ml of soil extracts per pot were applied 15 and 30 days after the commencement of the study. Identical volumes of sterilized water were applied on the same days to the Control pots. Greenhouse climatic conditions were passively controlled by opening roof and side windows when the internal air temperature was  $>30^{\circ}\text{C}$ , and by closing them when temperature was  $<20^{\circ}\text{C}$ . Irrigation was applied using manually operated valves for irrigation throughout the experiment to control that all pots were irrigated the same and plants suffered no hydric stress. Irrigation water was obtained from a desalination plant and electrical conductivity (EC) was  $0.6 - 1.2 \text{ dS m}^{-1}$ . No fertilizers were added during the experiment.

#### *Soil analyses*

The substrate in the pots was sampled at two different times, at the beginning (immediately following inoculation) and at the end of the experiment (at plant harvest). Substrate was sampled to determine the nutrient content at the beginning and end of the study. For microbial molecular analyses samples were taken at the end of the study. The substrate samples were handled as composite samples by combining substrate from ten replicate pots from each soil inoculum treatment.

***Substrate nutrient content***

Organic Matter and N contents were determined with a LECO Truspec C/N analyser (St. Joseph, MI, USA). Organic C was determined after removal of inorganic carbon with 2 M HCl (Schumacher, 2002). Phosphate ( $\text{PO}_4^{3-}$ ) and sulphate ( $\text{SO}_4^{2-}$ ) concentrations in water extract (1:10 v:v) were analysed by HPLC (Metrohm, HE, Switzerland). Nitrate ( $\text{NO}_3^-$ ) and ammonia ( $\text{NH}_4^+$ ) concentrations in the substrate were extracted with potassium chloride (KCl) (40 g moist soil; 200 ml 2 M KCl) and were determined with an automatic continuous segmented flow analyser (model SAN++, Skalar Analytical B.V., Breda, The Netherlands). Other elements were determined after acid digestion and with an inductively coupled plasma (ICP) emission spectrometer (ICAP 6500 DUO Thermo; Thermo Scientific, Wilmington, DE, USA). Substrate pH was measured in an 1:2.5 (w:v), aqueous solution with a pH-meter (Crison, Barcelona, Spain). Apart from the analysis of  $\text{NO}_3^-$  and  $\text{NH}_4^+$  conducted at the University of Almeria, all determinations were conducted at the CSIC-CEBAS (Centre of Edaphology and Applied Biology of Segura) “Ionomics” laboratory in Murcia, Spain.

***Plant traits, gas exchange rates and plant biomass***

Just before plant sampling, maximum leaf photosynthetic rate ( $A_{\max}$ ) and instantaneous gas exchange efficiency (iGEE) were measured in each of three fully expanded, mature leaves per plant, with no apparent damage. Analyses were done using the mean value of these three measurements per plant. We measured three plants per greenhouse soil inoculum; thus 15 plants per inocula treatment (CM, CMOM or ORG) and in three control plants, totalling 48 plants measured. Gas

exchange measurements were done using a LI-6400 IRGA (LiCor Biosciences, Inc., Lincoln, USA). Temperature and light conditions in the IRGA chamber were set at 25°C and 1500  $\mu\text{mol m}^{-2}\text{s}^{-1}$  PAR intensity, respectively, during measurement.  $i\text{GEE}$  was calculated by dividing  $A_{\text{max}}$  by stomatal conductance (Farquhar et al., 1989).

One fully expanded mature leaf per plant was collected to measure specific leaf area (SLA); another similar leaf was used to determine leaf dry matter content (LDMC) following standard protocols (Pérez-Harguindeguy et al., 2013). SLA was measured as the ratio between fresh leaf area and leaf dry mass. One mature leaf per plant was harvested, rehydrated overnight in the dark, and subsequently weighed and scanned for leaf area. Leaf area was measured using the Midebmp software (CSIC-EEZA, Almería, Spain). Leaves were dried at 60°C for 72 h and weighed. LDMC was calculated as the ratio between leaf dry and fresh mass.

The natural abundance carbon and N isotope ratios of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , respectively, and the total C and N contents of leaves were analyzed in two fully expanded leaves, per plant, that had no visible damage. Dry leaves were ground in a ball mill (model MM400, Retsch GmbH, Haan, Germany) at 3000 rpm for 1 minute to obtain a fine powder. Three mg of each sample was wrapped in a tin capsule (Model D1008, Elemental Microanalysis, United Kingdom). Leaf  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , and leaf C and N content (in percentage) were determined using a GC IsoLink – MS – Delta V continuous flow mass spectrometer (MS) system that included a ISQ-QD single quadrupole MS and a Trace 1310 gas chromatograph (Thermo Fisher Scientific™, Spain) at the Stable Isotope Analysis Lab at CIC (Scientific Instrumental Center), University of Granada (Spain). The isotopic abundance of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  was expressed in parts per thousand (‰) as:

$$\delta = (R_{\text{sample}} / R_{\text{standard}} - 1) \times 1000$$

where  $R_{\text{sample}}$  and  $R_{\text{standard}}$  are the molar ratios of heavy to light isotope of the sample and the international standard, respectively. Mass spectrometer precision was 0.15 ‰ for carbon and nitrogen, based on replicate analyses of standard reference materials.

At plant sampling, above- and below-ground plant tissues were separated and oven-dried at 60°C until constant weight and then weighed. Apart from shoot (S), root (R) and total biomass, the root-to-shoot ratio (R:S) was calculated as an indicator of biomass allocation. We did not wait until fructification for measuring fruit yield. Tomato plants have high nutritional requirements to reach fructification, and we did not include additional fertilization to avoid confound effects with those produced by the microbial communities from the different pot substrates. Nonetheless, Candido et al. (2015) analysed the effect of different microbial community inoculations on tomato plants and showed significant differences in total plant biomass at mid-growing season. These differences were also maintained in plant biomass at final-growing season and marketable tomato, being the total biomass as a proxy of fruit production.

#### ***DNA extraction and quantitative PCR***

DNA was extracted from 250 mg samples of substrate using the DNeasy Powersoil<sup>®</sup> Kit (Qiagen, Inc., Venlo, Netherlands), following the manufacturer's protocol. DNA concentration was estimated using Qubit Fluorometric Quantification (Thermo Scientific, USA); samples were stored at -80°C.

Quantitative PCR (qPCR) analyses were performed on the soil DNA extracts to measure the abundance of microbial marker genes for bacteria and fungi. The primer pairs used for the qPCR analyses were 515f (5'-GTGYCAGCMGCCGCGGTAA-3') and 806r (5'-GGACTACNVGGGTWTCTAAT-3') for bacteria (Walters et al., 2015), and ITS1 (5'-TCCGTAGGTGAACCTGCGG-3'; Gardes and Bruns, 1993) and ITS5.8S (5'-CGC TGC GTT CTT CAT CG-3'; Vilgalys and Hester, 1990) for fungi, respectively. Amplifications were performed by using a SYBR<sup>®</sup> Green (Sigma-Aldrich, USA) based qPCR method in a CFX96<sup>™</sup> Real-Time PCR Detection System (BioRad Laboratories, USA). Standard curves were prepared in every assay using 10-fold serial dilutions of stock solutions containing the target DNA molecules. The reaction mixture contained 10 µl of 2X PowerUp<sup>™</sup> SYBR<sup>™</sup> Green Master Mix (Applied Biosystems, USA), 1 µl of each primer (20 µM), 10-100ng of template DNA and nuclease free water (Ambion Thermofisher) up to 20 µl of final volume. Amplification conditions were as follows: 95°C for 10 min, bacteria: 35 cycles of 10 s at 95°C, 30 s at 57°C and 30 s at 72°C, fungi: 40 cycles of 15 s at 95°C, 30 s at 53°C and 1 min at 72°C, followed by melt curve from 60°C to 95°C at 0.5 °C increment. Triplicate reactions were performed for each DNA extract, standard curve, and negative control. PCR efficiency for different assays ranged between 75% and 95% with  $R^2 > 0.9$ . The specificity of amplified products was verified by melting curves and agarose gel electrophoresis analysis.



*Metabarcoding of prokaryotic and fungal soil communities*

Amplicon sequencing was performed using Earth Microbiome Project (EMP) standard protocols (<http://press.igsb.anl.gov/earthmicrobiome/protocols-and-standards>) at the facilities of Genyo in Granada, Spain. PCR was done in triplicate on the V4 region of the 16S rRNA gene using the primer pair 515f-806r and on the ITS1 region with the primer pair ITS1f-ITS2 (Walters et al., 2015). Barcoded PCR products were quantified using a Qubit dsDNA (Thermo Fisher Scientific) instrument and pooled in equal concentrations. The multiplexed DNA library was purified using Agencourt AMPure XP beads (Beckman Coulter). DNA quality and size were checked with a High Sensivity DNA Assay (Bioanalyzer 2100, Agilent) and sequenced in an Illumina MiSeq sequencing platform using the Illumina reagent kit V3 (600 cycles) generating 300 bp pair-end reads.

Demultiplexed pair-end Illumina reads were processed using QIIME 2 pipeline v.2019.4 (Bolyen et al. 2019). The cutadapt plugin (Martin, 2011) was used to trim primers. The data was denoised with the q2-dada2 plugin, which implements the DADA2 R library (Callahan et al., 2016), performing sequence quality control, truncation of the reads, stitching R1 and R2 reads, generation of amplicon sequence variants (ASV) and screening out potentially chimeric sequences. PCR negative controls, DNA extraction controls and a commercial mock community sample (ZymoBIOMICS Microbial Community Standard, Zymo Research) were also sequenced. After checking sequencing controls and the correct classification at genus level of the 8 bacterial and 2 fungal strains included in the mock sample (data not shown), control samples were excluded from the analysis. In the case of ITS data,

we only used the R1 reads, as the taxonomic classification of the mock community at genus level was not accurate combining R1 and R2 reads.

Taxonomy was assigned using the QIIME 2 Naïve Bayes method (Bokulich et al., 2018). The databases SILVA v.132 (Quast et al., 2013) and UNITE v8 dynamic (Kõljalg et al., 2005) were used to train the classifiers for 16S and ITS data, respectively. ASVs assigned to chloroplasts and mitochondria (16S data) and eukaryotic non-fungal lineages (ITS) were removed, as also ASVs not classified at phylum level. The total high-quality reads and the total ASVs obtained before and after rarefaction, as well as the different associated taxa are shown in Supplementary Table S1. The sequenced dataset has been deposited in the NCBI Biosample Dataset PRJNA629769.

#### *Statistical analysis*

The effects of the experimental treatments (soil inocula from different greenhouse managements added to pots) on substrate nutrient content and plant responses were analyzed with linear mixed models (LMM) with fertilization practice as the fixed factor and greenhouse ID as the random factor. In the case of substrate nutrient content, we also included “time”, beginning or end of the experiment, and the interaction between time and fertilization practice as additional fixed factors. When necessary, we selected a variance function structure to avoid heteroscedasticity (Pinheiro and Bates, 2000). The restricted maximum likelihood estimator (REML) was used to perform ANOVA. Post-hoc comparisons between treatment levels were performed using Fischer’s LSD tests. qPCR results were analyzed with linear models (LM), using the  $\log_{10}$  transformation of data. The

combined effects of biotic and abiotic factors on plant biomass were analyzed using a partial least squares regression (PLS) model, where pot substrate characteristics, and prokaryotic and fungal abundance were included as predictors and total biomass was the dependent variable.

Unless stated otherwise, statistical analyses were conducted with R 3.5.2 version (R Core Team<sup>®</sup>, 2018) using the interface implemented in the InfoStat<sup>®</sup> statistical software (Di Rienzo et al., 2019) or RStudio<sup>®</sup> (Version 1.1.463). Significance of differences between treatments were set at  $p < 0.05$ . Results throughout the text and figures and tables are mean values  $\pm$  1SE.

Calypso software (Zakrzewski et al., 2017), an online suite of analytical tools for microbiomes that integrates different R packages (<http://cgenome.net/calypso/>) was used to calculate alpha diversity indices on normalized 16S rRNA and ITS datasets. These were used to produce multivariate diagrams and to perform statistical tests on the microbiome data, using the ASV matrix and the taxonomic assignments generated by QIIME2 as input data. We then performed non-parametric tests for determining significant differences in alpha diversity using a Kruskal-Wallis test at a 95% confidence level and  $\beta$ -diversity using PERMANOVA and calculated a linear discriminant analysis (LDA) effect size (LEfSe) algorithm (Segata et al., 2011) to identify specific features (taxa) in soils with significant associations to different treatments ( $p < 0.05$ ). Potential presence of phytopathogens among the differentially abundant prokaryotic genera were investigated by using the method FAPROTAX v. 1.2.3, that have been updated to include a list of plant pathogens (Louca et al., 2016). Similarly, we used FUNGuild for the fungal dataset (Nguyen et al., 2016). Mantel tests based on Jaccard distance matrix index were used to analyze the correlation between the microbial communities' composition in the original greenhouse soils

(Usero et al. submitted) that were sampled to prepare the inocula and in pot substrates at the end of the experiment.

### 3. RESULTS

#### *Substrate chemical characteristics*

There were no significant differences in the chemical composition of pot substrate between treatments at the beginning of the study after soil inocula addition ( $t_0$ ), indicating that inoculum treatments did not affect substrate chemical composition (Table 1, Table S2). At the end of the study ( $t_f$ ), substrates of all inoculum treatments had more  $\text{NO}_3^-$  and  $\text{NH}_4^+$  than at  $t_0$ . The increase from  $t_0$  to  $t_f$  in  $\text{NO}_3^-$  content was higher in pots inoculated with ORG than with CM inoculum, suggesting that both mineralization of organic N and nitrification were enhanced by microbial communities from ORG inoculum. At the end of the study, the  $\text{NO}_3^-$  content in pots receiving CMOM inoculum was intermediate between those receiving ORG and CM inocula (Table 1). There were also differences in total N content at  $t_f$ , which were higher in CM than in ORG. Therefore, the different inocula resulted in differences in the forms of N of the pot substrate at the end of the study.

Organic C (as well as SOM) increased from  $t_f$  to  $t_0$  in CM and CMOM and were unaffected in ORG (Table 1). Consequently, at  $t_f$  there was a tendency to more organic C in CM and CMOM than in ORG pot substrates. The different inoculum treatments resulted in differences in net organic C accumulation that were presumably associated with OM decomposition from peat of substrates inoculated,

C consumption by microorganisms (CO<sub>2</sub> release), as well as organic C from dead microorganisms and roots (Khan et al., 2016).

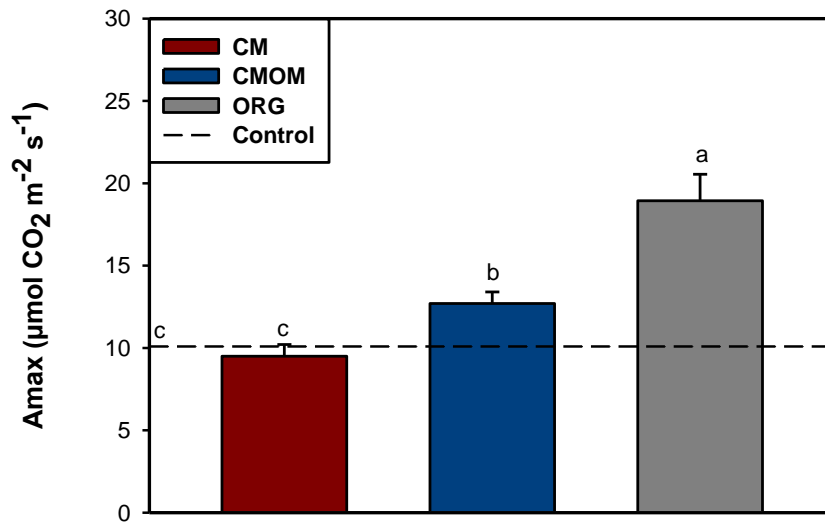
**Table 1:** Chemical substrate properties. Results are means  $\pm$  1SE, n=5. Different letters in a row indicate significant differences ( $p < 0.05$ ) among treatments after LSD post-hoc comparisons. The last six columns are F and p-value results after GLMM analysis. CM: Pots inoculated with conventionally managed soil (e.g. use of synthetic chemical fertilizers) which did not receive organic amendments; CMOM: Pots inoculated with conventionally managed soil (e.g. use of synthetic chemical fertilizers) which received organic amendments, and ORG: Pots inoculated with organic management soil which received yearly organic amendments and which the synthetic chemical fertilizers were not used.

| Variable                     | Unit   | Substrate beginning ( $t_0$ ) |                      |                        | Substrate final ( $t_t$ ) |                       |                       | Significance  |          |       |               |                 |             |
|------------------------------|--------|-------------------------------|----------------------|------------------------|---------------------------|-----------------------|-----------------------|---------------|----------|-------|---------------|-----------------|-------------|
|                              |        | Treatment                     |                      |                        | Treatment                 |                       |                       | F             |          |       | p-value       |                 |             |
|                              |        | CM                            | CMOM                 | ORG                    | CM                        | CMOM                  | ORG                   | Treatment (T) | Time (t) | T x t | Treatment (T) | Time (t)        | T x t       |
| pH                           |        | 6.62 $\pm$ 0.08 a             | 6.68 $\pm$ 0.35 a    | 6.67 $\pm$ 0.10 a      | 6.83 $\pm$ 0.15 a         | 6.74 $\pm$ 0.092 a    | 6.76 $\pm$ 0.26 a     | 0.02          | 2.68     | 0.39  | 0.98          | 0.11            | 0.68        |
| Total N                      | g/100g | 0.10 $\pm$ 0.04 c             | 0.09 $\pm$ 0.01 c    | 0.16 $\pm$ 0.07 bc     | 0.19 $\pm$ 0.06 a         | 0.15 $\pm$ 0.06 ab    | 0.10 $\pm$ 0.03 bc    | 1.74          | 9.31     | 4.61  | 0.19          | <b>0.01</b>     | <b>0.02</b> |
| Organic C                    | g/100g | 1.91 $\pm$ 0.90 c             | 1.87 $\pm$ 0.76 c    | 3.49 $\pm$ 1.84 bc     | 4.18 $\pm$ 1.70 a         | 3.94 $\pm$ 2.08 ab    | 2.31 $\pm$ 0.90 bc    | 1.40          | 9.68     | 3.16  | 0.27          | <b>&lt;0.01</b> | 0.06        |
| Total O.M.                   | g/100g | 3.30 $\pm$ 1.55 c             | 3.22 $\pm$ 1.31 c    | 6.01 $\pm$ 3.17 bc     | 7.21 $\pm$ 2.92 a         | 6.79 $\pm$ 3.58 ab    | 3.98 $\pm$ 1.55 bc    | 1.40          | 9.68     | 3.16  | 0.27          | <b>&lt;0.01</b> | 0.06        |
| Ca                           | g/100g | 0.11 $\pm$ 0.02 a             | 0.11 $\pm$ 0.018 a   | 0.20 $\pm$ 0.24 a      | 0.20 $\pm$ 0.24 a         | 0.09 $\pm$ 0.10 a     | 0.21 $\pm$ 0.09 a     | 0.63          | 2.50     | 0.98  | 0.54          | 0.13            | 0.39        |
| Fe                           | mg/kg  | 735.53 $\pm$ 53.37 a          | 780.08 $\pm$ 68.41 a | 1032.66 $\pm$ 667.59 a | 804.41 $\pm$ 852.00 a     | 444.63 $\pm$ 534.84 a | 876.31 $\pm$ 158.27 a | 0.67          | 0.11     | 0.87  | 0.52          | 0.74            | 0.43        |
| K                            | g/100g | 0.04 $\pm$ 0.01 a             | 0.03 $\pm$ 0.02 abc  | 0.03 $\pm$ 0.04 abc    | 0.04 $\pm$ 0.04 bc        | 0.01 $\pm$ 0.01 c     | 0.01 $\pm$ 0.01 c     | 4.52          | 2.20     | 0.08  | 0.02          | 0.15            | 0.92        |
| P                            | g/100g | 0.007 $\pm$ 0.001 a           | 0.008 $\pm$ 0.001 a  | 0.008 $\pm$ 0.007 a    | 0.007 $\pm$ 0.008 a       | 0.005 $\pm$ 0.004 a   | 0.008 $\pm$ 0.002 a   | 0.22          | 0.27     | 0.83  | 0.81          | 0.61            | 0.45        |
| S                            | g/100g | 0.020 $\pm$ 0.006 a           | 0.022 $\pm$ 0.004 a  | 0.052 $\pm$ 0.080 a    | 0.048 $\pm$ 0.082 a       | 0.022 $\pm$ 0.023 a   | 0.061 $\pm$ 0.057 a   | 0.49          | 2.23     | 0.62  | 0.62          | 0.15            | 0.55        |
| NO <sub>3</sub> <sup>-</sup> | mg/l   | 1.42 $\pm$ 0.13 c             | 1.54 $\pm$ 0.49 c    | 2.25 $\pm$ 1.18 c      | 2.98 $\pm$ 0.56 b         | 3.94 $\pm$ 0.59 ab    | 4.37 $\pm$ 0.90 a     | 5.94          | 116.94   | 5.00  | <b>0.01</b>   | <b>&lt;0.01</b> | <b>0.02</b> |
| NH <sub>4</sub> <sup>+</sup> | mg/l   | 0.62 $\pm$ 0.03 b             | 0.59 $\pm$ 0.07 b    | 0.93 $\pm$ 0.36 b      | 1.27 $\pm$ 0.09 a         | 1.28 $\pm$ 0.08 a     | 1.31 $\pm$ 0.15 a     | 0.91          | 451.19   | 0.23  | 0.42          | <b>&lt;0.01</b> | 0.80        |

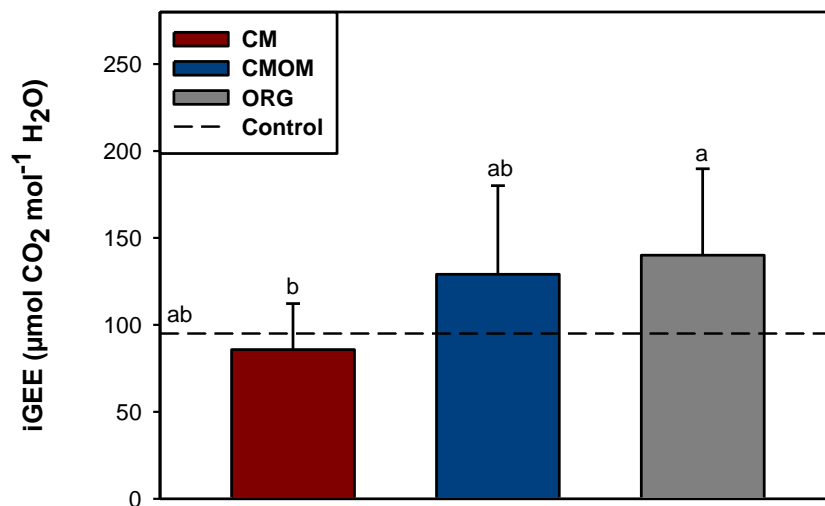
### *Plant responses*

The maximum photosynthetic rate ( $A_{\max}$ ) was highest in plants inoculated with ORG, followed by those inoculated with CMOM, and then by plants inoculated with CM and Control plants (Figure 1A). Instantaneous gas exchange efficiency (iGEE) was higher in plants inoculated with ORG than in plants inoculated with CM (Figure 1B); plants from the CMOM and Control treatments were intermediate but there were not significant differences between both treatments or with CM treatment. Plants in pots inoculated with ORG had a greater LDMC than those inoculated with CM (Table 2). Inoculum treatment did not affect SLA.

A)



B)



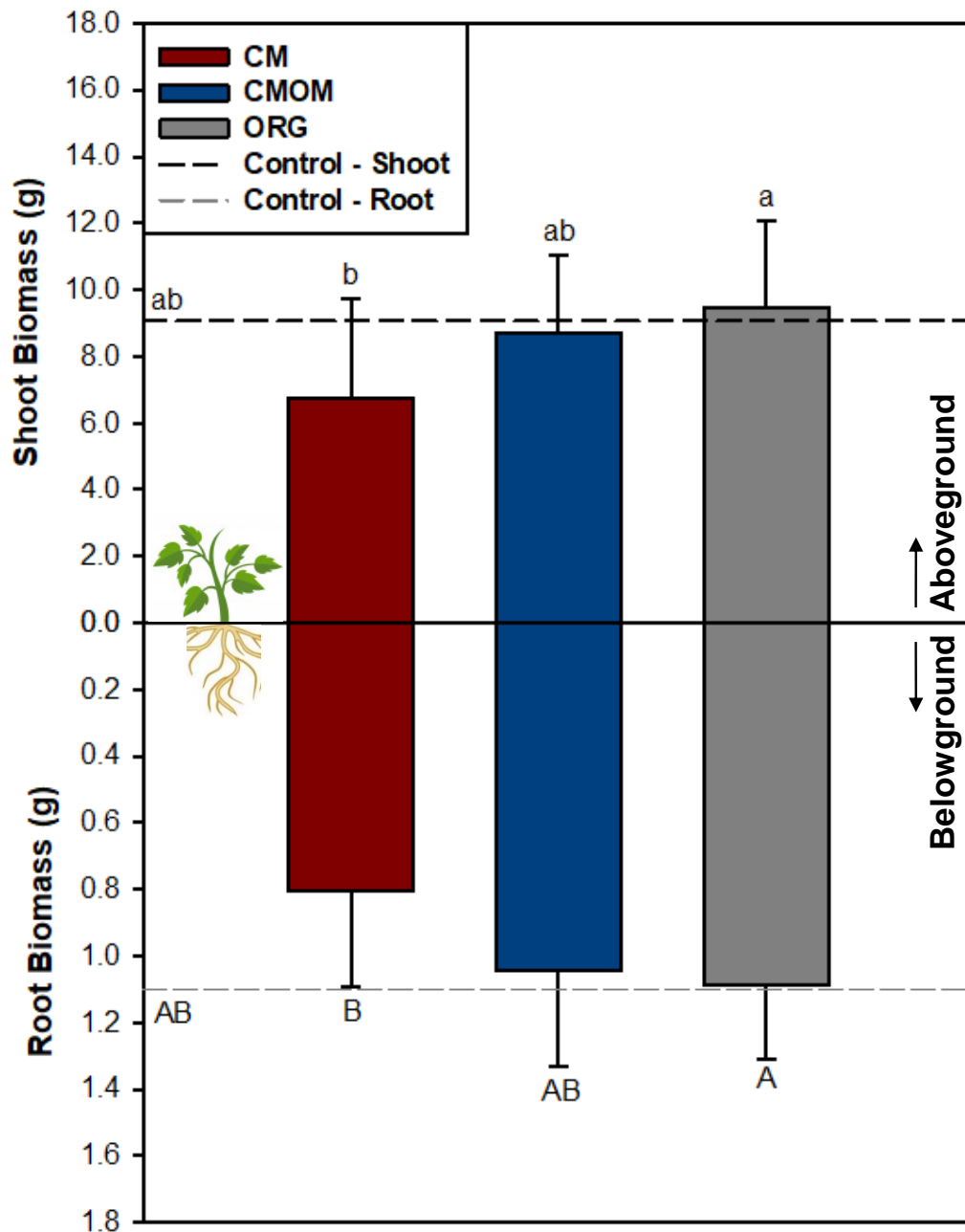
**Figure 1.** Maximum photosynthetic rate ( $A_{max}$ ; A) and instantaneous gas exchange efficiency (iGEE; B) at the end of the experiment. Bars represent mean values  $\pm 1$  SE;  $n=15$ . The dashed horizontal line is the mean  $A_{max}$  and iGEE of Control plants (no inoculated), respectively. Different letters across bars and above the mean Control line indicate significant differences ( $p < 0.05$ ) among treatments after Fischer LSD post-hoc comparison. CM: Pots inoculated with conventionally managed soil (e.g. use of synthetic chemical fertilizers) which did not receive organic amendments; CMOM: Pots inoculated with conventionally managed soil (e.g. use of synthetic chemical fertilizers) which received organic amendments, and ORG: Pots inoculated with organic management soil which received yearly organic amendments and which the synthetic chemical fertilizers were not used.



There were no differences between treatments in leaf  $\delta^{13}\text{C}$  values, leaf total N and C contents (Table 2). Leaves of plants inoculated with CM had the highest  $\delta^{15}\text{N}$  values (Table 2). There were no significant increases in total biomass (shoot plus root biomass) with ORG and CMOM inocula compared to the Control (Table 2). However, plants that received the CM inocula grew less than Control ones (Table 2). For both shoot and root biomass, there were no significant differences between ORG, CMOM and Control plants, and there were significant differences between ORG and CM plants (Figure 2). There were no differences in R:S between treatments (data not presented).

**Table 2:** Plant biomass and leaf traits. Results are means  $\pm$  SE. Different letters in a row indicate significant differences ( $p < 0.05$ ) among treatments after LSD post-hoc comparison. Legend of treatments as in Table 1.

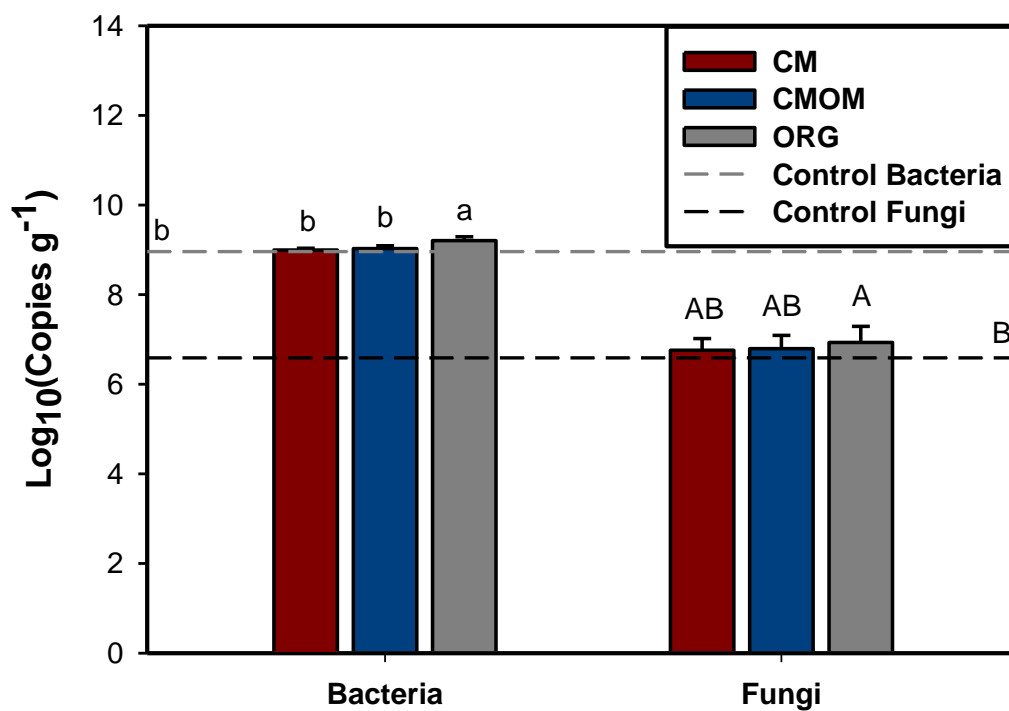
| Variable                       | Unit               | Treatment                  |                              |                             |                              |
|--------------------------------|--------------------|----------------------------|------------------------------|-----------------------------|------------------------------|
|                                |                    | CM                         | CMOM                         | ORG                         | Control                      |
| Total biomass                  | g                  | 7.54 $\pm$ 0.46 <b>b</b>   | 9.75 $\pm$ 0.36 <b>a</b>     | 10.57 $\pm$ 0.39 <b>a</b>   | 11.20 $\pm$ 0.67 <b>a</b>    |
| Specific Leaf Area (SLA)       | m <sup>2</sup> /kg | 23.48 $\pm$ 3.15 <b>a</b>  | 23.48 $\pm$ 2.84 <b>a</b>    | 22.61 $\pm$ 2.48 <b>a</b>   | 20.22 $\pm$ 0.34 <b>a</b>    |
| Leaf Dry Matter Content (LDMC) | mg/g               | 94.26 $\pm$ 12.50 <b>b</b> | 108.13 $\pm$ 11.22 <b>ab</b> | 115.75 $\pm$ 14.56 <b>a</b> | 103.86 $\pm$ 18.83 <b>ab</b> |
| $\delta^{15}\text{N}$          | ‰                  | 10.14 $\pm$ 0.53 <b>a</b>  | 8.87 $\pm$ 0.53 <b>b</b>     | 8.75 $\pm$ 0.38 <b>b</b>    | 8.84 $\pm$ 0.31 <b>b</b>     |
| $\delta^{13}\text{C}$          | ‰                  | -30.19 $\pm$ 0.14 <b>a</b> | -29.85 $\pm$ 0.13 <b>a</b>   | -30.07 $\pm$ 0.13 <b>a</b>  | -30.08 $\pm$ 0.2 <b>a</b>    |
| Leaf total N                   | %                  | 2.87 $\pm$ 0.62 <b>a</b>   | 2.55 $\pm$ 0.62 <b>a</b>     | 2.93 $\pm$ 0.44 <b>a</b>    | 2.99 $\pm$ 0.52 <b>a</b>     |
| Leaf total C                   | %                  | 38.48 $\pm$ 0.46 <b>a</b>  | 38.92 $\pm$ 0.47 <b>a</b>    | 39.41 $\pm$ 0.34 <b>a</b>   | 39.17 $\pm$ 0.33 <b>a</b>    |
| Leaf C:N                       |                    | 16.94 $\pm$ 2.00 <b>a</b>  | 17.54 $\pm$ 2.83 <b>a</b>    | 16.34 $\pm$ 2.00 <b>a</b>   | 16.29 $\pm$ 2.37 <b>a</b>    |



**Figure 2.** Shoot and root biomass per plant at the end of the experiment. Bars are mean values  $\pm 1$  SE;  $n=30$ . The horizontal line in the origin represents the soil surface. Values above the soil line represent shoot biomass and values below the soil line represents root biomass. The dashed horizontal line is the mean shoot or root biomass of Control plants (no inoculated). Different letters across bars and above the mean Control lines indicate significant differences ( $p < 0.05$ ) among treatments after Fischer LSD post-hoc comparison. Legend of treatments as in Figure 1.

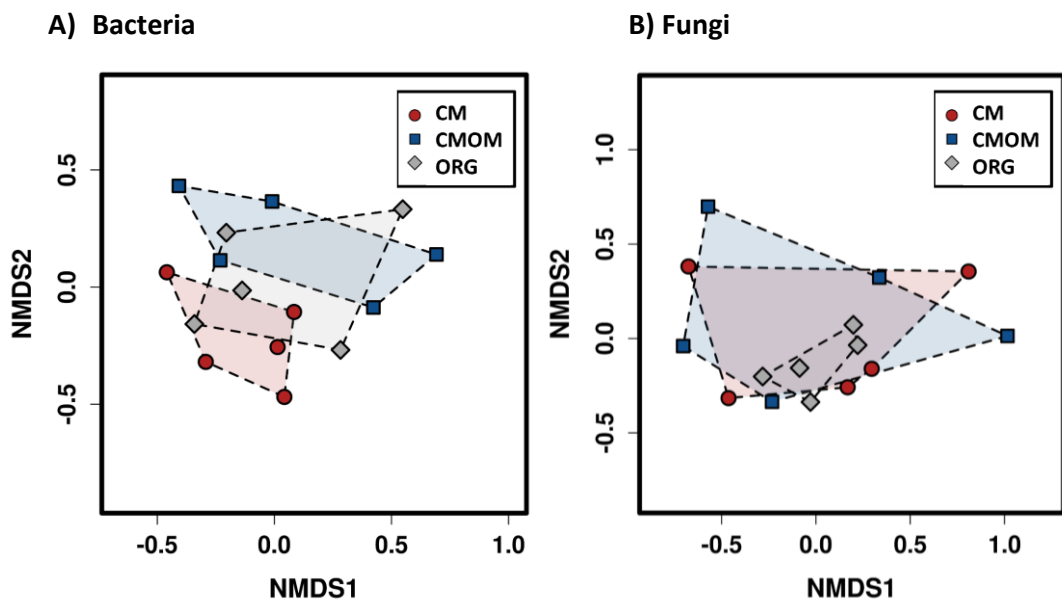
***Microbial community composition and structure in pot substrates at the end of the experiment***

Microbial abundance (determined by qPCR) showed differences among experimental treatments at the end of the experiment, being higher the prokaryote abundance in ORG than in the other two treatments and Control substrates (Figure 3). There were not differences in fungi abundance among treatments or in the fungi:prokaryote ratio (data not shown).



**Figure 3.** Soil bacterial and fungal abundance in pot-substrates at the end of the experiment determined by qPCR of marker genes. Bars represent mean values  $\pm 1$  SE;  $n=5$ . Different letters across bars and above the mean Control line indicate significant differences ( $p < 0.05$ ) among treatments after Fischer LSD post-hoc comparison. Legend of treatments as in Figure 1.

Alpha diversity analyses of the prokaryotic and fungal communities did not show differences across treatments (Table S3). However, beta diversity analysis revealed an overall effect of the treatments on the composition of the prokaryotic communities at the end of the experiment. The NMDS plot and PERMANOVA test based on Jaccard index showed a separation of CM and CMOM clusters, but the analysis based on Bray-Curtis index did not (Figure 4A, Table 3). In the case of the fungal communities, the beta diversity analysis did not show any effect of the treatments at community level (Figure 4B; Table 3).



**Figure 4.** Non-metric multidimensional scaling (NMDS) based on Jaccard distance matrices of prokaryotic (A; stress value 0.167) and fungal communities (B; stress value 0.124) of pot-substrates at the end of the experiment, n=5. Legend of treatments as in Figure 1.

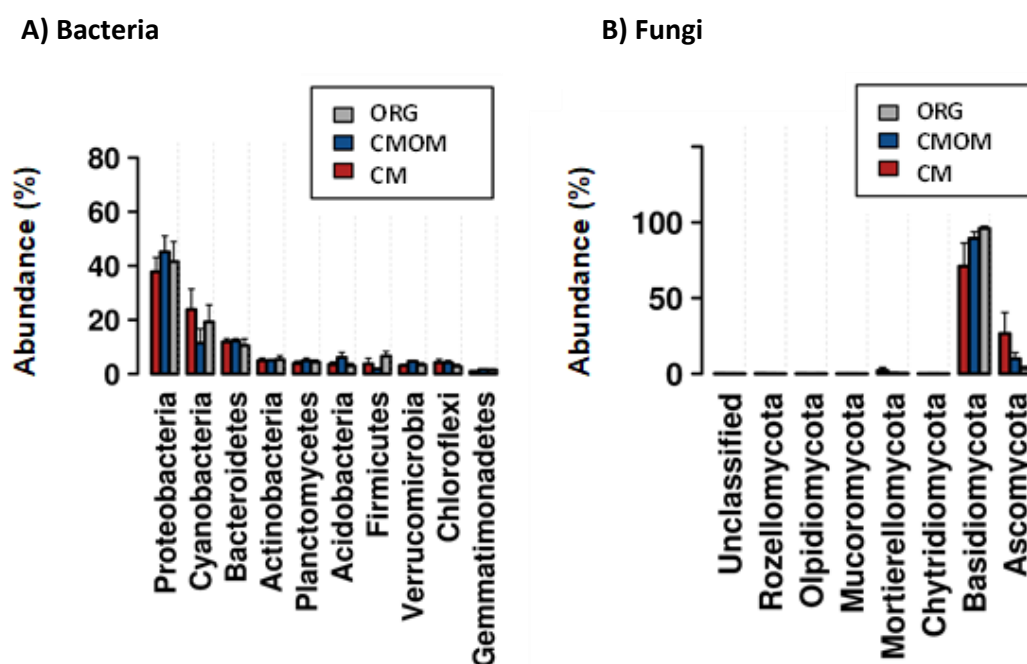
**Table 3.** PERMANOVA analyses of beta diversity based on Bray-Curtis and Jaccard distances comparing the three treatments. Legend of treatments as in Table 1.

| Factor <sup>a</sup>      | Prokaryote (16S rRNA) |         |          |             | Fungi (ITS) |         |          |         |
|--------------------------|-----------------------|---------|----------|-------------|-------------|---------|----------|---------|
|                          | Bray-Curtis           |         | Jaccard  |             | Bray-Curtis |         | Jaccard  |         |
|                          | Pseudo-F              | p-value | Pseudo-F | p-value     | Pseudo-F    | p-value | Pseudo-F | p-value |
| Management               | 1.07                  | 0.25    | 1.16     | <b>0.04</b> | 1.13        | 0.29    | 1.04     | 0.35    |
| Managements <sup>b</sup> | Pseudo-F              | p-value | Pseudo-F | p-value     | Pseudo-F    | p-value | Pseudo-F | p-value |
| CM-CMOM                  | 1.12                  | 0.23    | 1.88     | <b>0.04</b> | 0.89        | 0.62    | 0.79     | 0.93    |
| CM-ORG                   | 1.01                  | 0.48    | 1.22     | 0.08        | 1.39        | 0.13    | 1.10     | 0.27    |
| CMOM-ORG                 | 1.08                  | 0.33    | 1.19     | 0.13        | 1.09        | 0.31    | 1.28     | 0.14    |

<sup>a</sup>Effects of factor “Management” were assessed by PERMANOVA analysis taking into account all groups. Values represent the multivariate Pseudo-F and the p-value at 95% confidence level.

<sup>b</sup>Pairwise comparisons between management systems. Values represent the univariate Pseudo-F and the p-value at 95% confidence level assessed by PERMANOVA analysis.

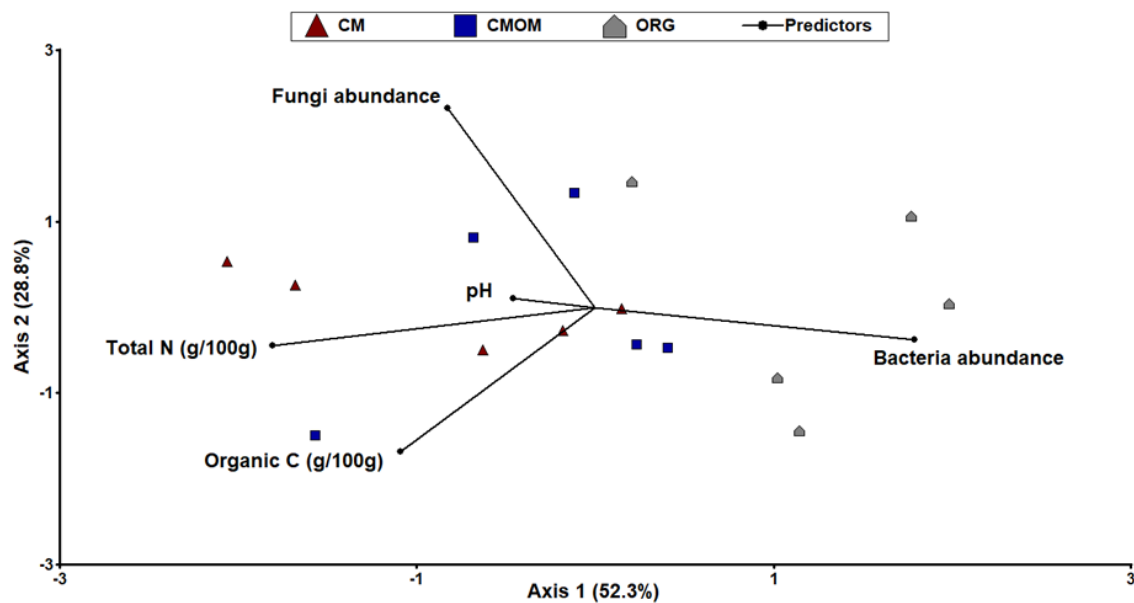
Overall, prokaryotic ASVs were assigned to 42 phyla (5 archaeal and 37 bacterial), but the 10 most abundant phyla accounted for more than 90% of the total number of reads. Predominant phyla were Proteobacteria, Cyanobacteria, Bacteroidetes, Actinobacteria, Planctomycetes and Acidobacteria (Figure 5A). Fungal ASVs were assigned to eight phyla but, similarly, the three most abundant phyla, Basidiomycota, Ascomycota and Mortierellomycota did account for more than 90% of fungal ASVs (Figure 5B).



**Figure 5.** Relative abundance of the ten most frequent prokaryotic phyla (A); and eight fungal phyla (B). Bars represent mean  $\pm 1$  SE; n=5. Legend of treatments as in Figure 1.

We detected two phyla, 21 families and 35 bacterial genera as differentially abundant among treatments at the end of the experiment (LEfSe, LDA score >2 and  $p < 0.05$ ; Figures S2A-S2C). Some of these bacterial taxa included abundant lineages clearly associated to different soil fertilizations (LDA >3,  $p < 0.05$ ), like the families Opitutaceae, Nitrosomonadaceae or Reyraneliaceae, (associated to CMOM) and Nodosilineaceae and Cyclobacteriaceae (associated to CM); and the genera *Arthronema* (associated to ORG), *Salinispira* (associated to CMOM), and *Nodosilinea* (associated to CM). *Nocardia*, a bacterial genera associated to CM treatment, contains at least one phytopathogenic species (Table S4). LEfSe identified only one fungal genus, *Olpidium*, associated to a specific treatment, CM (LEfSe, LDA score >2 and  $p < 0.05$ ; Figure S3). This fungal genus was confirmed by FUNGuild as potential phytopathogenic (Table S4).

The relationship between microbial abundance (qPCR), substrate nutrient content and other substrate characteristics on total plant biomass was analyzed using PLS. We included bacterial and fungal abundance, total N and organic C, and pH. Plants in ORG and CM treatments were clearly separated in the two axes, with CMOM in between. The main predictors were bacterial abundance, total N and organic C for Axis 1 (52.3% of variance explained) and fungi abundance for Axis 2 (28.8% of variance explained, Figure 6).



**Figure 6.** Partial Least Squares (PLS) regression analysis for total plant biomass as the response (dependent) variable and bacteria and fungi abundance (qPCR), pH, total N and total organic C as predictors. Legend of treatments as in Figure 1.

*Relation between original greenhouse soils communities used to prepare the inocula and pot substrate communities at the end of the experiment*

We compared the soil microbial community composition of the original greenhouse soils used for preparing the inocula (see details in Usero et al. submitted) with that of the final pot substrates and treatments using Mantel tests based on the Jaccard distance coefficient.

Bacterial community composition in the original greenhouse soils used to prepare inocula (with three type of soil fertilization treatments) were correlated ( $p=0.006$ , Mantel test) with communities in the pot substrates treated with different greenhouse soil inocula at the end of the experiment; i.e., bacterial community composition in pot substrates resembled the origin of their particular inoculum.

Contrary to what we found for bacteria, fungal community composition in original greenhouse soils used to prepare inocula and in pot substrates were



uncorrelated ( $p=0.856$ , Mantel test), showing that soil fungal communities in substrates at the end of the experiment differed significantly from soil communities in the original greenhouse soils used to prepare the inocula. This data suggests that factors other than soil fertilization had a strong influence on the final fungal community composition of treated pot substrates.

#### 4. DISCUSSION

We had hypothesized that differences in soil fertilization in intensive agricultural systems would lead to distinct microbial communities that, in turn, would affect crop nutrient uptake and growth under intensive greenhouse conditions. We also hypothesized that microbial communities associated to organic amendment would enhance plant growth due to better nutrient uptake and higher nutrient availability for plants. Beta diversity analysis of the microbial communities show that, indeed, the prokaryotic composition of the substrates at the end of the experiment diverged across treatments, with a clear separation of CM and ORG samples.

Soil microbial changes influenced organic C exchange in tomato plants, manifested in a higher photosynthetic rate in plants grown in substrates that received inocula from ORG soils. Furthermore, root and shoot biomass were higher in plants grown with the inoculum from ORG soils, than in those that received the CM soil inoculum. Similar results were reported in other studies using related methodology (Lozano et al., 2018). The results in the present study suggest that organic matter management has a role in regulating microbial communities in intensive agriculture soils

(Hartmann et al., 2015) which, in turn, can have a positive or negative effect on plant growth represented in our study as total biomass at mid-growing season, which has been reported as a proxy of final-growing season marketable tomato production (Candido et al., 2015).

Substrate N and organic C contents changed as the plants grew; these effects were probably due to differences in OM decomposition by soil microorganisms. The high peat content (66% by volume), and dead microorganisms and roots throughout the cropping cycle presumably provided decomposable organic matter. The different soil microbiota inocula appear to have affected the rate with which OM was decomposed in N and C. Notably, in ORG pot substrate, organic C and OM content remained constant throughout the study, presumably because the rates of organic matter accretion from root turnover was balanced by substrate respiration rate by microorganisms. By contrast, in CM and CMOM there were increases in OM, which can be explained by respiration rates being less than the rate of OM accretion (Bhowmik et al., 2017). This increase of organic C in CM and CMOM pot substrates through the experiment could be explained by the fact that there were less bacteria in CM and CMOM pots than in ORG ones, having less C consumption by microorganisms; however, as pot substrate was the same in all treatments there were almost the same contribution to organic C of peat and dead microorganisms and roots, leading to organic C accumulation in the substrates in CM and CMOM pots (Khan et al., 2016). Our results showed that contents of different forms of N were particularly different in CM and ORG substrates at the end of the experiment, showing strong links between microbial community and N availability. On our study, there was more  $\text{NO}_3^-$  accumulation in substrates treated with ORG inoculum than in substrates treated with CM inoculum, suggesting that microbial communities

habiting substrates with ORG inoculum had more N mineralization and nitrification, extracting  $\text{NO}_3^-$  from SOM faster. In substrates inoculated with CM inoculum, there was more total N than in substrates inoculated with ORG, showing that N was not extracted yet, and mineralization and nitrification had not been so fast. Nonetheless, there were similar contents of  $\text{NH}_4^+$  in all pot substrates at the end of the experiment. These differences may have influenced the differences found in plant growth across treatments (higher in ORG than in CM). These differential effects on substrate nutrient content across treatments at the end of the study can be attributed to the greenhouse soil microbiota extracts added throughout the experiment and the activity and evolution of these inocula microbial communities. Overall, prokaryotes are considered to be the most important group affecting soil nutrient cycles and soil organic matter decomposition (Bender and van der Heijden, 2015) which in turn have consequences for plant productivity.

The effect of treatments on plant physiology was also noticeable. Inocula from soils receiving organic amendments (CMOM and ORG) resulted in plants having maximum photosynthetic rate and instantaneous iGEE higher than CM and Control treatments. This is a likely consequence of higher nutrient availability and plant uptake or of microorganisms directly enhancing plant performance (Xu et al., 2001). SLA typically responds to stress conditions such as drought or nutrient limitation. However, the lack of SLA differences in our dataset suggests that plants were not stressed during the course of the experiment, and growth differences between treatments were only due to effects of microbial communities provided through inocula. Usually, SLA is positively correlated with soil N (Ordoñez et al., 2009) and negatively correlated with plant resource-use efficiency (Wright et al., 2004). Our plants grew in optimal conditions (enough water and nutrient supply,

mild temperatures) and therefore the lack of differences in SLA is not surprising. However, our results suggest that ORG plants were more efficient at resource-use than CM or Control plants, as they had higher photosynthetic rate and iGEE than CM, despite ORG substrates having greater  $\text{NO}_3^-$  content than CM.

It is important to highlight the differences in leaf  $\delta^{15}\text{N}$  in different fertilization regimes (Ma et al., 2018). Leaf  $\delta^{15}\text{N}$  in plants have been used as an indirect index of N cycling parameters. Variation in  $\delta^{15}\text{N}$  among treatments represent differences in foliar nitrogen uptake, soil nitrogen origin, and mycorrhizae fixation (Vallano and Sparks, 2013). Leaf  $\delta^{15}\text{N}$  was lower in CMOM and ORG than in CM plants. It could happen because we had plants that obtained their N from different origins. Indeed, our results point that N in soils were in different forms depending on the treatment, with differences in nitrates and total N that could have influenced leaf  $\delta^{15}\text{N}$  values, as higher content of nitrates in soils are related to lower leaf  $\delta^{15}\text{N}$  values (Craine et al., 2015). Furthermore, lower leaf  $\delta^{15}\text{N}$  values are related to mycorrhizal symbiosis (Craine et al., 2015), which could have been happening in plants growing in substrates inoculated with ORG and CMOM. This could explain the higher plant nutrient uptake and plant growth in ORG and CMOM treatments.

Long-term leaf water use efficiency ( $\delta^{13}\text{C}$ ) was similar across treatments. This index have been reported as an important indicator of plant water stress (Wei et al., 2016). In our study, plants were irrigated on demand and we did not find any sign of plant water stress across treatments, so no differences in water use efficiency were expected. The increase in LDMC in plants grown with CMOM and ORG inocula are similar to those reported by Yildirim (2007) with tomato plants. LDMC was correlated with photosynthetic rate, which was higher in CMOM and ORG than in

CM treatments. SLA and LDMC were not correlated in our experiment, in contrast to the results of Poorter et al. (2009). SLA and LDMC are associated to biological processes but can behave independently in response to similar conditions (Cornelissen et al., 2003). In our case, higher LDMC in ORG and CMOM treatments show that leaves are more resistant to physical hazard caused by pests (Cornelissen et al., 2003), being an important fact of resilience in stress situations.

The positive effect of microbial communities associated to organic management supports published reports showing that organic matter addition to greenhouse soils increases soil microbial diversity (Xia et al., 2015), plant nutrient uptake (Jacoby et al., 2017), plant growth (Bonanomi et al., 2016) and prevented the effects of pathogens (Crowder et al., 2010). Plants in pots inoculated with CM inoculum were smaller than those from any other treatment, even Control plants (without inoculation), suggesting that CM inoculum may have greater abundance of soil microbial pathogens or less plant growth promoting bacteria (Bonanomi et al., 2016).

Abundance of soil microorganisms measured by qPCR showed significant differences in prokaryotic abundance between treatments at the end of experiment, suggesting that ORG favored an increase in prokaryotic bacteria but not in fungal abundance; again supporting the idea that organic management favored some beneficial microbial taxa and functions, like free-living N-fixing bacteria (Wang et al., 2012). However, there were no differences in prokaryote or fungal alpha diversity, in contrast with results from Lori et al. (2017), who showed higher prokaryote abundance and alpha diversity in soils when organic amendments were applied. In contrast to Bonanomi et al. (2016) too, who showed an opposite pattern, with prokaryote abundance and alpha diversity being higher in conventional than in

organic managements. We expected a high variability in our data due to the different origin of soils (different greenhouses), as well as their different composition and texture. In addition, small microclimatic conditions may have contributed to the variability in microbial communities we found (Poeplau et al., 2015).

Soil community structure (beta diversity) differed at the end of the experiment. These differences were only significant by using the Jaccard index but not using the Bray-Curtis index. This fact suggests that differences in prokaryote community composition across treatments at the end of the experiment should be mostly attributed to low-abundance bacteria, as the Jaccard index uses presence/absence data and ignores abundance, while Bray-Curtis index considers relative abundances (Li et al., 2016). Our results support the previous finding that keystone root microbial species might be decreased in conventional farming under intensive conditions (Banerjee et al., 2019).

We found some microbial genera significantly associated to different treatments. For example, *Nitrospira*, associated to CMOM has been reported as the most important nitrite oxidizer genus (Daims et al., 2015). *Thauera*, linked to the ORG treatment, is associated with the N cycle (Shinoda et al., 2004). Both bacterial taxa could be responsible for the increased N availability in soils. However, and by contrast, we identified ITS sequences assigned to *Olpidium*, a fungal genus associated to CM. In this genus, there are species reported as pathogens, like *Olpidium brassicae*, an important vector transmitting the tobacco necrosis virus (TNV) which affects tomato plants (Hančinský et al., 2020). Therefore, it is likely that species in this genus could partly explain the negative effect of CM microbial communities on tomato plants.

## 5. CONCLUSIONS

Plants growing with inocula from greenhouse soils with organic amendments were positively influenced by changes in microbial community structure, while those growing with inocula from greenhouse soils where synthetic chemical fertilizers were used and with no organic amendments had negative effects. Therefore, our data suggest that organic amendments could enhance plant growth while the lack of organic amendments could have negative effects on plant growth because of its effects on soil microbial communities. These patterns provide a glimpse on the role of microbial communities in intensive agriculture, suggesting that management practices are key to sustain productivity without the negative effects of chemicals use in intensive agrosystems.

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## 7. SUPPLEMENTARY MATERIAL

**Table S1.** Total high-quality 16S and ITS reads, total ASVs obtained before and after normalization and taxa association.

|     | Total reads | Reads after normalization | Total ASVs | ASVs after normalization | Number of phyla | Number of families | Number of genera |
|-----|-------------|---------------------------|------------|--------------------------|-----------------|--------------------|------------------|
| 16S | 3,610,289   | 1,271,250                 | 22,088     | 21,528                   | 42              | 431                | 778              |
| ITS | 2,233,628   | 1,875,807                 | 1,882      | 829                      | 8               | 62                 | 81               |

**Table S2.** Chemical substrate properties not shown in Table 1. Results are means  $\pm$  1SE, n=5. Different letters in a row indicate significant differences ( $p < 0.05$ ) among treatments after LSD post-hoc comparisons. The last 6 columns are F and p-value results after GLMM analysis. Legend of treatments as in Fig. S2.

| Variable                      | Unit   | Substrate beginning ( $t_0$ ) |                        |                         | Substrate final ( $t_f$ ) |                         |                        | Significance  |          |       |               |                 |       |
|-------------------------------|--------|-------------------------------|------------------------|-------------------------|---------------------------|-------------------------|------------------------|---------------|----------|-------|---------------|-----------------|-------|
|                               |        | Treatment                     |                        |                         | Treatment                 |                         |                        | F             |          |       | p-value       |                 |       |
|                               |        | CM                            | CMOM                   | ORG                     | CM                        | CMOM                    | ORG                    | Treatment (T) | Time (t) | T x t | Treatment (T) | Time (t)        | T x t |
| CaCO <sub>3</sub>             | g/100g | 1.12 $\pm$ 0.89 a             | 4.22 $\pm$ 3.96 a      | 7.17 $\pm$ 6.34 a       | 7.33 $\pm$ 5.83 a         | 7.63 $\pm$ 9.38 a       | 3.59 $\pm$ 5.67 a      | 0.56          | 2.78     | 0.69  | 0.58          | 0.11            | 0.51  |
| Al                            | mg/kg  | 2248.67 $\pm$ 679.55 a        | 1926.32 $\pm$ 246.43 a | 2284.83 $\pm$ 1762.35 a | 1957.87 $\pm$ 2187.15 a   | 1093.45 $\pm$ 1317.86 a | 2038.19 $\pm$ 483.31 a | 0.74          | 0.49     | 0.63  | 0.49          | 0.49            | 0.54  |
| Cu                            | mg/kg  | 1.59 $\pm$ 0.29 a             | 1.71 $\pm$ 0.63 a      | 1.87 $\pm$ 1.59 a       | 1.48 $\pm$ 1.89 a         | 1.09 $\pm$ 1.19 a       | 1.73 $\pm$ 0.43 a      | 0.06          | 0.07     | 0.74  | 0.95          | 0.80            | 0.49  |
| Mg                            | g/100g | 0.020 $\pm$ 0.010 a           | 0.018 $\pm$ 0.002 a    | 0.032 $\pm$ 0.037 a     | 0.032 $\pm$ 0.038 a       | 0.013 $\pm$ 0.019 a     | 0.026 $\pm$ 0.003 a    | 0.87          | 0.79     | 0.72  | 0.43          | 0.38            | 0.50  |
| Mn                            | mg/kg  | 13.29 $\pm$ 0.57 a            | 13.03 $\pm$ 4.30 a     | 17.85 $\pm$ 12.86 a     | 14.49 $\pm$ 16.074 a      | 6.95 $\pm$ 9.012 a      | 12.92 $\pm$ 2.054 a    | 0.65          | 0.24     | 0.68  | 0.53          | 0.63            | 0.52  |
| Na                            | g/100g | 0.03 $\pm$ 0.02 b             | 0.03 $\pm$ 0.01 b      | 0.04 $\pm$ 0.01 b       | 0.05 $\pm$ 0.07 a         | 0.02 $\pm$ 0.02 ab      | 0.03 $\pm$ 0.02 ab     | 0.54          | 7.07     | 0.44  | 0.59          | <b>0.01</b>     | 0.65  |
| Pb                            | mg/kg  | 2.46 $\pm$ 0.70 a             | 2.31 $\pm$ 0.21 a      | 2.56 $\pm$ 1.89 a       | 1.91 $\pm$ 2.33 a         | 1.57 $\pm$ 1.63 a       | 2.41 $\pm$ 0.57 a      | 0.16          | 0.44     | 0.59  | 0.86          | 0.51            | 0.56  |
| Ti                            | mg/kg  | 22.71 $\pm$ 4.46 a            | 23.11 $\pm$ 3.04 a     | 27.84 $\pm$ 20.30 a     | 21.59 $\pm$ 25.71 a       | 13.25 $\pm$ 14.96 a     | 25.18 $\pm$ 5.25 a     | 0.48          | 0.30     | 0.72  | 0.62          | 0.59            | 0.50  |
| Zn                            | mg/kg  | 3.39 $\pm$ 0.65 a             | 3.31 $\pm$ 0.33 a      | 3.93 $\pm$ 3.61 a       | 3.47 $\pm$ 4.09 a         | 2.29 $\pm$ 2.088 a      | 3.99 $\pm$ 0.75 a      | 0.37          | <0.01    | 0.73  | 0.69          | 0.95            | 0.49  |
| Cl                            | mg/l   | 3.32 $\pm$ 0.065 c            | 3.43 $\pm$ 0.097 c     | 3.56 $\pm$ 0.075 c      | 87.07 $\pm$ 53.46 ab      | 95.69 $\pm$ 72.13 a     | 45.52 $\pm$ 22.58 bc   | 1.26          | 27.78    | 1.25  | 0.30          | <b>&lt;0.01</b> | 0.30  |
| SO <sub>4</sub> <sup>2-</sup> | mg/l   | 17.01 $\pm$ 2.64 b            | 20.62 $\pm$ 2.70 b     | 53.12 $\pm$ 58.21 b     | 77.13 $\pm$ 52.52 ab      | 70.85 $\pm$ 41.30 ab    | 130.73 $\pm$ 122.35 a  | 0.81          | 12.79    | 0.87  | 0.46          | <b>&lt;0.01</b> | 0.43  |

**Table S3.** Results of Kruskal-Wallis analysis of total ASV richness and Shannon index comparing the different treatments. Legend of treatments as in Fig. S2.

| Factor <sup>a</sup>      | Prokaryote (16S) |         |               |         | Fungi (ITS) |         |               |         |
|--------------------------|------------------|---------|---------------|---------|-------------|---------|---------------|---------|
|                          | Shannon          |         | Observed ASVs |         | Shannon     |         | Observed ASVs |         |
|                          | H                | p-value | H             | p-value | H           | p-value | H             | p-value |
| Management               | 1.94             | 0.38    | 2.24          | 0.33    | 2.78        | 0.25    | 2.38          | 0.30    |
| Managements <sup>b</sup> | H                | p-value | H             | p-value | H           | p-value | H             | p-value |
| CM-CMOM                  | 1.32             | 0.25    | 2.45          | 0.12    | 0.27        | 0.60    | 0.10          | 0.75    |
| CM-ORG                   | 0.27             | 0.60    | 0.01          | 0.92    | 2.45        | 0.12    | 1.58          | 0.21    |
| CMOM-ORG                 | 1.32             | 0.25    | 0.88          | 0.35    | 1.32        | 0.25    | 1.84          | 0.17    |

<sup>a</sup>Effects of factor “Management” were assessed by Kruskal-Wallis analysis taking into account all groups. Values represent the univariate H statistic and the p-value at 95% confidence level.

<sup>b</sup>Pairwise comparisons between management systems. Values represent the univariate H statistic and the p-value at 95% confidence level assessed by Kruskal-Wallis analysis.

**Table S4.** Prokaryotic and fungal functions associated to genus by LEfSe provided by FAPROTAX (prokaryotic function) and FUNGuild (Fungal guild). Legends of treatments as in Fig. S2.

| <b>Prokaryotic genus</b> | <b>Associated treatment</b> | <b>Function</b>                               | <b>Reference</b>   |
|--------------------------|-----------------------------|---|--|
| Nodosilinea              | CM                          | Unknown                                       |  |
| Brachymonas              | CM                          | Nitrate reduction                             | Hiraishi et al. 1995   |
| Algoriphagus             | CM                          | Unknown                                       |  |
| Marinibaculum            | CM                          | Unknown                                       |  |
| Hyphomonas               | CM                          | Unknown                                       |  |
| Pseudoxanthomonas        | CM                          | Unknown                                       |  |
| Rubinisphaera            | CM                          | Unknown                                       |  |
| Parasegetibacter         | CM                          | Unknown                                       |  |
| Persicitalea             | CM                          | Unknown                                       |  |
| Nocardia                 | CM                          | Plant Pathogen                                | UK National Collection of Plant Pathogenic Bacteria. NCPPB No: 954           |
| Magnetospira             | CM                          | Unknown                                       |  |
| Oceanibaculum            | CM                          | Unknown                                       |  |
| Chthonobacter            | CM                          | Unknown                                       |  |
| Salinispira              | CMOM                        | Unknown                                       |  |
| Alterococcus             | CMOM                        | Fermenter of monosaccharides or disaccharides | Hedlund and Shieh 2011   |
| Bauidia                  | CMOM                        | Unknown                                       |  |
| Sphingobacteriales       | CMOM                        | Plant Pathogen                                | UK National Collection of Plant Pathogenic Bacteria. NCPPB No: 4319 and 2493 |
| Sphingopyxis             | CMOM                        | Unknown                                       |  |
| Phaselicystis            | CMOM                        | cellulose-degrading                           | García et al. 2009   |
| Porticoccus              | CMOM                        | hydrocarbon-degrading                         | Gutierrez et al. 2012  |
| WWH121                   | CMOM                        | Unknown                                       |  |
| Nitrospira               | CMOM                        | Complete ammonia oxidation (comammox)         | van Kessel et al. 2015   |
| Reyranella               | CMOM                        | Oxidase activity                              | Pagnier et al. 2011  |
| Ferruginibacter          | CMOM                        | Catalase and oxidase activity                 | Lim et al. 2009  |
| CL50029                  | ORG                         | Unknown                                       |  |
| Arthronema               | ORG                         | Unknown                                       |  |
| Thauera                  | ORG                         | Denitrifier                                   | Mechichi et al. 2002   |
| Marmoricola              | ORG                         | Unknown                                       |  |
| <b>Fungal genus</b>      | <b>Associated treatment</b> | <b>Guild</b>                                  | <b>Reference</b>   |
| Olpidium                 | CM                          | Plant Pathogen                                | Devasahayam and Henry 2009   |

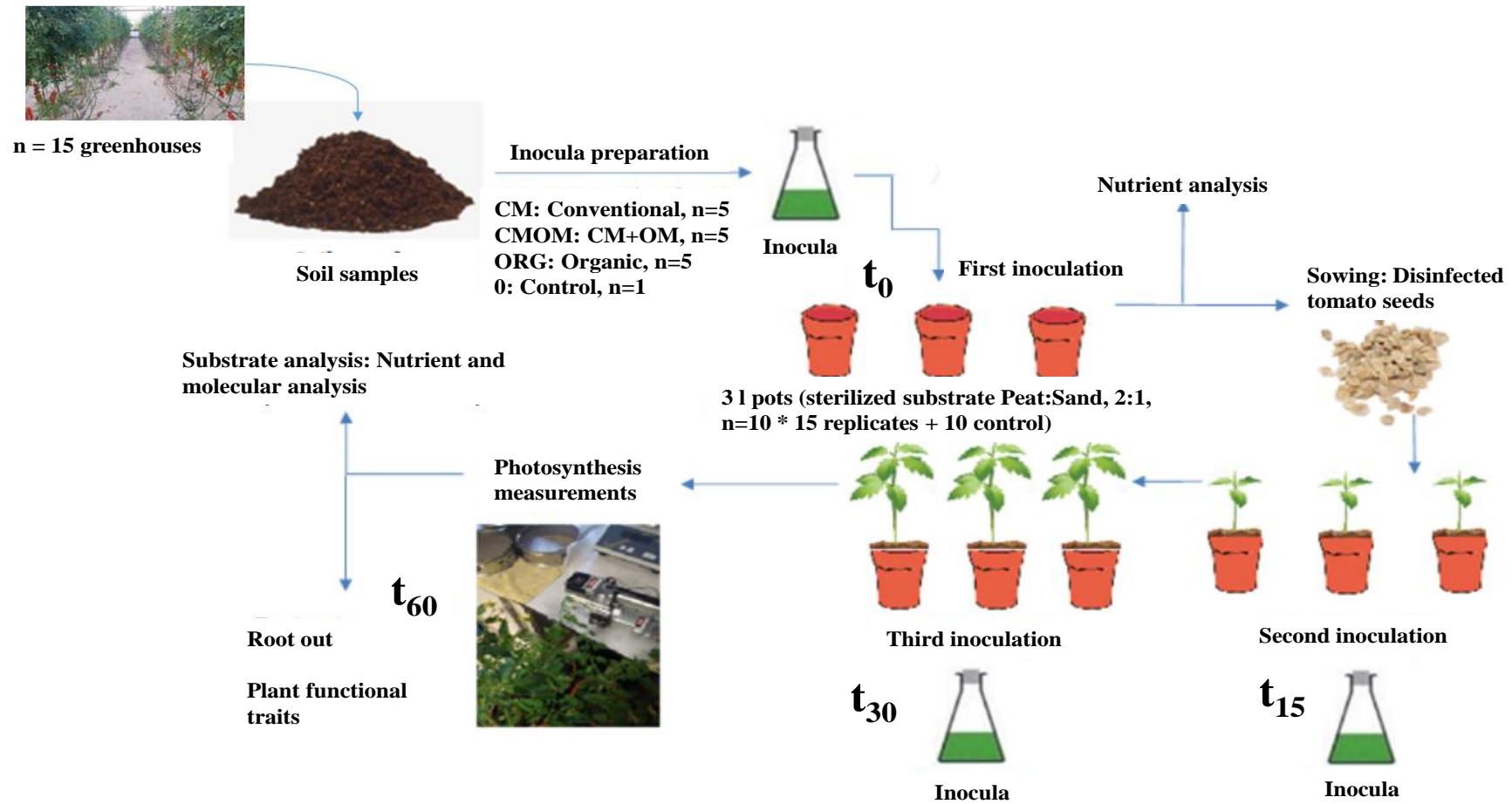
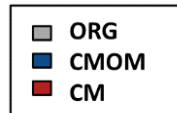
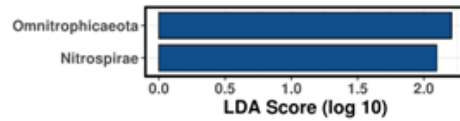
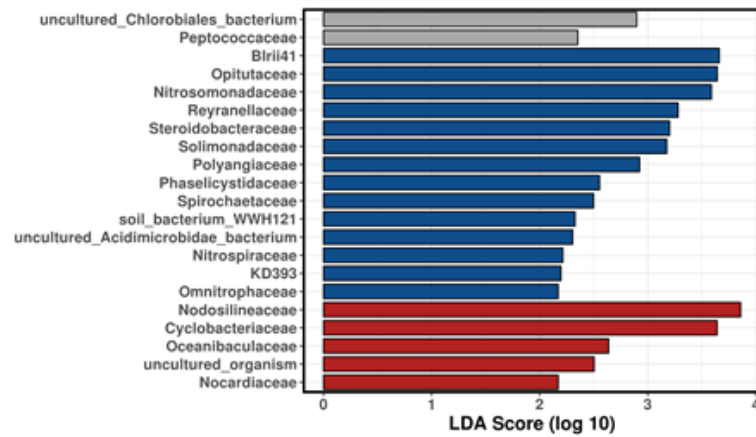


Figure S1. Experimental design and variables measured.

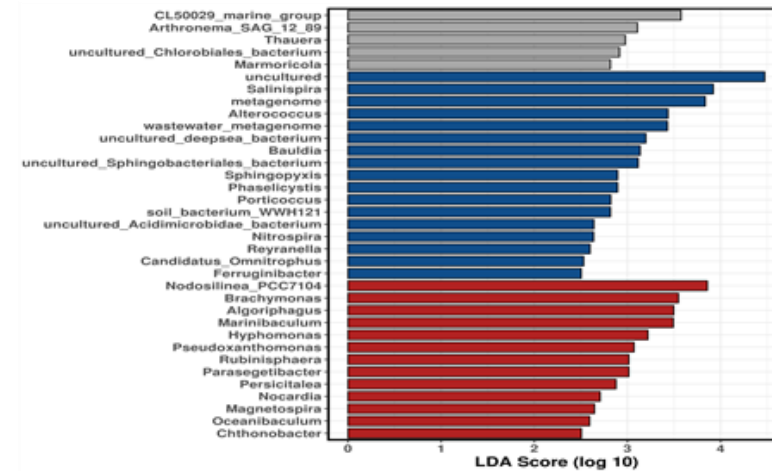
A)



B)

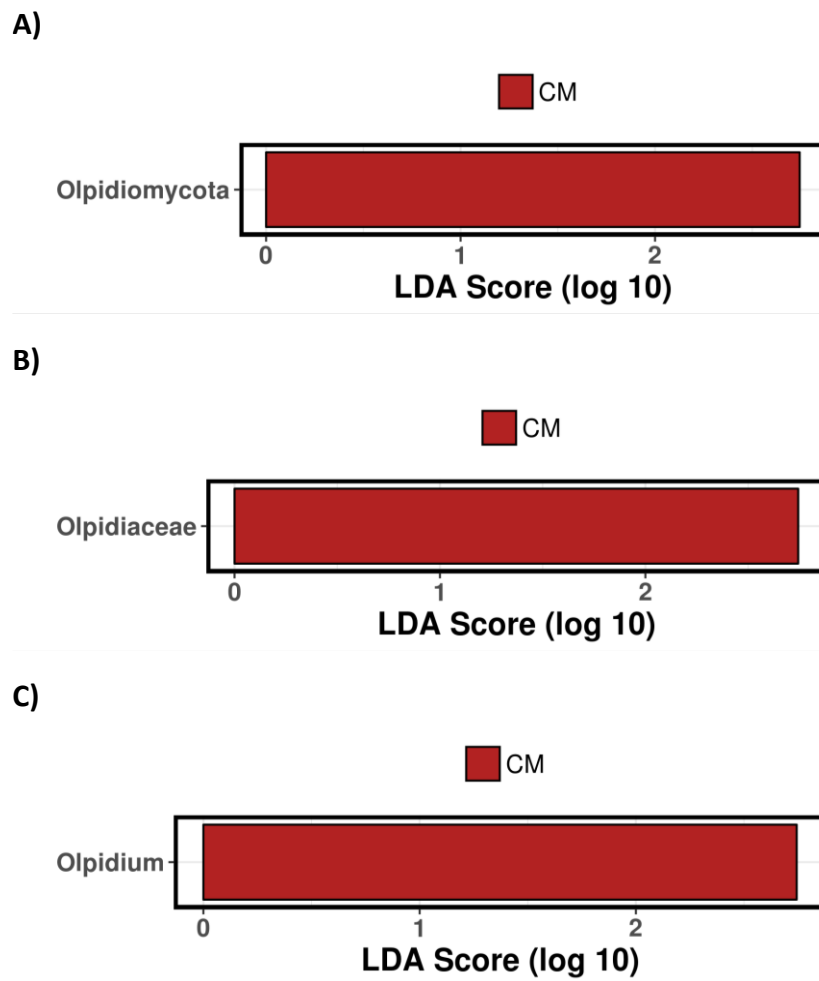


C)



**Figure S2.** Prokaryotic phyla (A), families (B) and genera (C) associated to different treatments (LDA>2, p<0.05). CM: Pots inoculated with conventionally managed soil and no OM application; CMOM: Pots inoculated with conventionally managed soil and OM application, and ORG: Pots inoculated with fully organic management soil with yearly OM application and no chemicals added.





**Figure S3.** Fungal phyla (A), families (B), genera (C) associated to CM treatment (LDA>2,  $p<0.05$ ). Legend of treatments as in Fig. S2.

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# CAPÍTULO IV

## Effects of different soil disinfection techniques on soil microbial communities in intensive greenhouse agriculture





# **EFFECTS OF DIFFERENT SOIL DISINFECTION TECHNIQUES ON SOIL MICROBIAL COMMUNITIES IN INTENSIVE GREENHOUSE AGRICULTURE**

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*(En revisión en Biology and Fertility of Soils)*

## **ABSTRACT**

Intensive greenhouse agriculture is becoming very important all around the world to feed a growing population. This type of agriculture is linked to monocultures and is origin of several environmental problems. One of these problems concerns the disinfection of soil prior to planting new crops. The impact of chemicals used to disinfect soils is under review in the European Union, with many products being prohibited. There are environmental-friendly alternatives; however, there is little information on their effectiveness. We addressed the effect of different soil disinfection techniques on microbial communities and the effects of the latter on plant growth and productivity. The different disinfection techniques tested were i) chemical disinfection (with 1,3-dicholopropene, CD); ii) solarization (thermal disinfection using a plastic cover, SOL), and iii) passive disinfection (no plants growing for one month, PD). After disinfecting greenhouses with the three different techniques, we extracted the soil microbial community from two depths in each greenhouse (n=3 greenhouses per disinfection technique). We then added these

inocula to pots with sterilized substrate, and planted tomato plants grown from disinfected seeds. The plants grew for three months in a common greenhouse. At the end of study, we measured photosynthetic rate, root and shoot biomass, leaf traits, and fruit production. Our data showed that different disinfection techniques led to different soil microbial communities, and each had a different effect on plant growth and fruit production. Plants growing with extracts of CD and SOL treatments grew better than plants grown with PD extracts, and had higher fruit production. Overall, our data show that disinfection by solarization is an effective and sustainable soil disinfection alternative to the application of chemicals that may soon be banned.

**KEYWORDS:** dichloropropene, soil microbial communities, solarization, tomato production.

## 1. INTRODUCTION

Feeding a growing world population is one of the most important challenges humanity will face in a near future (Fraser, 2020), and ensuring global food supply requires sustainable intensive agriculture (Beltran-Peña et al., 2020). In intensive agriculture, soil management has been shown to be essential to increase production and to control soil-borne pathogens (Usero et al., 2021). However, the use of chemicals to disinfect soils has increased in parallel to intensification, causing health and environmental problems (Barry et al., 2012). European policies that regulated the use of disinfection chemicals in 2009 allowed only two products (EC-Regulation 1107/2009), Dazomet and metam-sodium/metam-potassium (the metam products are under review). However, the presence of soil-borne pathogens led the European Union (EU) to give exceptional authorization to other chemicals, allowing member states the possibility of restricted continued use. In Spain, the use of 1,3-dichloropropene has been authorized exceptionally until 2022 for some crops (MAPA, 2020), but this authorization includes the need of a transition to alternative disinfection techniques, which are revised every year by regional governments. 1,3-dichloropropene is an effective product to control soil-borne fungal pathogens (Qiao et al., 2010). However, several problems linked to its use have been identified. For instance, it has a long-term impact on human health, increasing cancer risk in workers exposed to its volatile compounds (Beauvais, 2015). It also produces environmental issues, like groundwater contamination (Ruzo, 2006), and the release of contaminants to the atmosphere (Yates and Ashworth, 2018). Moreover, 1,3-dichloropropene has important effects on soil microbial communities (Dangi et al., 2017), decreasing not only the presence of pathogens but also the absolute abundance

of microorganisms (Cheng et al., 2020). Application of this chemical also decreases bacterial diversity (Hoshino and Matsumoto, 2007), affecting soil functions like nitrogen mineralization and nitrification (Yan et al., 2013), decreasing the relative abundance of bacteria involved in the N cycle (Fang et al., 2019) and several enzymatic processes (Hussain et al., 2009).

The intensive production in greenhouses, such as in south-eastern (SE) Spain needs yearly soil disinfection to maintain crop production economically viable by controlling soil-borne pathogens. In this regard, 1,3-dichloropropene is a good chemical alternative to banned fumigants, like Methyl-bromide (Chellemi and Mirusso, 2006). However, finding an effective sustainable alternative to these chemicals is urgently needed to maintain crop production while avoiding environmental pollution and human health problems.

Solarization and biosolarization have been assessed as non-chemical alternatives to soil disinfection (Rubin et al., 2007). Solarization is a process that increases soil temperature through plastic mulching, leading to a reduction of microbial communities by heat (Katan, 2014). In the case of biosolarization, the effect of solarization is combined with the application of fresh manure, in which decomposition increases soil temperature and volatile compound generation that further contribute to disinfect the soil (Flores et al., 2008). However, biosolarization is more expensive than solarization, and yearly applications are not economically viable (Bach et al., 2016; Rowlings et al., 2019). For this reason, solarization is more widespread. It represents a potential reduction of more than 50% in costs compared with 1,3-dichloropropene use (Lombardo et al., 2012). Furthermore, when compared to other chemicals applications, solarization has shown a positive effect on tomato production after three years of application (Scopa et al., 2009).



In this study, we analyzed the effects of different disinfection techniques on the composition of surviving soil microbial communities. We then performed an experiment to assess the different effects of these soil microbial communities on tomato plant growth and production. For this purpose, we used an experimental approach consisting of tomato plants treated with soil extracts from commercial greenhouses that were obtained immediately after soil disinfection. We tested three disinfection approaches, all of them widely used locally: chemical disinfection (i.e., application of 1,3-dichloropropene), solarization, and passive disinfection (absence of intervention or watering during an appreciable period of time). We hypothesized that: i) surviving microbial communities associated to different disinfection techniques differ in composition; ii) consequently, these communities produce differential effects on plant growth and tomato production; iii) active disinfection (chemical or solarization) has stronger and more positive effects on crop production than passive disinfection. We also hypothesized that iv) there would not be relevant differences between chemical disinfection and solarization, showing that the latter is a good alternative to the former.

## **2. MATERIAL AND METHODS**

### ***Greenhouse selection, disinfection techniques and soil sampling***

Nine commercial greenhouses from Almeria, Spain that grew tomato crops were selected in September 2017. Different disinfection techniques had been applied in these greenhouses in July 2017, i.e., two months before the planting of the next tomato crop. Three types of disinfection techniques were used in different

greenhouses: 1) Passive disinfection that consisted of one month with no crop cultivation (PD); 2) Chemical disinfection (CD) using a product containing 1,3-dichloropropene applied by irrigation, followed by soil covered for seven days with transparent 0.05 mm thick polyethylene plastic sheet. After that, the greenhouse remained 21 days with no crop cultivation as a safety period. 3) Solarization (SOL) by covering moistened soil with a transparent 0.05 mm thick polyethylene plastic sheet for 30 days, while greenhouse is totally closed to reach high temperature. Each disinfection technique was applied on three of the selected greenhouses. Additionally, we took into account the type of soil fertilization management in each greenhouse (Table S1, Appendix 1, Appendix 2).

Soils were sampled 30 days after previous crop harvest in the PD treatment, after the safety period in CD, and immediately after removing the plastic sheet in SOL. All greenhouses used the local “enarenado” technique, i.e., artificial soil system in which a 8–10 cm layer of coarse sand mulch is placed over the soil (Thompson et al., 2007). Soils were sampled at two different depths, (1) from the first 10 cm after removing the sand mulching, and (2) between 10 and 20 cm depth. For each depth, soil was sampled from 10 randomly located points in each greenhouse and samples were combined to make two composite samples (one per depth) per greenhouse. The equipment for soil sampling was sterilized with ethanol between samples. All samples were immediately placed in a cool box at 5°C and rapidly transferred to the laboratory.

### ***Preparation of soil microbial community inoculum***

Soil microbial communities were extracted from each soil sample by mixing 0.5 L of soil in 1 L of deionized, sterilized water. The soil suspension was filtered through a 0.5 mm sieve to remove soil particles while allowing the passing of fungal spores and hyphae and soil bacteria (Rodríguez-Echeverría et al. 2013). One extract was prepared from each greenhouse and soil depth, totaling 18 inocula (9 greenhouses x 2 depths).

### ***Experimental design***

We assessed the effect of soil extracts on tomato plants growing in pots that received the greenhouse soil inocula before seed sowing. 150 ml of inoculum was added to 3 L polyethylene pots filled with a peat and sand mix (2:1 v/v) previously autoclaved three times at 121°C for 60 min. Six replicate pots were prepared for each individual inoculum, making a total of 108 inoculated pots (3 soil disinfection techniques x 3 greenhouses x 2 depths x 6 replicates). In addition, we included six pots that only received 150 ml of deionized, sterilized water as a Control treatment. After inoculation, three hybrid tomato seeds of a commercial variety (Hulk F1<sup>®</sup>, CapGen Seeds, Vicar, Spain) were sown in each pot to assure that at least one plant established. After seedling establishment, we left one plant per pot. Before sowing, seeds were disinfected in 70% ethanol for one minute, cleaned with sterilized water, disinfected with 5% sodium hypochlorite solution for five minutes, washed again with sterilized water, and blotted dry with paper towels (Rodríguez-Echeverría et al., 2013).

The experiment was from December 2017 to April 2018. Pots were randomly placed in the greenhouse and relocated randomly every 15 days to avoid environmental gradients. Two additional inoculations of 150 ml of soil inocula per pot were applied 15 and 30 days after the beginning of the experiment, applying the same volume of sterilized water to Control pots. Greenhouse climatic conditions were passively controlled by opening the roof and side windows when the internal air temperature was  $>30^{\circ}\text{C}$ , and by closing them when temperature was  $<20^{\circ}\text{C}$ . Watering was applied using manually operated valves throughout the experiment, taking care that all pots received the same amount of water and that plants suffered no water stress. Water was obtained from a desalination plant, and electrical conductivity (EC) was  $0.6\text{-}1.2\text{ dS m}^{-1}$ . No fertilizers were added during the experiment.

### *Substrate sampling*

Pots substrate was sampled after the first inoculation to check that the nutrient content received with the inocula was the same for all pots, and for DNA analysis of microbial communities associated to the different disinfection techniques. Composite samples were obtained for each greenhouse by combining samples from all pots receiving the same soil inoculum, including control pots, and each composite sample was separated in two subsamples, one for nutrient content and another for DNA analysis. The subsample used for nutrient content was dried and sent for analysis, and the subsample for DNA analysis was directly transferred to the lab to extract DNA before storage.

***Substrate nutrient content***

Total N content was determined with a LECO Truspec analyzer (St. Joseph, MI, USA). Organic C was determined following Schumacher (2002), using 2M HCl to remove inorganic C. Nitrate ( $\text{NO}_3^-$ ) and ammonia ( $\text{NH}_4^+$ ) were extracted using 2M KCl solution (i.e., by mixing 40 g of substrate with 200 ml of KCl solution), and concentration was determined with an automatic continuous segmented flow analyzer (model SAN<sup>++</sup>, Skalar Analytical B.V., Breda, The Netherlands). P, K and Ca were determined after acid digestion in an inductively coupled plasma (ICP) emission spectrometer (ICAP 6500 DUO; Thermo Scientific, Wilmington, DE, USA). Substrate pH was measured with a pH-meter (Crison, Barcelona, Spain) in a 1:2.5 solution in water. Analysis of  $\text{NO}_3^-$  and  $\text{NH}_4^+$  were conducted at the Department of Agronomy, University of Almería. Other determinations were conducted at the CSIC-CEBAS “Ionomics” lab in Murcia, Spain.

***Plant traits, gas exchange rates, plant biomass and crop production***

Maximum leaf photosynthetic rate ( $A_{\text{max}}$ ) and instantaneous gas exchange efficiency (iGEE) were measured before harvest.  $A_{\text{max}}$  was measured using an IRGA LI-6400 (LiCor Bioscience, Lincoln, USA) in three fully expanded, mature leaves per plant, with no apparent damage. For statistical analyses, we used the mean value of these three measurements per plant. IRGA chamber parameters were set at 25°C and 1,500  $\mu\text{mol m}^{-2}\text{s}^{-1}$  PAR intensity during measurements. iGEE was calculated by dividing  $A_{\text{max}}$  by stomatal conductance (Farquhar et al., 1989).

Two fully expanded, mature leaves were collected per plant, one used to calculate the specific leaf area (SLA) and the other to determine leaf dry matter

content (LDMC), both following standard protocols (Pérez-Harguindeguy et al., 2013). SLA is the ratio between fresh leaf area and leaf dry mass. Leaf area was measured using the Midebmp software (CSIC-EEZA, Almería, Spain). Leaf saturated mass was weighed after leaving each leaf inside a dark container with the petiole inserted in water-soaked cotton for 24 h. Fresh leaves were dried at 60°C for 72 h and weighed. LDMC is the ratio between leaf dry and fresh mass.

We collected, counted and weighed all tomato fruits, obtaining individual fruit mass and total fresh mass production per plant. After measurements, fruits were oven-dried at 60°C until constant weight, and then weighed to determine dry mass.

After fruit harvest, above- and below-ground plant tissues were separated and oven-dried at 60°C until constant weight and then weighed. Shoot (S), root (R), and total biomass (including shoot and root biomass, and excluding fruit biomass) were calculated, as well as the root-to-shoot ratio (R:S).

### ***DNA extraction and quantitative PCR***

DNA was extracted using the DNeasy Powersoil<sup>®</sup> Kit (Qiagen, Inc., Venlo, Netherlands), from 250 mg of each substrate sampled after inoculation. DNA concentration was estimated using Qubit Fluorometric Quantification (Thermo Scientific, USA); samples were stored at -80°C.

Quantitative PCR (qPCR) analyses were performed on DNA extractions to measure the abundance of microbial marker genes for prokaryotes and fungi. The primer pairs used for the qPCR analyses were 515f (5'-GTGYCAGCMGCCGCGGTAA-3') and 806r (5'-GGACTACNVGGGTWTCTAAT-3') for bacteria (Walters et al., 2015),

and ITS1 (5'-TCCGTAGGTGAACCTGCGG-3'; Gardes and Bruns, 1993) and ITS5.8S (5'-CGC TGC GTT CTT CAT CG-3'; Vilgalys and Hester, 1990) for fungi, respectively. Amplifications were performed by using a SYBR<sup>®</sup> Green (Sigma-Aldrich, USA) based on qPCR method in a CFX96<sup>™</sup> Real-Time PCR Detection System (BioRad Laboratories, USA). Standard curves were prepared in every assay using 10-fold serial dilutions of stock solutions containing the target DNA molecules. The reaction mixture contained 10 µl of 2X PowerUp<sup>™</sup> SYBR<sup>™</sup> Green Master Mix (Applied Biosystems, USA), 1 µl of each primer (20 µM), 10-100 ng of template DNA and nuclease free water (Ambion Thermofisher) up to 20 µl of final volume. Amplification conditions were as follows: 95°C for 10 min and then for bacteria: 35 cycles of 10 s at 95°C, 30 s at 57°C, and 30 s at 72°C. For fungi: 40 cycles of 15 s at 95°C, 30 s at 53°C and 1 min at 72°C, followed by melt curve from 60°C to 95°C at 0.5 °C increment. Triplicate reactions were performed for each DNA extract, standard curve, and negative control. PCR efficiency for different assays ranged between 75% and 95% with  $R^2 > 0.9$ . The specificity of amplified products was verified by melting curves and agarose gel electrophoresis analysis.

### ***Metabarcoding of prokaryotic and fungal soil communities***

Amplicon sequencing was performed using Earth Microbiome Project (EMP) standard protocols (<https://earthmicrobiome.org/protocols-and-standards/>) at the facilities of Genyo in Granada, Spain. PCR was done in triplicate on the V4 region of the 16S rRNA gene using the primer pair 515f-806r and on the ITS1 region with the primer pair ITS1f-ITS2 (Walters et al. 2015). Barcoded PCR products were quantified using a Qubit dsDNA (Thermo Fisher Scientific) instrument and pooled

in equal concentrations. The multiplexed DNA library was purified using Agencourt AMPure XP beads (Beckman Coulter). DNA quality and size were checked with a High Sensivity DNA Assay (Bioanalyzer 2100, Agilent) and sequenced in an Illumina MiSeq sequencing platform using the Illumina reagent kit V3 (600 cycles) generating 300 bp pair-end reads.

Demultiplexed pair-end Illumina reads were processed using QIIME 2 pipeline v.2019.4 (Bolyen et al., 2019). The cutadapt plugin (Martin, 2011) was used to trim primers. The data was denoised with the q2-dada2 plugin, which implements the DADA2 R library (Callahan et al., 2016), performing sequence quality control, truncation of the reads, stitching R1 and R2 reads, generation of amplicon sequence variants (ASV) and screening out potentially chimeric sequences. PCR negative controls, DNA extraction controls and a commercial mock community sample (ZymoBIOMICS Microbial Community Standard, Zymo Research) were also sequenced. After checking sequencing controls and the correct classification at genus level of the 8 bacterial and 2 fungal strains included in the mock sample (data not shown), control samples were excluded from the analysis. In the case of ITS data, we only used the R1 reads, as the taxonomic classification of the mock community at genus level was not accurate combining R1 and R2 reads.

Taxonomy was assigned using the QIIME 2 Naïve Bayes method (Bokulich et al., 2018). The databases SILVA v.132 (Quast et al., 2013) and UNITE v8 dynamic (Kõljalg et al., 2005) were used to train the classifiers for 16S and ITS data, respectively. ASVs assigned to chloroplasts and mitochondria (16S data) and eukaryotic non-fungal lineages (ITS) were removed, as also ASVs not classified at



phylum level. The sequenced dataset has been deposited in the NCBI Biosample Dataset PRJNA629769.

### *Statistical analysis*

We used disinfection technique (PD, CD and SOL), soil depth (0-10 cm and 10-20 cm) and their interaction as fixed factors, and greenhouse ID as random factor, in linear mixed models (LMM). We analyzed the effects of experimental treatments on nutrient content in pots after inoculation, on qPCR  $\log_{10}$ -transformed results, and on plant data at harvest (plant traits, gas exchange rates, plant biomass, and crop production). When necessary, we selected a variance function structure to avoid heteroscedasticity. Post-hoc comparisons were performed using Fisher's LSD test for each factor.

Unless stated otherwise, statistical analyses were conducted with R 3.5.2 version (R Core Team<sup>®</sup>, 2018) using the interface implemented in the InfoStat<sup>®</sup> statistical software (Di Rienzo et al., 2019) and RStudio<sup>®</sup> (Version 1.1.463). Significance of differences between treatments were set at  $p < 0.05$ . Results throughout the text and figures and tables are mean values  $\pm$  1SE.

Calypso software (Zakrzewski et al., 2017), an online suite of analytical tools for microbiomes that integrates different R packages (<http://cgenome.net/calypso/>) was used to calculate  $\alpha$ -diversity indices on normalized 16S rRNA and ITS datasets. These were used to produce multivariate diagrams and to perform statistical tests on the microbiome data, using the ASV matrix and the taxonomic assignments generated by QIIME2 as input data. We then performed LMM for determining significant differences in  $\alpha$ -diversity indices at a 95% confidence level, and analysis

of  $\beta$ -diversity using PERMANOVA (ADONIS function from vegan package in R).

In all the cases, the greenhouse ID was set as random factor.

### 3. RESULTS

#### *Assessment of initial effect of inocula on substrate chemical characteristics*

Pot substrates inoculated with different soil extracts showed similar nutrient content (Table S2) with no significant differences in chemical composition, nor with control pots (Table S3). Therefore, inocula effects were produced by their microbial communities rather than by nutrient additions, as shown in previous studies using the same experimental approach (Usero et al., 2021).

#### *Substrate microbial communities after inoculation*

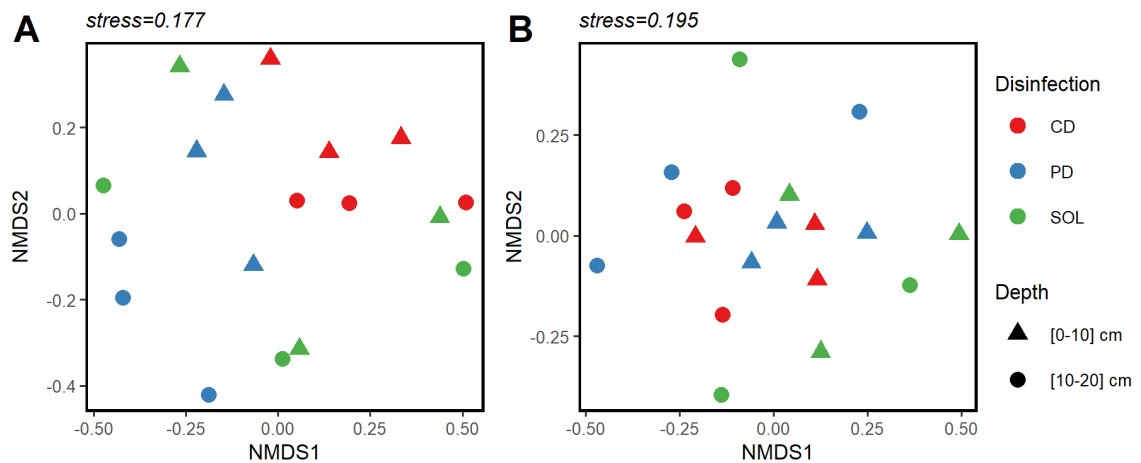
After inoculation, substrates showed differences in fungal abundance (determined by qPCR) among treatments (Table 1). Attending to disinfection techniques, SOL presented the highest and Control the lowest fungal abundances, whereas PD and CD were in between. There were no difference in prokaryotic abundance (determined by qPCR) among soil disinfection techniques, but the Control substrates had lower abundances compared to any of the disinfection treatments (Table 1). In the case of the fungi:prokaryote ratio, there were differences between SOL and CD, being PD in between. There were also differences between SOL and PD when compared to Control (Table 1). Attending to depth where soils were collected, there were no significant effects

**Table 1.** Prokaryotic and fungal abundance in pot substrates after inoculation. Results represent mean values  $\pm 1$  SE for each variable and soil inocula (n=3 substrate samples per soil disinfection technique and soil depth, n=18 substrates in total). Numbers with different letters in the same column and within each treatment indicate significant differences ( $p < 0.05$ ) among inocula treatments (disinfection and soil depth) after Fisher LSD post-hoc comparisons. For disinfection techniques, legend as in Table 1. For depth, [0-10]: Soil collected from the first 10 cm of soil profile, and [10-20]: Soil collected from 10 to 20 cm of soil depth. Control represents pot substrates inoculated with sterilized deionized water. F: F-statistic; df: degrees of freedom. The interaction “Disinfection treatment x Soil depth” did not render statistically significant results ( $p > 0.05$ ).

| Variable   | Disinfection technique |                   |                    |                   | F    | df | Depth             |                   | F    | df |
|--|------------------------|-------------------|--------------------|-------------------|------|----|-------------------|-------------------|------|----|
|  | CD                     | SOL               | PD                 | Control           |      |    | [0-10] cm         | [10-20] cm        |      |    |
| Prokaryotic abundance<br>( $\text{Log}_{10}(\text{Copies g}^{-1})$ ) | 8.74 $\pm$ 0.13 A      | 9.04 $\pm$ 0.13 A | 8.75 $\pm$ 0.04 A  | 8.16 $\pm$ 0.07 B | 1.70 | 3  | 8.64 $\pm$ 0.17 A | 8.53 $\pm$ 0.17 A | 0.40 | 1  |
| Fungal abundance<br>( $\text{Log}_{10}(\text{Copies g}^{-1})$ )      | 5.04 $\pm$ 0.01 C      | 6.15 $\pm$ 0.13 A | 5.63 $\pm$ 0.16 B  | 4.39 $\pm$ 0.15 D | 3.93 | 3  | 5.49 $\pm$ 0.20 A | 5.91 $\pm$ 0.20 A | 2.83 | 1  |
| Fungi:Prokaryote ratio   | 0.60 $\pm$ 0.02 BC     | 0.68 $\pm$ 0.01 A | 0.64 $\pm$ 0.02 AB | 0.54 $\pm$ 0.02 C | 2.44 | 3  | 0.62 $\pm$ 0.02 A | 0.67 $\pm$ 0.02 A | 3.20 | 1  |

of soil depth on prokaryote or fungal abundances, nor on the fungi:prokaryote ratio. However, there were differences of both depths when compared to Control (Table 1). The interaction between disinfection techniques and soil depths had no influence on prokaryote or fungal abundance, nor on fungi:prokaryote ratios.

Results of  $\alpha$ -diversity of prokaryotic and fungal communities (ASV richness and Shannon index) did not show differences across disinfection techniques, soil depths or the interaction between these factors (Table S4). By contrast, the analysis of  $\beta$ -diversity revealed an overall effect of disinfection technique and soil depth on the composition of the prokaryotic communities. NMDS based on the Bray-Curtis dissimilarity index clearly separated PD and CD samples, as well as the two depths treatments within these two disinfection techniques (Figure 1A). PERMANOVA analyses confirmed the differences between CD and PD prokaryotic community compositions ( $p=0.001$ ), as well as between soil inocula depths ( $p\text{-value}=0.005$ ). The interaction between disinfection technique and depth was not significant ( $p\text{-value}=0.954$ ). In the case of the fungal communities,  $\beta$ -diversity analyses only show significant effect of depth on fungal  $\beta$ -diversity (Figure 1B; Table 2).



**Figure 1.** Non-metric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarity index results among pot substrates prokaryotic (A) and fungal communities (B) after inoculation. Legend for the disinfection techniques is as follows. PS: Passive disinfection (one month with no cultivation or plastic cover), CD: Chemical disinfection (1,3-dichloropropene application), and SOL: Solarization. Legend for soil depths, [0-10]: Soil collected from the first 10 cm of the soil profile after removing sand layer, and [10-20]: Soil collected from 10 to 20 cm of soil depth.

**Table 2.** PERMANOVA analysis results of pot substrate prokaryotic and fungal communities comparing the different inocula treatments. Legend of inocula treatments as in Table 1.

| Factor <sup>a</sup>                     | Prokaryote (16S rRNA)          |                |       | Fungi (ITS) |                |       |       |
|---|--------------------------------|----------------|-------|-------------|----------------|-------|-------|
|   | F                              | R <sup>2</sup> | p     | F           | R <sup>2</sup> | p     |       |
| <b>Disinfection technique</b>           | 1.287                          | 0.144          | 0.031 | 1.181       | 0.137          | 0.109 |       |
| <b>Depth</b>                            | 1.744                          | 0.097          | 0.004 | 1.347       | 0.078          | 0.012 |       |
| <b>Disinfection technique X Depth</b>   | 0.803                          | 0.090          | 0.660 | 0.736       | 0.086          | 0.805 |       |
| <b>Pairwise comparisons<sup>b</sup></b> |                                |                |       |             |                |       |       |
| <b>PD-CD</b>                            | Disinfection technique         | 1.598          | 0.131 | 0.001       | 1.189          | 0.105 | 0.189 |
|   | Depth                          | 1.609          | 0.132 | 0.002       | 1.404          | 0.124 | 0.102 |
|   | Disinfection technique X Depth | 0.949          | 0.078 | 0.598       | 0.706          | 0.062 | 0.934 |
| <b>CD-SOL</b>                           | Disinfection technique         | 1.203          | 0.108 | 0.162       | 1.149          | 0.106 | 0.233 |
|   | Depth                          | 1.199          | 0.108 | 0.168       | 0.957          | 0.088 | 0.520 |
|   | Disinfection technique X Depth | 0.721          | 0.065 | 0.961       | 0.766          | 0.070 | 0.907 |
| <b>PD-SOL</b>                           | Disinfection technique         | 1.093          | 0.096 | 0.300       | 1.162          | 0.104 | 0.250 |
|   | Depth                          | 1.502          | 0.132 | 0.011       | 1.121          | 0.100 | 0.290 |
|   | Disinfection technique X Depth | 0.758          | 0.067 | 0.909       | 0.877          | 0.079 | 0.673 |

<sup>a</sup>Effects of factors were assessed by PERMANOVA analysis taking into account all groups. Values represent the univariate F statistic, the variability explained (R<sup>2</sup>) and the p-value.

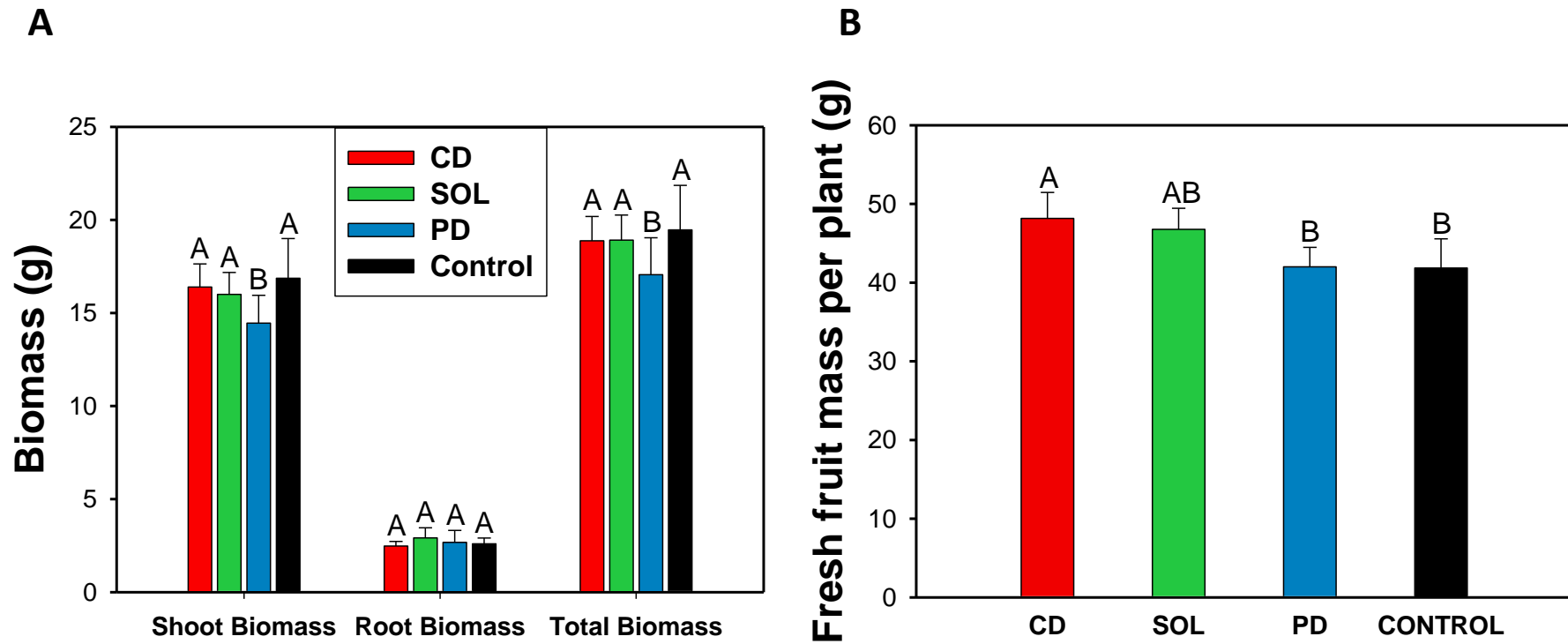
<sup>b</sup>Pairwise comparisons between disinfection techniques. Values represent the multivariate F statistic, the variability explained (R<sup>2</sup>) and the p-value assessed by PERMANOVA analysis.

Predominant prokaryotic and fungal phyla were similar in all treatments, being the most common prokaryotic phyla Proteobacteria, Firmicutes, Bacteroidetes, Chloroflexi, Actinobacteria and Gemmatimonadetes (Figure S1) and the most common fungal phyla Ascomycota, Basidiomycota, Olpidiomyota and Mortierellomycota (Figure S2). In both cases, these phyla accounted for more than 90% of the total number of reads.

***Effect of inocula treatments on photosynthesis, gas exchange and plant traits***

Inocula treatments did not have any effect on plant physiological responses. There were no differences of disinfection technique or depth in  $A_{max}$ , nor between inocula treatments and Control plants. iGEE did not differ among inocula treatments either (Table S5). Regarding plant functional traits, plants in pots watered with inocula from surface soil had the highest SLA values, whereas plants growing in substrates watered with inocula from sub-surface soils and Control pots had similar SLA values (Table S5). SLA of tomato plants were similar across soil disinfection techniques.

There were significant effects of disinfection techniques on shoot and total plant biomass (Figure 2A). Plants growing in pots inoculated with PD had the lowest shoot and total plant mass, whereas plants growing in pots inoculated with CD and SOL, as well as Control pots, had similar shoot and total plant masses (Figure 2A). There were no other effects on plant biomass (Table S5).



**Figure 2.** Shoot, root and total biomass per plant at the end of the experiment (A) and weight of fresh tomato fruit set per plant (B). Bars are mean values  $\pm 1$  SE; n=18. Different letters across bars within each plant variable measured indicate significant differences ( $p < 0.05$ ) among treatments after Fisher LSD post-hoc comparison. Legend of treatments as in Fig. 1

*Effect of inocula treatments on crop production*

There were significant effects of the different disinfection techniques on fresh crop production, i.e., total fresh mass of tomato fruits per plant (Table S6, Figure 2B). Tomato plants growing in pots inoculated with CD had a higher fresh fruit mass per plant than plants growing in pots inoculated with PD or control plants, being SOL in between (Figure 2B). There were no other differences in crop production or tomato fruit mass (Table S6).

#### **4. DISCUSSION**

We hypothesized that soil microbial communities associated to the different disinfection techniques in intensive greenhouse agriculture would differ in composition, and that the different microbial compositions would influence plant growth and tomato production, with better results in active (chemical or thermal) than in passive disinfection. We also hypothesized that solarization (thermal disinfection) could be a good alternative to chemical disinfection, not showing differences between both techniques. Results supported our hypotheses, showing that soil microbial communities differed depending on the disinfection technique used, and their inocula had an effect on plant biomass and production, with higher productivity in plants inoculated with solarized or chemically disinfected soils.

The impact of chemical disinfection on prokaryotic communities was evident in soils disinfected with 1,3-dichloropropene compared to soils with passive disinfection. Solarized soils had prokaryotic communities more variable, in



agreement with Yun et al. (2020), who showed that chemical disinfection is more selective than solarization concerning prokaryotes survival, as shown also by  $\beta$ -diversity data. PERMANOVA analyses, however, showed not only significant differences between CD and SOL soils, but also marginal differences between SOL and PD soils too, showing that prokaryotic community is influenced by disinfection technique. In fungal communities,  $\beta$ -diversity analysis did not show a clear pattern related to disinfection type, suggesting that fungal communities do not seem to be much influenced by soil disinfection technique (Neilson et al., 2020).

We found an important influence of depth in prokaryotic and fungal communities, emphasizing the importance of environmental factors (i.e., radiation, oxygen content, temperature, or humidity) on soil community composition and structure (Eilers et al., 2012) and the dissimilar impact of disinfection techniques at different depths. On the one hand, Oz et al. (2017) reported that solarization has the maximum temperature in the first five cm of soil, being 4-10°C higher than at 30 cm depth. On the other hand, 1,3-dichloropropene penetration in soil depends on soil texture and porosity, and concentration reaches a maximum between 10 and 30 cm deep (Ashworth and Yates, 2007). All these factors influence microbial composition, with clear effects on prokaryotic and fungal communities at surface and subsurface soil.

Different soil inocula, and thus microbial composition, influenced plant growth, with an important effect on crop production at the end of experiment. Differences in microbial communities affected SLA, shoot biomass and fresh fruit biomass, but not  $A_{\max}$ , instantaneous gas exchange or root biomass.  $A_{\max}$  and gas exchange vary depending on phenological stage, and at harvest, plants were in the fruiting phase, a period in which differences in photosynthetic rates are lower than in previous stages (Dobrescu et al., 2016). Depth of soil extracts influenced SLA in

chemically disinfected and solarized soils. Since SLA is negatively related to resource use efficiency (Wright et al., 2004), differences could be explained by differences in microbial communities at different depths. Microbial communities in the first 10 cm coexist with a high root density (almost 90% of roots are on the first 10 cm of soil in these greenhouses; Zapata-sierra et al. (2021), and they are interacting with plants most likely with higher resource use efficiency. There was a significant effect of microbial communities associated to different disinfection techniques on plant biomass. Plants that received PD inocula grew less than in the other treatments, highlighting the importance of disinfection in intensive greenhouse agriculture, where there are problems of pathogen accumulation (Chellemi et al., 2013; De Corato et al., 2020). Active disinfection (chemical and thermal) can amend pathogens accumulation in soils (Castello et al., 2017; Ruzo, 2006), thereby benefiting plant growth and crop production (Gill et al., 2017). In our experiment, differences in total biomass were due to differences in shoot biomass, not in root biomass, most likely due to limitations of pot size (Poorter et al., 2012). The higher growth in plants treated with CD and SOL inocula resulted in higher fresh fruit mass per plant and higher crop production. This result highlights again the importance of disinfecting soils before transplanting to ensure a production economically sustainable. Potential losses due to pathogens could represent more than 20% of crops (Oerke, 2006).

The environmental disadvantages of chemical disinfection will make it disappear in a near future. Environmental and health problems derived from its use are evident (e.g., Ajwa et al., 2010; Li and Jennings, 2017; Sande et al., 2011), and they have to be applied under strict regulations, resulting in logistic problems and higher prizes. By contrast, solarization does not have such drawbacks and costs are lower

(Lombardo et al., 2012). Our results show that solarization led to a production similar to that reached with chemical disinfectants, being much cheaper. Therefore, solarization is an alternative to chemical disinfection healthy for the environment and for humans, and cheaper. Biosolarization was not assessed in our experiment, but it is demonstrated as a good alternative too (Achmon et al., 2018). However, a yearly biosolarization could not be economically viable (Bach et al., 2016; Rowlings et al., 2019), and an alternation between solarization and biosolarization could be the best alternative for farmers.

## 5. CONCLUSIONS

Different disinfection techniques led to differences in soil microbial community composition at prokaryotic and fungal level, having an important effect on plants. Our data show that solarization equals the results of chemical disinfection with 1,3-dichloropropene, being an environmentally-friendlier alternative to chemical disinfection, avoiding human health risks and being more economically sustainable.

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## 7. APPENDIX 1

### **Analyzing the effect of soil management on plant biomass and fresh fruit mass production**

This experiment was performed using inocula from soils of diverse greenhouses subjected to different disinfection techniques (our experimental treatment). These disinfections were done in the period between two crop cultivation cycles. These greenhouses had also different histories of soil management and fertilization, from chemical fertilization to organic fertilization, with different effects on soil microbial community composition (Usero et al. 2021) prior to the disinfection. Thus, the aim of this analysis is to assess the potential effect of the different soil managements before the disinfection on experimental tomato plants growth and production, resulting in a possible interaction of the results assessed analyzing the different disinfection techniques.

The six greenhouses analyzed in the present study had the following soil management histories: (i) Two were yearly treated with a chemical fertilization during the crop cycle before disinfection (CF). (ii) Two other received chemical fertilization during the crop cycle before disinfection, and an organic matter amendment one year before the crop cultivation (CF+OM). And, finally, (iii) soils of the last two greenhouses received an organic fertilization and an organic matter amendment one year before the cultivation (OF+OM). Soils of these group of six greenhouses were treated either with chemical disinfection (n=3) or solarization (thermal disinfection; n=3, see Table 1 in main text).

We analyzed if the greenhouse soil inocula added to pots had different effects on plant biomass and fresh fruit mass per plant depending on the greenhouse soil

management and irrespective of the soil disinfection they received. These potential differences in plant responses were analyzed with linear mixed models (LMM), with greenhouse soil management (“Management”) as fixed factor, and greenhouse ID as the random factor. Depth was not taken into account for the analysis. Control plants were included in the analyses and we selected a variance function structure to model and avoid heteroscedasticity when necessary. The restricted maximum likelihood estimator (REML) was used to perform ANOVA. Post-hoc comparisons were performed using DGC test for each factor.

Our results showed that there were no differences either in plant biomass or fresh fruit mass per plant across the different management levels (Appendix 1 Table 1). Thus, in our study, greenhouse soil disinfection (either solarization or chemical disinfection) cancelled any differential effect of greenhouse soil management on plant growth.

**Appendix 1 Table 1.**

| Variable                       | Management   |              |              |              | F    | dF | p    |
|--------------------------------|--------------|--------------|--------------|--------------|------|----|------|
|                                | CF           | CF+OM        | OF+OM        | Control      |      |    |      |
| Total biomass (g)              | 18.74±1.01 A | 19.45±1.01 A | 18.50±1.01 A | 19.47±1.73 A | 0.19 | 3  | 0.89 |
| Fresh fruit mass per plant (g) | 44.79±4.10 A | 47.01±4.43 A | 37.19±4.52 A | 49.03±3.92 A | 1.41 | 3  | 0.39 |

Results represent mean values  $\pm 1$  SE. Different letters indicate significant differences ( $p < 0.05$ ) among managements after DGC post-hoc comparison. CF: Chemical fertilization; CF+OM: Chemical fertilization + Organic matter amendment one year before; OF+OM: Organic fertilization + Organic matter amendment one year before.



### **Analyzing the effect of disinfection technique on plant biomass and fresh fruit mass production for one specific management**

To reinforce the idea that the different greenhouse soil disinfections cancel any differential effect of greenhouse soil management on plant growth, we performed an additional analysis. In this case, we assessed the potential effects of inocula from different soil disinfection techniques on plant biomass and fresh fruit mass per plant, but selected only those greenhouses that received the same soil management (but different disinfection).

Thus, in this analysis we selected three greenhouses: one with a chemical disinfection (CD), one with solarization (SOL), and one with passive disinfection (PD). These greenhouses had the same management (CF: Chemical fertilization) during the last crop cycle (Table 1 in main text).

As with previous section, we performed linear models (LM), with disinfection technique as the fixed factor and plant biomass and fresh fruit mass per plant being the response variables. Depth was not taken into account for the analysis. Control plants were included in the analyses and we selected a variance function structure to avoid heteroscedasticity when necessary. The restricted maximum likelihood estimator (REML) was used to perform ANOVA. Post-hoc comparisons were performed using DGC test for each factor.

Results show that on greenhouse soil disinfection technique had a distinct effect on plant biomass, whereas the effects on fresh fruit mass per plant were more complex (Appendix 1 Table 2). Passive disinfection had a detrimental effect on plant biomass (plant biomass was less than that of control plants), whereas the other disinfection techniques had similar effects to the control treatment. Fresh fruit mass

per plant results were similar to those obtained for all greenhouses analyzed in main study (taking into account 9 greenhouses instead of these 6). Disinfection technique had influence on fresh fruit mass per plant, showing that disinfection had greater effects on plant growth than the management applied the year before. Furthermore, we had similar results for only one original soil management than for the whole experiment presented in the main text (nine greenhouses with different soil management histories).

### Appendix 1 Table 2.

| Variable                  | Disinfection technique |               |               |              | F    | dF | p     |
|---------------------------|------------------------|---------------|---------------|--------------|------|----|-------|
|                           | CD                     | SOL           | PD            | Control      |      |    |       |
| Total biomass (g)         | 17.73±1.02 A           | 19.75±1.02 A  | 15.14±0.59 B  | 19.47±1.44 A | 6.83 | 3  | <0.01 |
| Fresh fruit per plant (g) | 55.04±5.86 A           | 45.32±2.45 AB | 40.44±3.01 BC | 37.19±2.38 C | 3.71 | 3  | 0.02  |

Results represent mean values  $\pm 1$  SE. Different letters indicate significant differences ( $p < 0.05$ ) among managements after DGC post-hoc comparison. CD: Chemical disinfection; SOL: Solarization; NSD: Non-disinfected soils.

### Conclusion

In this analysis, we assessed the potential effect of different soil managements applied during the year before disinfection on tomato-plant responses in our experimental study. We show that, although the effects of different soil management on soil inocula composition were evident (Fig. 1), the disinfection applied on each soil cancelled away the potential effects of original soil management on plant growth and fresh fruit mass per plant, prevailing the influence of each disinfection technique on the soil inocula effects on plant responses. These analyses help us to simplify the statistical analysis applied in the main text.

## 8. SUPPLEMENTARY MATERIAL

**Table S1.** Types of soil disinfection techniques applied after tomato crop harvest and soil fertilization management during the crop cycle on the different greenhouse analyzed in this study. Legend of disinfection techniques, PD: Passive disinfection (one month with no cultivation or plastic cover), CD: Chemical disinfection (1,3-dichloropropene application), and SOL: Solarization.

| Greenhouse ID | Disinfection technique | Fertilization management information                            |
|---------------|------------------------|---|
| 1             | PD                     | Chemical fertilization  |
| 2             | PD                     | Chemical fertilization  |
| 3             | PD                     | Chemical fertilization  |
| 4             | CD                     | Chemical fertilization and Organic matter application last year |
| 5             | CD                     | Chemical fertilization  |
| 6             | CD                     | Chemical fertilization and Organic matter application last year |
| 7             | SOL                    | Certified organic management                                    |
| 8             | SOL                    | Certified organic management                                    |
| 9             | SOL                    | Chemical fertilization  |

**Table S2.** Pot-substrate chemical properties after inoculation of greenhouse soil inocula subjected to different disinfection techniques. Values represent mean  $\pm$ 1 SE, n=6 (three greenhouses per disinfection technique and two soil depth per greenhouse). PD: Passive disinfection (one month with no cultivation or plastic cover), CD: Chemical disinfection (1,3-dichloropropene) and SOL: Solarization. Control represents pot-substrate inoculated with sterilized deionized water.

| Variable   | CD              | SOL             | PD              | Control         |
|--|-----------------|-----------------|-----------------|-----------------|
| pH   | 6.66 $\pm$ 0.04 | 6.62 $\pm$ 0.04 | 6.64 $\pm$ 0.04 | 6.50 $\pm$ 0.09 |
| Total N (g 100g <sup>-1</sup> )                    | 0.09 $\pm$ 0.01 | 0.10 $\pm$ 0.01 | 0.08 $\pm$ 0.01 | 0.09 $\pm$ 0.01 |
| Organic C (g 100g <sup>-1</sup> )                  | 1.49 $\pm$ 0.13 | 1.47 $\pm$ 0.13 | 1.31 $\pm$ 0.13 | 1.57 $\pm$ 0.24 |
| Ca (g 100g <sup>-1</sup> )                         | 0.10 $\pm$ 0.01 | 0.10 $\pm$ 0.01 | 0.11 $\pm$ 0.01 | 0.10 $\pm$ 0.02 |
| K (g 100g <sup>-1</sup> )                          | 0.03 $\pm$ 0.01 | 0.03 $\pm$ 0.01 | 0.03 $\pm$ 0.01 | 0.01 $\pm$ 0.02 |
| P (g 100g <sup>-1</sup> )                          | 0.01 $\pm$ 0.00 | 0.01 $\pm$ 0.00 | 0.01 $\pm$ 0.00 | 0.01 $\pm$ 0.00 |
| NO <sub>3</sub> <sup>-</sup> (mg L <sup>-1</sup> ) | 1.40 $\pm$ 0.09 | 1.45 $\pm$ 0.09 | 1.43 $\pm$ 0.09 | 1.50 $\pm$ 0.19 |
| NH <sub>4</sub> <sup>+</sup> (mg L <sup>-1</sup> ) | 0.60 $\pm$ 0.02 | 0.63 $\pm$ 0.02 | 0.59 $\pm$ 0.02 | 0.57 $\pm$ 0.05 |

**Table S3.** Results from the GLM were the different substrate chemical properties were the response variables and the Soil disinfection technique, Soil depth (Depth) and their interaction were included as the fixed factors in the model. Values represent the univariate Fisher's F statistic and associated p-value.

| Variable  | Factor                         | F-value | p-value |
|---|--------------------------------|---------|---------|
| pH  | Disinfection technique         | 0.90    | 0.49    |
|   | Depth                          | 1.53    | 0.28    |
|   | Disinfection technique X Depth | 0.68    | 0.69    |
| Total N<br>(g 100 g <sup>-1</sup> )                   | Disinfection technique         | 2.74    | 0.14    |
|   | Depth                          | 0.48    | 0.64    |
|   | Disinfection technique X Depth | 2.23    | 0.27    |
| Organic C<br>(g 100 g <sup>-1</sup> )                 | Disinfection technique         | 0.49    | 0.70    |
|   | Depth                          | 2.45    | 0.16    |
|   | Disinfection technique X Depth | 1.34    | 0.44    |
| Ca<br>(g 100 g <sup>-1</sup> )                        | Disinfection technique         | 0.05    | 0.98    |
|   | Depth                          | 0.47    | 0.64    |
|   | Disinfection technique X Depth | 0.94    | 0.57    |
| K<br>(g 100 g <sup>-1</sup> )                         | Disinfection technique         | 0.44    | 0.73    |
|   | Depth                          | 3.03    | 0.11    |
|   | Disinfection technique X Depth | 1.49    | 0.40    |
| P<br>(g 100 g <sup>-1</sup> )                         | Disinfection technique         | 0.33    | 0.81    |
|   | Depth                          | 0.36    | 0.71    |
|   | Disinfection technique X Depth | 0.27    | 0.92    |
| NO <sub>3</sub> <sup>-</sup><br>(mg L <sup>-1</sup> ) | Disinfection technique         | 0.10    | 0.96    |
|   | Depth                          | 0.84    | 0.47    |
|   | Disinfection technique X Depth | 0.54    | 0.76    |
| NH <sub>4</sub> <sup>+</sup><br>(mg L <sup>-1</sup> ) | Disinfection technique         | 0.60    | 0.64    |
|   | Depth                          | 0.42    | 0.67    |
|   | Disinfection technique X Depth | 3.97    | 0.14    |

**Table S3.** Results of the statistical analysis of ASV richness and Shannon index for the different fixed factors (A; legend of fixed factors in Supp. Table 1) and Fisher LSD post-hoc comparisons across “Disinfection technique” levels (B). In A, values represent the univariate Fisher’s F statistic and corresponding p-value. In B, values represent mean  $\pm$  1 SE. Legend of disinfection techniques as in Table S2.

**A**

| <b>Prokaryote</b> |                                |         |         |
|-------------------|--------------------------------|---------|---------|
| Variable          | Factor                         | F-value | p-value |
| Shannon index     | Disinfection technique         | 0.10    | 0.90    |
|                   | Depth                          | 1.70    | 0.24    |
|                   | Disinfection technique X Depth | 0.69    | 0.54    |
| ASV Richness      | Disinfection technique         | 0.01    | 0.99    |
|                   | Depth                          | 1.66    | 0.25    |
|                   | Disinfection technique X Depth | 1.77    | 0.25    |

| <b>Fungi</b>  |                                |         |         |
|---------------|--------------------------------|---------|---------|
| Variable      | Factor                         | F-value | p-value |
| Shannon index | Disinfection technique         | 1.11    | 0.39    |
|               | Depth                          | 2.68    | 0.15    |
|               | Disinfection technique X Depth | 1.68    | 0.26    |
| ASV Richness  | Disinfection technique         | 0.26    | 0.78    |
|               | Depth                          | 3.06    | 0.13    |
|               | Disinfection technique X Depth | 0.48    | 0.64    |

**B****Post-hoc comparisons for “Disinfection technique”**

| <b>Prokaryote</b> |                        |                        |                        |
|-------------------|------------------------|------------------------|------------------------|
| Variable          | CD                     | SOL                    | PD                     |
| Shannon index     | 5.95 $\pm$ 0.24 A      | 5.82 $\pm$ 0.24 A      | 5.95 $\pm$ 0.24 A      |
| Richness          | 1384.84 $\pm$ 197.45 A | 1350.72 $\pm$ 197.45 A | 1935.86 $\pm$ 197.45 A |

| <b>Fungi</b>  |                      |                      |                     |
|---------------|----------------------|----------------------|---------------------|
| Variable      | CD                   | SOL                  | PD                  |
| Shannon index | 3.15 $\pm$ 0.43 A    | 2.87 $\pm$ 0.43 A    | 2.26 $\pm$ 0.43 A   |
| Richness      | 104.34 $\pm$ 17.96 A | 109.57 $\pm$ 17.96 A | 91.73 $\pm$ 17.96 A |

**Table S4.** Results of analyses of root:shoot ratio, maximum photosynthetic rate (Amax), instantaneous gas exchange efficiency (iGEE) and specific leaf area (SLA) of tomato plants at the end of the experiment (A). Mean  $\pm$ 1 SE values of these response variables of tomato plants growing in pot substrates that received inocula of greenhouse soils from different depths (Depth) and that received different disinfection treatments (disinfection techniques) (B). In A, values represent the univariate F statistic and the associated p-value. Values in bold represent differences among inocula treatments (in this case, greenhouse soil depth at which soil inocula was sampled). Legend of disinfection techniques as in Table S2. For depth, [0-10]: Soil collected from the first 10 cm of soil profile, and [10-20]: Soil collected from 10 to 20 cm of soil depth.

**A**

| Variable  | Factor                         | F-value | p-value       |
|---|--------------------------------|---------|---------------|
| Root:shoot ratio  | Disinfection technique         | 0.73    | 0.57          |
|   | Depth                          | 0.50    | 0.48          |
|   | Disinfection technique X Depth | 2.19    | 0.11          |
| Amax<br>( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ )        | Disinfection technique         | 0.84    | 0.4759        |
|   | Depth                          | 0.01    | 0.9597        |
|   | Disinfection technique X Depth | 0.09    | 0.9135        |
| iGEE<br>( $\mu\text{mol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$ ) | Disinfection technique         | 2.63    | 0.1511        |
|   | Depth                          | 0.24    | 0.6247        |
|   | Disinfection technique X Depth | 0.35    | 0.7034        |
| SLA<br>( $\text{m}^2 \text{ kg}^{-1}$ )                               | Disinfection technique         | 4.17    | 0.0733        |
|   | Depth                          | 11.02   | <b>0.0019</b> |
|   | Disinfection technique X Depth | 2.43    | 0.1006        |

**B**

| Variable   | Disinfection technique |                    |                    |                    | Depth              |                    |
|--|------------------------|--------------------|--------------------|--------------------|--------------------|--------------------|
|  | CD                     | SOL                | PD                 | Control            | [0-10]             | [10-20]            |
| Root:shoot ratio   | 0.15 $\pm$ 0.02        | 0.19 $\pm$ 0.02    | 0.18 $\pm$ 0.02    | 0.16 $\pm$ 0.04    | 0.17 $\pm$ 0.01    | 0.18 $\pm$ 0.01    |
| Amax ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ )        | 2.51 $\pm$ 0.58        | 2.36 $\pm$ 0.27    | 2.07 $\pm$ 0.58    | 2.17 $\pm$ 0.33    | 2.32 $\pm$ 0.16    | 2.31 $\pm$ 0.17    |
| iGEE ( $\mu\text{mol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$ ) | 286.78 $\pm$ 90.00     | 325.14 $\pm$ 99.43 | 234.01 $\pm$ 76.31 | 184.89 $\pm$ 85.64 | 291.81 $\pm$ 31.92 | 312.14 $\pm$ 31.70 |
| SLA ( $\text{m}^2 \text{ kg}^{-1}$ )                               | 5.36 $\pm$ 0.17        | 5.81 $\pm$ 0.31    | 5.38 $\pm$ 0.11    | 4.90 $\pm$ 0.39    | 5.94 $\pm$ 0.20    | 5.09 $\pm$ 0.10    |

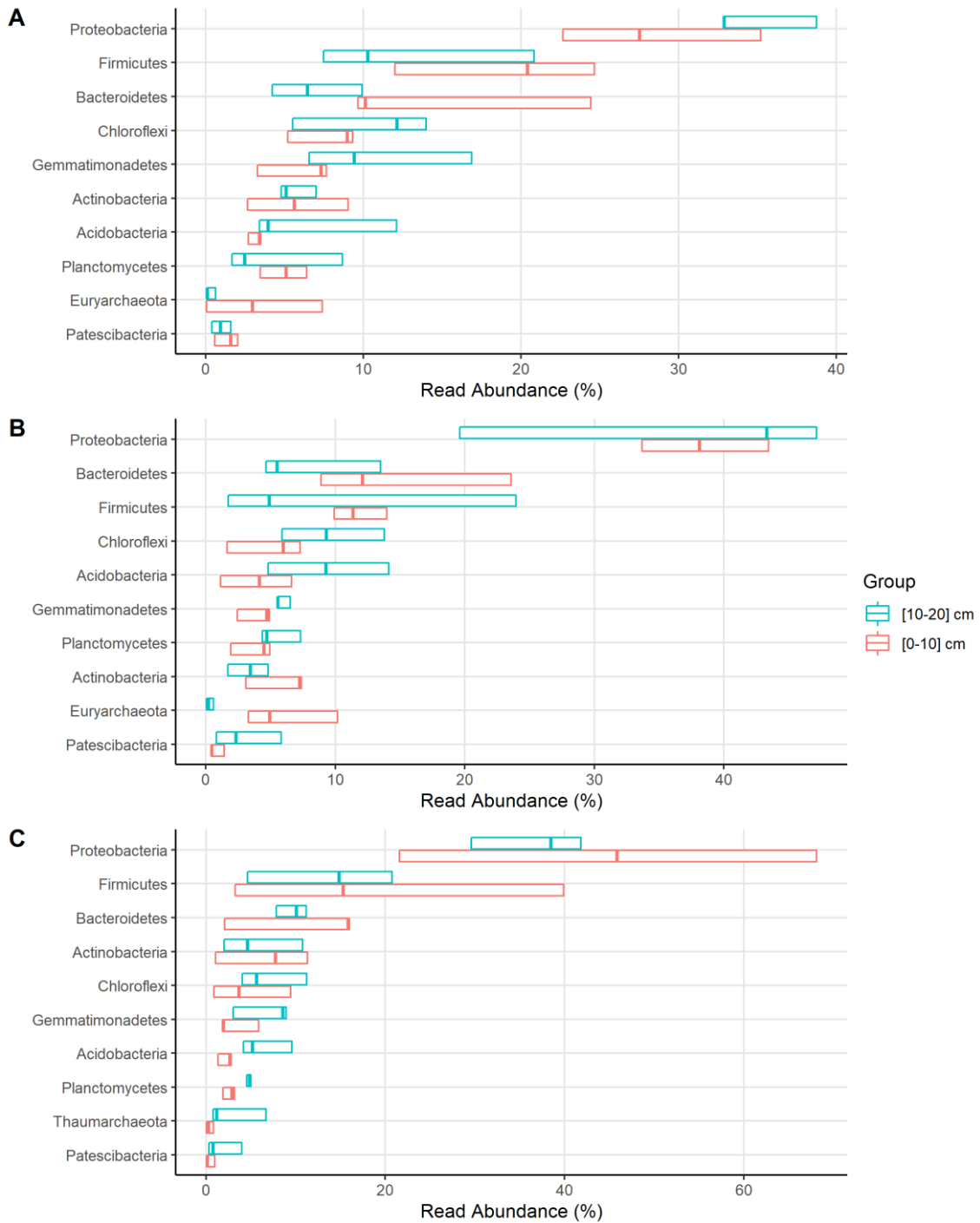
**Table S5.** Results of analyses of number of fruits, fresh fruit mass per plant, dry fruit mass per plant, fresh mass per fruit and dry mass per fruit at the end of the experiment (A), and values of the different disinfection techniques for the different variables (B). Fresh fruit mass per plant is not included in Table B as it is graphed in Figure 2 in the main manuscript. In A, values represent the univariate F statistic and associated p-value. In B, values represent mean  $\pm$ 1 SE. Legend of disinfection techniques as in Table S1.

**A**

| Variable                           | Factor                         | F-value | p-value |
|------------------------------------|--------------------------------|---------|---------|
| Number of fruits                   | Disinfection technique         | 1.76    | 0.2547  |
|                                    | Depth                          | 0.16    | 0.6864  |
|                                    | Disinfection technique X Depth | 0.17    | 0.8480  |
| Fresh fruit mass per plant (g)     | Disinfection technique         | 7.00    | 0.0270  |
|                                    | Depth                          | 1.99    | 0.1615  |
|                                    | Disinfection technique X Depth | 0.17    | 0.8453  |
| Dry fruit mass per plant (g)       | Disinfection technique         | 1.69    | 0.1786  |
|                                    | Depth                          | 0.87    | 0.3539  |
|                                    | Disinfection technique X Depth | 1.59    | 0.2098  |
| Fresh mass fruit <sup>-1</sup> (g) | Disinfection technique         | 0.95    | 0.4365  |
|                                    | Depth                          | 0.19    | 0.6653  |
|                                    | Disinfection technique X Depth | 0.45    | 0.6372  |
| Dry mass fruit <sup>-1</sup> (g)   | Disinfection technique         | 0.79    | 0.4545  |
|                                    | Depth                          | 0.28    | 0.5998  |
|                                    | Disinfection technique X Depth | 2.18    | 0.1178  |

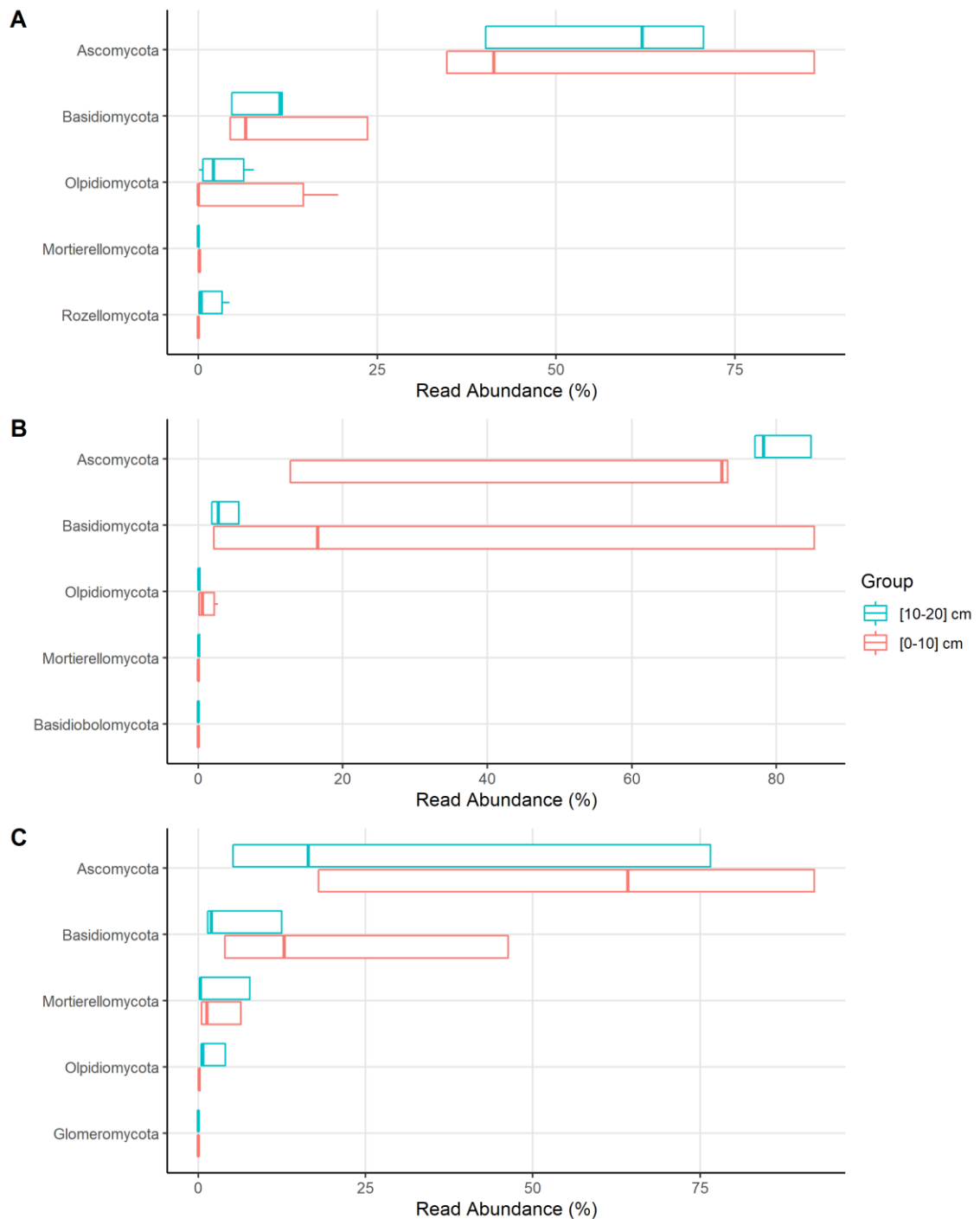
**B**

| Variable                           | CD              | SOL             | PD              | Control         |
|------------------------------------|-----------------|-----------------|-----------------|-----------------|
| Number of fruits                   | 6.33 $\pm$ 0.53 | 6.17 $\pm$ 0.53 | 5.00 $\pm$ 0.50 | 7.00 $\pm$ 1.03 |
| Dry fruit mass per plant (g)       | 4.65 $\pm$ 0.33 | 4.31 $\pm$ 0.25 | 3.99 $\pm$ 0.25 | 4.17 $\pm$ 1.02 |
| Fresh mass fruit <sup>-1</sup> (g) | 8.45 $\pm$ 0.81 | 8.38 $\pm$ 0.88 | 9.15 $\pm$ 0.81 | 8.42 $\pm$ 1.91 |
| Dry mass fruit <sup>-1</sup> (g)   | 0.78 $\pm$ 0.06 | 0.78 $\pm$ 0.06 | 0.79 $\pm$ 0.06 | 0.67 $\pm$ 0.15 |



**Figure S1.** Relative abundance of the ten most frequent prokaryotic phyla of the pot-substrates inoculated with greenhouse soil inocula that received different disinfection techniques: PD (A), CD (B) and SOL (C). Values distribution of relative abundances are shown with box-plots that include the median (line within the box); and quantiles Q1 and Q3 (limits of the box). Legend of disinfection techniques as in Table S1. Legends of depth as in Table S4.





**Figure S2.** Relative abundance of the five most frequent fungal phyla of the pot-substrates inoculated with greenhouse soil inocula that received different disinfection techniques: PD (A), CD (B) and SOL (C). Values distribution of relative abundances are shown with box-plots that include the median (line within the box); and quantiles Q1 and Q3 (limits of the box). Legend of disinfection techniques as in Table S1. Legends of depth as in Table S4.



# CAPÍTULO V

## Discusión general





## DISCUSIÓN GENERAL

El objetivo de esta tesis es evaluar el efecto que tiene el aporte de materia orgánica y la desinfección del suelo de invernaderos de Almería sobre sus comunidades microbianas y el de éstas sobre el cultivo. Conocer estos efectos es esencial para la sostenibilidad del sistema agronómico intensivo, indispensable en un mundo globalizado con una población en crecimiento y cada vez más demandante de alimentos.

El aporte de materia orgánica incrementó la respiración del suelo durante todo el ciclo productivo (Capítulo II), que se ha mostrado como un indicador fiable de la actividad de los microorganismos (Curiel-Yuste et al., 2007) y de la calidad del suelo (Bünemann et al., 2018). En nuestro caso, se ha visto una correlación positiva entre la respiración del suelo y la producción de tomate, mostrando que la respiración puede ser usada como indicador indirecto de la producción (Lamprey et al., 2019; Mbuthia et al., 2015). A este respecto cabe destacar el efecto del aporte de materia orgánica sobre las características nutricionales del suelo, que se tradujo en niveles superiores de nitrógeno total, así como de nitratos y amonio, elementos esenciales para el crecimiento de la planta (Trandel et al., 2018). Esto puede contribuir a que se disminuya el aporte externo como fertilizante químico (Luan et al., 2019), lo cual se traduciría en un ahorro para el agricultor (Mohamad et al., 2018), además de una importante mejora medioambiental. Si bien no hubo diferencias entre tratamientos en cuanto a diversidad de las comunidades microbianas dentro de los invernaderos ( $\alpha$ ), sí se obtuvieron diferencias en diversidad entre tratamientos ( $\beta$ ) debido a los distintos aportes de materia orgánica. Esto muestra las diferencias que surgen entre comunidades con manejos diferentes de materia orgánica, pudiendo conllevar

diferencias funcionales que afecten a las interacciones de los microorganismos con las plantas (Banerjee et al., 2019) así como al crecimiento y producción del cultivo. Es interesante notar que, aunque no se observaron plantas enfermas, en los suelos sin aporte de materia orgánica había una mayor cantidad de organismos potencialmente patógenos que podrían afectar al crecimiento de las plantas. El manejo ecológico, por su parte, mostró una mayor dispersión en los resultados obtenidos para la diversidad  $\alpha$  y  $\beta$ , mostrando cómo la composición de la comunidad microbiana es más variable en el manejo ecológico que en el convencional. Esto se debe, probablemente, a los diferentes productos orgánicos certificados que hay en el mercado, y que tienen un efecto muy diverso sobre la comunidad microbiana del suelo (Malusa et al., 2012; Zhang et al., 2015).

Si bien los resultados anteriores mostraron el claro efecto de la materia orgánica sobre la comunidad microbiana del suelo y sobre la producción, era primordial comprender los efectos de la propia comunidad microbiana sobre la asimilación de nutrientes, capacidad fotosintética y crecimiento vegetativo del cultivo. Por ello, en el Capítulo III se buscó minimizar la heterogeneidad ambiental y del suelo para evidenciar el efecto de las comunidades microbianas sobre la planta. En este experimento, las plantas de tomate crecieron en un sustrato homogéneo en macetas a las que se inocularon comunidades microbianas de suelos de invernadero bajo distintos manejos de materia orgánica. Los resultados obtenidos mostraron que las comunidades microbianas asociadas al cultivo ecológico, aunque muy diferentes entre sí, tuvieron un efecto muy positivo sobre las plantas de tomate, incrementando la fotosíntesis y el crecimiento vegetativo y radicular, confirmando los resultados mostrados en el meta-análisis de Lori et al. (2017). Además, cuando comparamos las plantas crecidas con comunidades microbianas de invernaderos convencionales con

plantas control, observamos que el no aportar materia orgánica produjo un efecto depresor de las comunidades microbianas y una acumulación de microorganismos patógenos. Los patógenos disparan en la planta los sistemas de defensa (Ghabooli et al., 2013; Wang et al., 2019), que afectan también a los microorganismos beneficiosos mediante la exudación de metabolitos (Hu et al., 2018), lo que disminuye a su vez el crecimiento de la planta.

El otro manejo agronómico que se analiza en esta tesis es la desinfección del suelo (Capítulo IV). En este caso, a diferencia del aporte de materia orgánica, tenemos un efecto mucho más drástico, inmediato y concentrado en el tiempo. Así, en el Anexo 1 del Capítulo IV se observa como el efecto que se obtenía con el aporte de la materia orgánica en el suelo queda minimizado con esta desinfección, mostrando que ésta provoca una disminución indiscriminada de microorganismos, ya sean patógenos o beneficiosos, obteniendo una comunidad diferente a la que teníamos antes de la desinfección. Además, las comunidades microbianas difirieron en composición y estructura según la técnica de desinfección usada, observándose que la desinfección química fue la más selectiva y la solarización la más variable en cuanto a sus efectos sobre la comunidad microbiana (Yun et al., 2020). Sin embargo, los efectos sobre las plantas provocados por la inoculación de las comunidades microbianas asociadas a las diferentes desinfecciones muestran que no hay diferencias en crecimiento y producción entre la desinfección química y la solarización, evidenciando que la solarización es una buena alternativa a la desinfección química, evitando múltiples problemas medioambientales y sobre la salud humana (Ajwa et al., 2010; Li and Jennings, 2017; Sande et al., 2011). La solarización por su parte, además de ser menos perjudicial para el medio ambiente, tiene un costo menor (Lombardo et al., 2012), por lo que ayuda a la sostenibilidad

económica del sector. La desinfección pasiva (sin uso plástico ni aplicación de desinfectante químico), sin embargo, tuvo consecuencias negativas para el crecimiento y producción de las plantas, sugiriendo que una desinfección activa de los suelos de invernaderos es necesaria, ya sea térmica o química, para el mantenimiento del sistema productivo, probablemente debido a que el monocultivo y la intensificación conllevan un incremento de patógenos (Chellemi et al., 2013; De Corato et al., 2020), como hemos visto en anteriores capítulos. Esto puede conllevar pérdidas productivas de más del 20% en suelos sin desinfectar comparado con los suelos desinfectados (Oerke, 2006).

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# CAPÍTULO VI

## Conclusiones





## CONCLUSIONES

Las principales conclusiones de la presente tesis, en el contexto de invernaderos de Almería son las siguientes:

1. El manejo de la materia orgánica tiene un efecto directo e importante sobre las comunidades microbianas del suelo, afectando a su composición, estructura y actividad.
2. Las comunidades microbianas asociadas a la aplicación de materia orgánica en el suelo tienen un efecto positivo sobre el crecimiento de la planta, así como sobre su producción.
3. Las comunidades microbianas asociadas al manejo ecológico del suelo tienen un efecto sobre el crecimiento de la planta, mostrando una mayor fotosíntesis y un mayor crecimiento en comparación con las plantas que crecieron bajo el efecto de las comunidades microbianas asociadas a suelos sin aplicación de materia orgánica.
4. Las comunidades microbianas asociadas al manejo del suelo sin aplicación de materia orgánica tuvieron un efecto negativo sobre el crecimiento de las plantas, mostrando además una mayor concentración de organismos patógenos.

5. Las diferentes técnicas de desinfección del suelo tienen efectos distintos sobre las comunidades microbianas del suelo, conllevando diferencias en composición y en la estructura de la comunidad.
  
6. Las comunidades microbianas asociadas a la desinfección térmica (solarización) y química (1,3-dicloropropeno) del suelo tienen un efecto positivo sobre el crecimiento y la producción de la planta en comparación con las comunidades microbianas asociadas a una desinfección pasiva.
  
7. No se encontraron diferencias entre la desinfección térmica (solarización) y química (1,3-dicloropropeno) a nivel de crecimiento o producción de planta, por lo que se concluye que la solarización es la práctica más sostenible, tanto medioambientalmente como económicamente.



