



The living soil: a bit of what happens in this environment. An emphasis on phytopathogens

El suelo vivo: un poco de lo que ocurre en este entorno. Un énfasis en los fitopatógenos

 Ana Luisa Olivas-Tarango¹,  Hilda Karina Sáenz-Hidalgo^{1,2},  Aarón Alejandro Porras-Chavira¹,
 Teresita de Jesus Ruiz-Anchondo¹,  Gerardo Leyva-Mir³,
 Socorro Héctor Tarango-Rivero⁴,  Graciela Dolores Avila-Quezada^{1*}

¹Universidad Autónoma de Chihuahua, calle Escorza 900, CP 31000, Chihuahua, Chihuahua, México.

²Centro de Investigación en Alimentación y Desarrollo AC., av. 4 sur 3820, CP 33084, Delicias, Chihuahua, México.

³Universidad Autónoma Chapingo, km 38.5 carr. Mexico-Texcoco, CP 56230, Chapingo, Edo. de Mexico, México.

⁴Comité de la Nuez del Estado de Chihuahua, calle Trasviña y Retes 3505, San Felipe II Etapa, CP 31203, Chihuahua, Chihuahua, México.

ABSTRACT: Soil is an ecosystem with a carbon pool that supports biological diversity. In this review, we present how significant is the symbiosis between the plant root and the macro and microorganisms of the soil, as well as the benefits it generates to achieve an ecological balance and maintain low populations of plant pathogens in food production. For instance, earthworms, collembola, mealybugs and oribatid mites greatly influence the functioning of the soil system, as they build and maintain soil structure and actively participate in nutrient cycling through mineralization and humification processes, in addition to consuming pathogens. On the other hand, microorganisms such as mycorrhizal fungi, which benefit by absorbing the nutrients of the plant and help it absorb minerals from the soil, provide protection to the roots against phytopathogens. Mycorrhizal fungi induce changes in the plant and then the plant responds by producing exudates from the roots that reduce or repel plant pathogens. Another example is the *Trichoderma* fungus, known as a biocontrol agent for producing secondary metabolites with antimicrobial activity against plant pathogens. Biological control agents and their secondary metabolites are potential approaches currently being used to reduce or replace agrochemicals. Finally, integrated crop management promotes competition and balance essential to maintaining soil health and ensuring food production.

Key words: earthworms, fungi, symbiosis, *Trichoderma*.

RESUMEN: El suelo es un ecosistema con una reserva de carbono que sustenta la diversidad biológica. En esta revisión, presentamos cuán significativa es la simbiosis entre la raíz de la planta y los macro y microorganismos del suelo, así como los beneficios que genera para lograr un equilibrio ecológico y mantener bajas poblaciones de fitopatógenos en la producción de alimentos. Por ejemplo, las lombrices de tierra, colémbolos, cochinillas y ácaros oribátidos influyen, en gran medida, en el funcionamiento del sistema del suelo, ya que construyen y mantienen la estructura del suelo y participan activamente en el ciclo de nutrientes, a través de procesos de mineralización y humificación, además de consumir fitopatógenos. Por otro lado, microorganismos como los hongos micorrízicos, que se benefician al absorber los nutrientes de la planta, la ayudan a absorber los minerales del suelo y brindan protección a las raíces frente a los fitopatógenos. Los hongos micorrízicos inducen cambios en la planta y luego la planta responde produciendo exudados de las raíces que reducen o repelen a los patógenos. Otro ejemplo es el hongo *Trichoderma*, conocido como agente de biocontrol para la producción de metabolitos secundarios con actividad antimicrobiana contra fitopatógenos. Los agentes de control biológico y sus metabolitos secundarios son enfoques potenciales que se utilizan actualmente para reducir o reemplazar los agroquímicos. Finalmente, el manejo integrado de cultivos promueve la competencia y el equilibrio esenciales para mantener la salud del suelo y asegurar la producción de alimentos.

Palabras clave: anélidos, hongos, simbiosis, *Trichoderma*.

*Author for correspondence: gdavila@uach.mx; gavilaq@gmail.com

Received: 26/07/2022

Accepted: 21/11/2022

Conflict of interest: The authors declare that they have no conflict of interest.

Author contributions: **Conceptualization-** Graciela Dolores Avila-Quezada, Socorro Héctor Tarango-Rivero, Gerardo Leyva-Mir. **Research-** Graciela Dolores Avila-Quezada, Gerardo Leyva-Mir, Teresita de Jesus Ruiz-Anchondo. **Methodology-** Ana Luisa Olivas-Tarango, Hilda Karina Saenz-Hidalgo, Aaron Alejandro Porras-Chavira. **Supervision-** Graciela Dolores Avila-Quezada, Socorro Héctor Tarango-Rivero. **Initial draft writing, final writing and editing, and data curation-** Teresita de Jesus Ruiz-Anchondo, Graciela Dolores Avila-Quezada, Socorro Héctor Tarango-Rivero, Gerardo Leyva-Mir.

This is an open access article distributed under the terms of the Creative Commons Attribution-NonCommercial (BY-NC 4.0).

<https://creativecommons.org/licenses/by-nc/4.0/>



INTRODUCTION

Feeding the world's population is a priority issue, therefore the 2030 Agenda for Sustainable Development of the United Nations includes within its 17 Sustainable Development Goals, the goal *zero hunger* (1).

Achieving this is challenging, as plants are exposed to many soil conditions that could affect growth and production. For instance, pests and diseases are one of the biggest challenges crop growers face every year. In addition, emerging diseases constitute one of the greatest risks due to the devastation they cause in agricultural production (2-5).

It is known that the excessive application of agrochemicals have an immediate effect on what is desired to achieve during agricultural production (6); however, this is achieved with environmental consequences and damage to the health of agricultural workers and consumers. Sustainable technologies must be used to produce the food demanded by the population without affecting natural resources.

The soil, because it shelters a great biodiversity, is considered the basis for the production of healthy foods. Microbial diversity has several roles, one of which is the solubility of minerals to make them more available to plants. For example, phosphate solubilizing bacteria contribute up to 50 % of the element solubilization (7). Some organisms such as mycorrhizal fungi carry the elements to roots through their hyphae (8), even endomycorrhizae deposit them in the interarbuscular space (inside the plant).

This microbial activity promotes fertile soil and a balance of organisms and microorganisms. For instance, the earthworm improves the soil structure while reducing the populations of phytopathogens (Figure 1). Also the fungus *Trichoderma* has a broad spectrum of action that allows it to reduce a large number of plant pathogens.

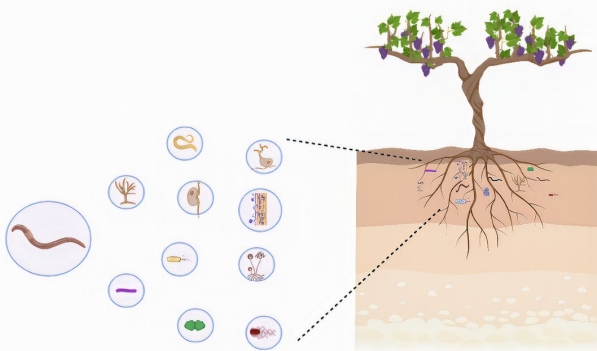


Figure 1. Earthworms and other microorganisms, members of the soil ecosystem in equilibrium, each with a specific task

DEVELOPMENT

Soil organisms

Earthworms, by its ability to dig galleries and produce demographic profiles and relationships with the soil

microflora, are a key component in the nutrient cycling in soils. Their physical activities and resultant chemical effects, promote short and rapid cycles of nutrients and assimilable carbohydrates (9).

Moreover, in agriculture the addition of vermicompost is a common practice. Vermicompost has an essential role to promote life in the soil by improving the texture and promoting satisfactory levels of macro and micronutrients (10). It contains many compounds rich in beneficial microorganisms and growth hormones that function as biofertilizing and biological control agent against plant pests and pathogens (11). In addition, during vermicomposting, the Californian Red worm (*Eisenia foetida*) ingests organic matter, which progressively decomposes and fragments. This matter is made up of microorganisms including a large number of fungi. The mucous substances yielded by earthworms have strong antimicrobial and antifungal activity (12). Through their skin secretions and antimicrobial protein, they control microorganisms (13), thus reducing the populations of soil plant pathogens.

The surface of the earthworm's skin contains antimicrobial peptides that protect it from the environment. It discharges peptides such as lysozyme through its skin, resulting in antimicrobial activity. In addition, the body wall and intestinal secretion have been shown to reduce *Fusarium oxysporum* (12).

Earthworms feed on soils that contain organic materials, live microorganisms, and insects. Once the food is ingested, it is modified in the earthworm body to facilitate its absorption. When entering through the mouth, the material is swallowed by the pharynx which is a force pump (Figure 2). After that, the muscles contract and move the food up the esophagus. Then, it goes to the crop (which contracts more than the gizzard) where it is stored and moves towards the gizzard. This is a strong muscle that grinds the material into very small parts, where the enzyme secretion take part in breaking down the products. The finely crushed material goes through the digestion process in the intestine. Here more enzymes are added to promote the breakdown into simple molecules (14). Enzymes include protease, lipase, amylase, lichenase, cellulase and chitinase (15). All this process achieves partially the elimination of plant pathogens.

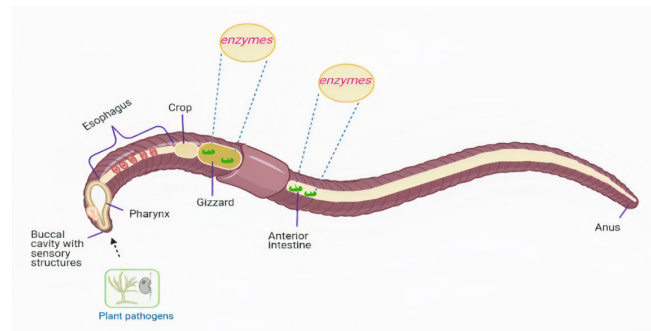


Figure 2. Earthworm's body organs, where the decomposing of ingested organic matter occurs, due to enzymatic activity

Earthworms as *Eisenia foetida* is reported to control nematodes as *Pratylenchus* sp in tomato (16), *Meloidogyne javanica* in cucumber (17), and *Meloidogyne hapla* in tomato (18).

Other researchers found that the earthworm *Lumbricus terrestris* fed on sclerotia of *Sclerotinia sclerotiorum* when they were hydrated (19). *L. terrestris* consumed an average of 61 % of sclerotia that were hydrated for 13 weeks. Besides, worm humus and arbuscular mycorrhizal fungi improve the quality of fruits (20).

Soil microorganisms, interactions and microenvironments

The biological structure of the soil is made up of a large number of bacteria, actinomycetes and fungi (21). All of them are associated with organic matter and polymeric microbial materials such as enzymes and extracellular polysaccharides that they themselves produce.

Microorganisms are found in dense tissues of clay or humified organic matter, in mucigel deposits, in micropores, or in carbohydrate-rich root plants. At these sites, microorganisms temporarily survive adverse conditions.

In this review we address two types of microorganisms that benefit plants and that are generally found naturally in soils in symbiosis with plants, and that can be used to enrich soils, such as mycorrhizal fungi and *Trichoderma* spp.

Once the micro and macroelements are solubilized by bacteria, they are transferred through the hypha of the mycorrhizal fungus to the previously mycorrhizal root. Phosphate transporter enzymes of the fungus and the plant are involved in this process (8).

The protection against plant pathogens that mycorrhizal fungi confer on plants has been demonstrated (22, 23). In the rhizosphere, microorganisms compete for space and nutrients. In addition, mycorrhizae also stimulate the biochemical defense mechanisms of plants (22).

The interactions between mycorrhizae and plants are self-regulating, in fact, when mineral nutrients are available in the soil, the colonization of mycorrhizae is reduced (24). Apparently, all microbial populations in the soil are self-regulating, even the plant regulates microorganisms in its rhizosphere. Thus, by adding microorganisms to the soil, they can be active for months or a year and disappear after that time. Some authors found that by incorporating the ectomycorrhizal fungus *Pisolithus tinctorius*, it protected *Pinus sylvestris* seedlings from the attack of *Fusarium moniliforme* and *Rhizoctonia solani*; this protection lasted one year (25).

It is very interesting to know the symbiosis in depth. The interaction begins through signals, and depending on the requirements of the plant and other as yet unknown factors, soil microorganisms regulate themselves.

Endomycorrhizal fungi are also root protectors against pathogens. For instance, a mixture of Arbuscular mycorrhizal fungi (AMF) composed by *Glomus aggregatum*, *Gigaspora margarita* and *Glomus intraradices* suppressed

root rot by *Fusarium solani* in *Phaseolus vulgaris* under greenhouse conditions (26).

Even endomycorrhizal fungi can control nematodes such as *Meloidogyne incognita* (27) and *Meloidogyne javanica* (28).

The reduction in the penetration of *M. incognita* in endomycorrhized plants may be due to the fact that AMF induce changes in the plant, and in response, the roots produce exudates, which suggests that exudates affect the motility of nematodes in the soil.

Other possibilities are the production of nematicidal compounds, increased lignification of the roots, changes in the composition of the cell wall and activation of the defense mechanisms of plants.

The accumulation of phenolic compounds, such as phytoalexins and flavonoids and isoflavonoids has been demonstrated in mycorrhizal roots in the presence of the nematode. AMF can also increase the activity of defense enzymes such as peroxidase, polyphenoloxidase, superoxide dismutase, chitinase and β 1,3 glucanase (27). In general, AMF naturally present in soil may be highly beneficial to sustainable agriculture, maintaining plant production by reducing pathogens.

Moreover, *Trichoderma* is a beneficial fungus that has demonstrated efficiency in the control of root pathogens (29) including nematodes (30), due to its ability to secrete volatile and non-volatile compounds, and secondary metabolites. Its direct mechanism includes competition, mycoparasitism, antibiosis, and induction of plant resistance mechanisms, as well as indirect mechanisms such as the inactivation of the enzymes produced by the pathogen (31, 33).

Among secondary metabolites are terpenes, pyrones, gliotoxin, gliovirin, and peptaibols (34). Antifungal metabolites produced by *Trichoderma* are epipolythiodioxopiperazines, peptaibols, pyrones, butenolides, pyridones, azaphilones, koniginins, steroids, anthraquinones, lactones, trichothecenes, and other (35, 36).

The expression of genes related to secondary metabolites in *Trichoderma* spp. depends on factors such as pH signaling, velvet complex proteins and communication signals with other microorganisms (37).

These metabolites exhibit bioactivity against plant pathogens as *Macrophomina phaseolina*, *Pythium* spp., *Sclerotium rolfsii*, *Rhizoctonia solani*, *Fusarium oxysporum*, *Verticillium dahliae*, *Botrytis cinerea*, *Ascochyta citrullina*, *Phytophthora parasitica*, *P. cinnamomi*, *Leptosphaeria maculans*, *Clavibacter* spp., *Gaeumannomyces graminis*, *Colletotrichum gloeosporioides*, among others (34, 35, 38-40).

Plants, microorganisms and carbon

Plants take carbon dioxide from the atmosphere and exude some carbon as a sugary substance through their roots. This secretion feeds the microorganisms in the soil. When plants die, microorganisms break down carbon and

use it for metabolism. This microbial decomposition releases carbon dioxide, therefore the soil stores more carbon when it is full of microbial life (41, 42).

Mycorrhizal fungi produce mucilaginous substances (8) such as glomalin. This is a very stable recalcitrant glycoprotein, with a half-life of up to 42 years, and constitutes the largest component of soil organic matter (43), it also promotes soil aggregation. Mycorrhizal fungi transfer more carbon to the soil than other microorganisms (44) (Figure 3).

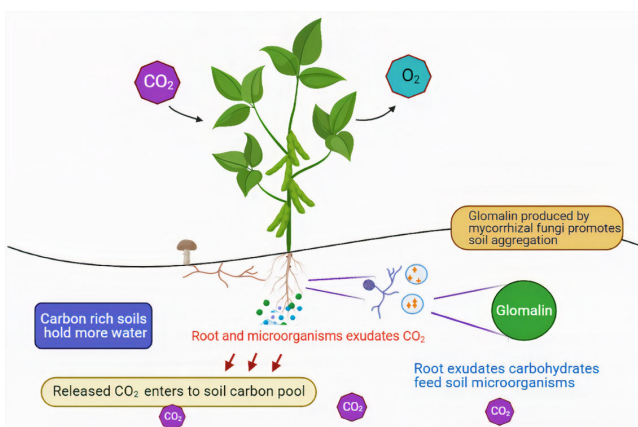


Figure 3. Carbon dioxide (CO₂) scheme from entering the tree canopy to its filtration into the soil, and the activity of microorganisms

Some of the carbon remains in the soil from days to a few years. Microorganisms can digest this carbon, thus emitting carbon dioxide. Thus is how carbon can remain for years or decades in a site (45). An important agricultural activity is the application of compost to the soil. Compost harbors microorganisms and can retain carbon for centuries.

Minimum tillage causes that the soil carbon is not exposed to oxygen and the soil aggregates remain intact, protecting their carbon (45-47).

Soil carbon sequestration is a natural way to remove carbon dioxide from the atmosphere, and this can be achieved with sustainable agricultural practices. These practices will improve the ability of soils to store carbon and help minimize the effects of global warming.

CONCLUSIONS

- This review presents how plants drawn CO₂ from the air, synthesize carbohydrates, which exude from roots, to feed, attract or repel microorganisms. Additionally, the important activity of soil organisms and microorganisms for the plant benefit is highlighted, focusing on earthworms, mycorrhizal fungi and *Trichoderma* since they can reduce plant pathogens populations. All of them within their specialty, achieve by competition for space, or with physical and chemical mechanisms, reduce soil plant pathogens.
- Earthworms, mycorrhizal fungi and *Trichoderma*, naturally present in soil may be highly beneficial to

sustainable agriculture, maintaining plant production and biological balance in soils. We conclude that integrated crop management promotes competition and balance, essential to maintaining soil health and ensuring food production. Finally, knowledge of the diversity of edaphic biota in agroecosystems allows the implementation of strategies for land use.

ACKNOWLEDGE

The authors thank the Postgraduate programs of National Council of Science and Technology (Conacyt), of the Faculty of Agrotechnological Sciences of the Autonomous University of Chihuahua, Mexico.

BIBLIOGRAPHY

1. ONU. Objetivos del Desarrollo Sostenible de la Agenda 2030 ONU. 2021 [citado 20/07/2021]. Disponible en: <https://www.un.org/sustainabledevelopment/>
2. Avila-Quezada G, Silva-Rojas HV, Sánchez-Chávez E, Leyva-Mir G, Martínez-Bolaños L, Guerrero-Prieto V, et al. Seguridad alimentaria: la continua lucha contra las enfermedades de los cultivos. *Tecnociencia Chihuahua*. 2016;10(3):133-142.
3. Cintora-Martínez EA, Leyva-Mir SG, Ayala-Escobar V, Avila-Quezada G, Camacho-Tapia M, Tovar-Pedraza JM. Pomegranate fruit rot caused by *Pilidiella granati* in Mexico. *Australasian Plant Disease Notes*. 2017;12(1):4.
4. García-González T, Sáenz-Hidalgo HK, Silva-Rojas HV, Morales-Nieto C, Vancheva T, Koebnik R, et al. *Enterobacter cloacae*, an emerging plant-pathogenic bacterium affecting chili pepper seedlings. *The Plant Pathology Journal*. 2018;34(1):1-10.
5. Avila-Quezada GD, Esquivel JF, Silva-Rojas HV, Leyva-Mir G, García-Avila C, Noriega-Orozco L, et al. Emerging plant diseases under a changing climate scenario: Threats to our global food supply. *Emirates Journal of Food and Agriculture*. 2018;30(6):443-450.
6. Sánchez-Chávez E, Silva-Rojas HV, Leyva-Mir G, Villareal-Guerrero F, Jiménez-Castro J, Molina-Gayoso E, et al. An effective strategy to reduce the incidence of *Phytophthora* root and crown rot in bell pepper. *Interciencia*. 2017;42(4):229-235.
7. Galvez ZYA, Burbano VEM. Solubilización de fosfatos: una función microbiana importante en el desarrollo vegetal. *NOVA Publicación en Ciencias Biomédicas*. 2015;12(21):67-79.
8. Madrid-Delgado G, Orozco-Miranda M, Cruz-Osorio M, Hernández-Rodríguez A, Rodríguez-Heredia R, Roa-Huerta M, et al. Pathways of phosphorus absorption and early signaling between the mycorrhizal fungi and plants. *Phyton International Journal of Experimental Botany*. 2021;90(5):1321-1338.
9. Le Bayon RC, Bullinger-Weber G, Schomburg A, Turberg P, Schlaepfer R, Guenat C. (2017). Earthworms as ecosystem engineers: A review. *Earthworms: Types, Roles and Research*. NOVA Science Publishers, New York, 129-178.

10. Sánchez-Rosales R, Hernández-Rodríguez A, Ojeda-Barrios D, Robles-Hernández L, González-Franco A, Parra-Quezada R. Comparison of three systems of decomposition of agricultural residues for the production of organic fertilizers. *Chilean Journal of Agricultural Research*. 2017;77(3):287-292.
11. Sulaiman ISC, Mohamad A. The use of vermiwash and vermicompost extract in plant disease and pest control. In: *Natural Remedies for Pest, Disease and Weed Control*. Academic Press; 2020. p. 187-201.
12. Andleeb S, Ejaz M, Awan UA, Ali S, Kiyani A, Shafique I, et al. In vitro screening of mucus and solvent extracts of *Eisenia foetida* against human bacterial and fungal pathogens. *Pakistan Journal of Pharmaceutical Sciences*. 2016;29(3):969-977.
13. Prakash M, Gunasekaran G. Antibacterial activity of the indigenous earthworms *Lampito mauritii* (Kinberg) and *Perionyx excavatus* (Perrier). *The Journal of Alternative and Complementary Medicine*. 2011;17:167-170.
14. Jouni F. Synergistic interaction earthworm-microbiota: a role in the tolerance and detoxification of pesticides?. *Agricultural sciences*. Université d'Avignon. 2018. English. ffnNT: 2018AVIG0699ff. [citado 20/07/2021]. Disponible en: <https://tel.archives-ouvertes.fr/tel-02074579/document>
15. Edwards CA, Fletcher KE. Interactions between earthworms and microorganisms in organic-matter breakdown. *Agriculture, Ecosystems & Environment*. 1988;24(1-3):235-247.
16. Nath G, Singh K. Combination of vermicomposts and biopesticides against nematode (*Pratylenchus* sp.) and their effect on growth and yield of tomato (*Lycopersicon esculentum*). *IIOAB Journal*. 2011;2:27-35.
17. Rostami M, Oliá M, Arabi M. Evaluation of the effects of earthworm *Eisenia fetida*-based products on the pathogenicity of root-knot nematode (*Meloidogyne javanica*) infecting cucumber. *International Journal of Recycling of Organic Waste in Agriculture*. 2014;3(2):58.
18. Edwards CA, Arancon NQ, Emerson E, Pulliam R. Suppressing plant parasitic nematodes and arthropod pests with vermicompost teas. *Biocycle*. 2007;48(12):38-39.
19. Euteneuer P, Wagentristl H, Steinkellner S, Scheibreithner C, Zaller JG. Earthworms affect decomposition of soil-borne plant pathogen *Sclerotinia sclerotiorum* in a cover crop field experiment. *Applied Soil Ecology*. 2019;138:88-93.
20. Charles NJ, Martín Alonso NJ. Uso y manejo de hongos micorrizicos arbusculares (HMA) y humus de lombriz en tomate (*Solanum lycopersicum* L.), bajo sistema protegido. *Cultivos Tropicales*. 2015;36(1):55-64.
21. González-Escobedo R, Muñoz-Castellanos LN, Muñoz-Ramírez ZY, Guigón López C, Avila-Quezada GD. Microbial community analysis of rhizosphere of healthy and wilted pepper (*Capsicum annum* L.) in an organic farming system. *Microbial Ecology*. 2021; Por asignar
22. Zhang H, Franken P. Comparison of systemic and local interactions between the arbuscular mycorrhizal fungus *Funnelformis mosseae* and the root pathogen *Aphanomyces euteiches* in *Medicago truncatula*. *Mycorrhiza*. 2014;24:419-430.
23. Song Y, Chen D, Lu K, Sun Z, Zeng R. Enhanced tomato disease resistance primed by arbuscular mycorrhizal fungus. *Frontiers in Plant Science*. 2015;6:786.
24. Azcón R, Ambrosano E, Charest C. Nutrient acquisition in mycorrhizal lettuce plants under different phosphorus and nitrogen concentration. *Plant Science*. 2003;165(5):1137-1145.
25. Chakravarty P, Unestam T. Differential influence of ectomycorrhizae on plant growth and disease resistance in *Pinus sylvestris* seedlings. *Journal of Phytopathology*. 1987;120(2):104-120.
26. Eke P, Adamou S, Fokom R, Nya VD, Fokou PVT, Wakam LN, et al. Arbuscular mycorrhizal fungi alter antifungal potential of lemongrass essential oil against *Fusarium solani*, causing root rot in common bean (*Phaseolus vulgaris* L.). *Heliyon*. 2020;6(12):e05737.
27. da Silva Campos MA. Bioprotection by arbuscular mycorrhizal fungi in plants infected with Meloidogyne nematodes: A sustainable alternative. *Crop Protection*. 2020;135:105203.
28. Sharma M, Saini I, Kaushik P, Al Dawsari MM, Al Balawi T, Alam P. Mycorrhizal fungi and *Pseudomonas fluorescens* application reduces root-knot nematode (*Meloidogyne javanica*) infestation in eggplant. *Saudi Journal of Biological Sciences*. 2021;28(7): 3685-3691.
29. Stummer BE, Zhang Q, Zhang X, Warren RA, Harvey PR. Quantification of *Trichoderma afroharzianum*, *Trichoderma harzianum* and *Trichoderma gamsii* inoculants in soil, the wheat rhizosphere and in planta suppression of the crown rot pathogen *Fusarium pseudograminearum*. *Journal of Applied Microbiology*. 2020;129(4):971-990.
30. TariqJaveed M, Farooq T, Al-Hazmi AS, Hussain MD, Rehman AU. Role of *Trichoderma* as a biocontrol agent (BCA) of phytoparasitic nematodes and plant growth inducer. *Journal of Invertebrate Pathology*. 2021;107626.
31. Pozo-Serrano J, Cruz ERDL, Teresa-Cardoso M, Rodríguez-Pérez A, García-Pupo J, Pérez-Tejeda Y, et al. Efectividad antagónica In vitro de *Trichoderma* sp., frente a *Stemphylium lycopersici*. *Cultivos Tropicales*. 2019;40(3).
32. Köhl J, Kolnaar R, Ravensberg WJ. Mode of action of microbial biological control agents against plant diseases: relevance beyond efficacy. *Frontiers in Plant Science*. 2019;10:845.
33. Vinale F, Sivasithamparam K, Ghisalberti EL, Woo SL, Nigro M, Marra R. Trichoderma secondary metabolites active on plants and fungal pathogens. *The Open Mycology Journal*. 2014;8(1):127-139.
34. Vinale F, Ghisalberti EL, Sivasithamparam K, Marral R, Ritieni A, Ferracane R, Woo S, Lorito M. Factors affecting the production of *Trichoderma harzianum* secondary metabolites during the interaction with different plant pathogens. *Letters in Applied Microbiology*. 2009;48(6):705-711.
35. Khan RAA, Najeeb S, Hussain S, Xie B, Li Y. Bioactive secondary metabolites from *Trichoderma* spp. against phytopathogenic fungi. *Microorganisms*. 2020;8(6), 817.

36. Sonkar P, Chandra R, Singh R, Kumar S. Study on management of *Fusarium oxysporum* through different mode of action of *Trichoderma* spp. *International Journal of Current Trends Science and Technology*. 2018;8:20192-20200.
37. Macheleidt J, Mattern DJ, Fischer J, Netzker T, Weber J, Schroeckh V, et al. Regulation and role of fungal secondary metabolites. *Annual Review of Genetics*. 2016;50:371-392.
38. Shyamli S, Prem D, Rs T, Atar S. Production and antifungal activity of secondary metabolites of *Trichoderma virens*. *Pesticide Research Journal*. 2005;17(2):26-29.
39. Shi M, Chen L, Wang XW, Zhang T, Zhao PB, Song XY, Sun CY, Chen XL, Zhou BC, Zhang YZ. Antimicrobial peptaibols from *Trichoderma pseudokoningii* induce programmed cell death in plant fungal pathogens. *Microbiology*. 2012;158:166-175.
40. Sha S, Liu L, Pan S, Wang WM. Isolation and purification of antifungal components from *Trichoderma harzianum* ferment broth by high-speed counter-current chromatography. *Chinese Journal of Biological Control*. 2013;29(1):83-88.
41. Marler TE, Krishnapillai MV. Vertical strata and stem carbon dioxide efflux in *Cycas* trees. *Plants*. 2020;9(2):230.
42. Chikov VI, Akhtyamova GA, Khamidullina LA. Ecological significance of the interaction of photosynthesis light and dark processes. *American Journal of Plant Sciences*. 2021;12(04):624.
43. Ferrero Holtz EW, Gonzalez MG, Giuffré L, Ciarlo E. Glomalins and their relationship with soil carbon. *International Journal of Applied Science and Technology*. 2016;6(2):69-73.
44. Kaiser C, Kilburn MR, Clode PL, Fuchslueger L, Koranda M, Cliff JB, et al. Exploring the transfer of recent plant photosynthates to soil microbes: mycorrhizal pathway vs direct root exudation. *New Phytologist*. 2015;205(4):1537-1551.
45. Kittredge J. Soil Carbon Restoration: Can Biology do the Job?. NE Organic farming association, Massachusetts Chapter, 16. 2015. [citado 20/07/2021]. Disponible en: https://www.unifiedfieldcorporation.com/wp-content/uploads/2015/11/2015_White_Paper_web.pdf
46. Olivas-Tarango AL, Tarango-Rivero SH, Ávila-Quezada GD. Pecan production improvement by zinc under drip irrigation in calcareous soils. *Terra Latinoamericana*, 2021;39:1-12.
47. Tarango-Rivero SH, Ávila-Quezada GD, Jacobo-Cuellar JL, Ramírez-Valdespino CA, Orrantia-Borunda E, Rodríguez-Heredia R, Olivas-Tarango AL. Chelated zinc and beneficial microorganisms: A sustainable fertilization option for pecan production. *Revista Chapingo. Serie horticultura*, 2022;28(3):145-159.