

REVIEW [REVISIÓN]

THE SOIL BIOTA: IMPORTANCE IN AGROFORESTRY AND AGRICULTURAL SYSTEMS

[LA BIOTA DEL SUELO: IMPORTANCIA EN SISTEMAS AGROFORESTALES Y AGRÍCOLAS]

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SUMMARY

The biological component of soil is important for the maintenance and functioning of ecosystems. Currently there have been some studies on the diversity of soil biota and their role in key soil processes. Microorganisms are critical to the functioning of biological systems and the maintenance of life on the planet, since they participate in metabolic, ecological and biotechnological processes on which we depend for survival and for facing future challenges. Soil organisms maintain soil processes such as carbon capture and storage, nutrient cycling, nitrogen fixation, water infiltration, aeration, and organic matter degradation. The effects of these ecosystem services are not yet fully explored, especially soil microorganisms (bacteria and fungi), and macroorganisms (earthworms).

Key words: Processes; carbon capture and storage; organic matter; microorganisms.

RESUMEN

El componente biológico de suelo es importante para el mantenimiento y el funcionamiento de los ecosistemas. De momento no se han realizado algunos estudios sobre la diversidad de la biota del suelo y su papel en los procesos clave del suelo. Los microorganismos son esenciales para el funcionamiento de los sistemas biológicos y el mantenimiento de la vida en el planeta, ya que participan en los procesos metabólicos, ecológicos y biotecnológicos de los que dependemos para sobrevivir y para poder afrontar los retos del futuro. Los organismos del suelo mantienen los procesos del suelo, como la captura y almacenamiento de carbono, el ciclo de nutrientes, fijación de nitrógeno, la infiltración del agua, la aireación y la degradación de la materia orgánica. Los efectos de estos servicios de los ecosistemas no están completamente exploradas, especialmente los microorganismos del suelo (bacterias y hongos), y macroorganismos (lombrices de tierra).

Palabras clave: Procesos, captura y almacenamiento de carbono; la materia orgánica; microorganisms.

INTRODUCTION

The intense perturbation on soils caused by population increases has been recorded in many parts of the tropics, can lead to lower crop yields as well as promote the invasion of difficult to control weeds. One of the options for stopping this process is land use through agroforestry systems (Jenkins *et al.*,

2004). In almost all traditional farming systems, including livestock systems, trees are interspersed with crops or managed zonally by alternating trees and crops and/or pasture. That is, they are agroforestry systems and even with the modernization of the agricultural region, agricultural landscapes still contain a high number of trees. These trees fulfill many purposes such as production (timber, firewood,

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fodder, fruits and medicines) as well as services (shade for crops and/or animals, protection in the case of windbreaks). In addition, trees increase the biodiversity of the agroecosystems by creating homes for other organisms in their branches, roots and litter (Reyes and Valery, 2007). Agroforestry techniques are used in regions with diverse ecological, economic and social conditions, as well as in regions with fertile soils where agroforestry systems can be very productive and sustainable. Equally, these practices have a high potential to maintain and improve productivity in areas that present problems of low fertility and excess or shortage of soil moisture (Musálem, 2001).

Agroforestry can also play an important role in conserving biodiversity in deforested and fragmented landscapes, providing habitats and resources for plant and animal species, maintaining the connection of the landscape (and, thereby, facilitating the movement of animals, seeds and pollen), making landscape living conditions less harsh for the inhabitants of the forest, reducing the frequency and intensity of fires, potentially reducing effects on remaining adjacent fragments, and providing buffer zones to protected areas (Jenkins *et al.*, 2004). The objective of this report is about some services microorganisms that contribute to different ecosystems.

The ecosystem-service

An ecosystem-service is defined as goods, functions and processes of an ecosystem that provide benefits to the human population (Boyd and Banzhaf, 2005; Balvanera and Cotler, 2007). The agro-forestrygrazing system is a production system (production services) for beneficial services: soil formation, nutrient cycling and primary production. Soils are also involved in regulating services (climate regulation on greenhouse gas fluxes and C capture, flood control, detoxification, protection of plants against parasites). This influences the dynamics of organic matter and the wide effects on soil physical properties (Table 1) (Jenkins *et al.*, 2004).

The microbial component of soil is important for health, maintenance, function and quality of ecosystems (Olalde and Aguilera, 1998). The role of the organisms is the transformation and availability of organic matter for plants, an activity without which the world would be a huge dump. Others have played a significant role in relation to man, and productivity, participating in agriculture, food processing and medicine production (van Eekeren, 2010).

	Goods/services	Ecosystem process	Soil biota contribution
Production	Pest and disease regulation	Interaction plants-	Reduction and control of
		organisms	pathogenic organisms
	Increase food Nutrient cycles	Biofertilizers Biopesticides Phytostimulators o Bioremediators CO ₂ and N fixation Organic matter degradation Carbon capture	Carbon and nitrogen storage
Environmental	Climate regulation	Ecosystem conservation	Reduced global warming
	Air quality regulation		
Contamination	Water cycle	Maintenance of plantations	Water quality and conservation
	Biodegradation		Transformation of harmful compounds into substances with lesser impact

Table 1. Ecosystem services of the soil biota.

Biological involvement in the process for formation of soil aggregates is important for their activity, mesofauna excrements, trapping of particles by roots and glues produced by fungi, mainly hyphae structures of arbuscular mycorrhizal fungi that trap and bind primary particles for the development of aggregates, and bacteria. Aggregates that form it are generally stable in water (González-Chávez *et al.*, 2004, van Eekeren, 2010). The importance of aggregates in the ecosystem is for soil stability and structure, participating in processes such as infiltration, aeration, water holding capacity, less encrusting of the soil surface and greater resistance to erosion (González-Chávez *et al.*, 2004).

The concept of ecosystem services is a newly formed, so there is a need to develop methodologies to identify, quantify and rank (if possible) the provided services. It is essential to identify the relationships between services and ecosystem processes that regulate them, to know the perception of the players, to model scenarios of loss of services and the potential population affected, coupled with an economic valuation study (Almeida-Leñero *et al.*, 2007). Only this will generate solid management proposals to conserve and restore ecosystems without forgetting that the main goal should be human welfare (Almeida-Leñero *et al.*, 2007).

Agricultural production

The relationships established by soil microorganisms may benefit to the plants when they occur in the area close to their roots (rhizosphere) characterized by having a large number of organic compounds that are exuded by the plants (Kloepper, 1994). Beneficial soil biota around the root, set and accelerates biochemical processes affecting growth and development of vegetation, and it is related to an increase in available nutrients and the production of growth substances while inhibiting parasitic organisms and pathogens (Lara and Echeverría, 2007).

Reyes and Valery (2007) studied the phosphate solubilizing, which varied with soil physical and chemical conditions and plant species. Where microbial population density showed a low rhizosphere/soil ratio opposed to one with high physical and chemical degradation caused by mining and by the corn shade house trial, the *Azotobacter* strain MF1b significantly increased the dry weight in the NK chemical treatments and phosphate rock with K, giving an agricultural service as a strain with potential use in soil fertility.

Ecosystems agricultural same ecological property, the cycling of nutrients in the soil, is considered as an ecosystem service. In agricultural fields, food

production depends on the cycling of nutrients in the soil (fertility), but also of various human interventions such as spraying of agricultural chemicals, raw material processing and food distribution. Developing appropriate indicators may provide a better understanding and quantifying of the link between the benefits provided by ecosystems and their ecological properties (Quétier *et al.*, 2007).

Earthworms provide production services to the ecosystem by digesting organic matter through their mutual interaction with the microflora registred into their digestive tract. The effects caused by the worms can be seen at different time and space scales. In short time, such as digestion for the worm, organic residues is fractionated, and some nutrients (nitrogen, phosphorus and potassium) can be assimilated by plants are released to the soil (Lavelle *et al.*, 1997).

Thus earthworms affect the nitrogen cycle directly by consuming and assimilating inorganic and organic-N. The worms can process large amounts of organic matter, with the consumption rate of Aporrectodea tuberculata ranging from 5 to 13 mg g⁻¹ organic matter g⁻¹ per worm per day⁻¹, while for Lumbricus *terrestris* goes from 14 to 2.7 mg g^{-1} per day⁻¹. The efficiency of assimilated nitrogen (^{15}N) ranges from 10 to 26% in A. tuberculata and 25-30% in L. Brussaard (1999) terrestris. estimated that consumption by earthworms may be 11.8 to 17.1 Mg organic matter ha⁻¹ per yr⁻¹; this can amount to 19-24% of organic waste matter yields. Geophagus earthworms can ingest huge amounts of land. The population of *Pontoscolex corethrurus* in grasslands of "Plan de las Hayas" Veracruz, can ingest of 400 Mg per ha per year, which means a worm of this kind can ingest from 1 to 3 times its own weight per day (Lavelle et al., 1997).

Bacteria

Kloepper (1994) used the term plant growth promoting rhizobacteria to refer to rhizobacteria capable in plants. This is a crucial feature for microbial inoculum selection for use in agriculture and food, mainly as biofertilizers, biopesticides, phytostimulators or bioremediators (Lugtenber *et al.*, 2001; Peña and Reyes, 2007).

The use of rhizosphere microorganisms in biotechnology for the human community has been implemented by inoculating seeds and plants (Peña and Reyes, 2007). Exploited and abandoned soils from a phosphate rock mine, where populations were 29% for fungi and 13% for cultivable calcium phosphate dissolving bacteria for plants under field conditions (Reyes *et al.*, 2006).

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Biological nitrogen fixation is carried out exclusively by prokaryotes, which have the ability to reduce atmospheric nitrogen (N₂) to ammonium (NH₄) that can be used by plants, contributing to, and improving productivity of crops (Zehr *et al.*, 2003, Philippot and Germon 2005). Several studies have demonstrated the importance and effect of the presence of nitrogenfixing bacteria in agricultural and ecosystems processes, as well as sustainable land use (Mantilla-Paredes *et al.*, 2009).

Arbuscular mycorrhizal fungi (AMF)

Mycorrhizae type of symbiosis between the fungi and plant roots; however, not all fungi are mycorrhizal, some are also saprophytic (Barker, 2009). With the establishment of arbuscular mycorrhizal fungi in the root system (Figure 1), the morphological and physiological integration of the symbiosis is satisfied, and will determine mutuality and nutrient exchange in both symbionts (Jones and Smith, 2004).

The benefit provided by AMF to the human community is the colonization of roots for absorption of some essential plant nutrients such as phosphorus and potassium. Also absorption of low mobility nutrients in the soil such as Cu and Zn, increasing plant tolerance to abiotic soil stress conditions and protection from pathogens (Smith and Read, 1997). The mutualistic symbiosis between fungi and plants is seen in the forage crops, ornamentals, fruits, vegetables and maple and other forests and pine (van Den Heijden., 1998).

The use of AMF in agriculture contributes to improve plant nutrition; however, the monoculture condition of agroecosystems, may be causing a decrease in the diversity of AMF and as a result (Figure 2), these microorganisms could be providing a beneficial effect even though limited to the hosts (Alarcon, 2007).

Another role for which AMF in ecosystems provide to plant is adaptability, establishment and growth. As to the soil stability, hyphae allow the aggregation of soil particles, which prevent soil erosion (Abbott and Gazey, 1994). Moreover, the activity of AMF allows the presence of microbial populations to be modified, participating as regulatory agents of beneficial and pathogenic microbiota, thus, influencing the dynamics of organic carbon and soil fertility (Alarcón, 2007).

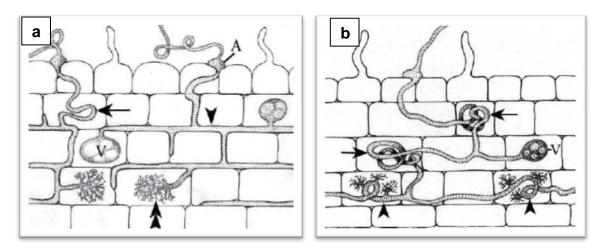


Figure 1. Types of arbuscular mycorrhizal association. a) Type Arum, characterized by hyphae that grow in an intercellular form (arrow head). b) Type Paris, characterized by hyphae with intracellular growth (arrow head). Vesicles (V), Appressorium (A), hyphae (arrows) y arbuscules (two arrowheads). Modified from Barrer (2009).

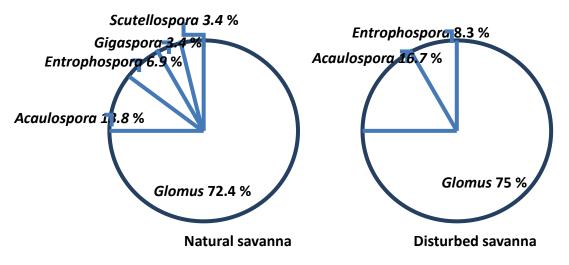


Figure 2. Percentage of the genus of AMF in natural and disturbed savanna (Lovera and Cuenca, 2007).

Antagonistic fungi, the case of *Trichoderma* spp

Trichoderma spp. has been widely used as antagonistic fungal agents against several pests as well as plant growth enhancers. Faster metabolic rates, antimicrobial metabolites, and physiological conformation are key factors which chiefly contribute to antagonism of these fungi. Mycoparasitism, spatial and nutrient competition, antibiosis by enzymes and secondary metabolites, and induction of plant defence system are typical biocontrol actions of these fungi. On the other hand, Trichoderma spp. has also been used in a wide range of commercial enzyme productions, namely, cellulases, hemicellulases, proteases, and -1,3-glucanase. The classification of the genus, Trichoderma, antagonic mechanisms and role in plant growth promotion has been well documented. However, fast paced current research in this field should be carefully updated for the foolproof commercialization of the fungi (Verma et al., 2007).

Previously, Cook (1993) classified the mycoparasitic interactions as: (i) replacement (unilateral antagonism), (ii) deadlock (mutual antagonism), and (iii) intermingling (no antagonism), with lack of explanation at microscopic level. However, more recently the understanding of mycoparasitism has considerably improved (Yedidia *et al.*, 1999). Interestingly, the studies were carried out at genetic (Zeilinger et al., 1999; Brunner et al., 2003) and microscopic (Benhamou et al., 1999) levels. However, a broader concept concerning living plants (with the exception of preservation of wood, where Trichoderma spp. alone kill plant pathogenic fungi; discussed later) would be that after being treated with mycoparasites, plants induce defense mechanisms on their own. Further, this phenomenon leads to production of fungal inhibitory compounds by plants in addition to *Trichoderma* spp., thereby, facilitating mycoparasitism. Moreover, the mycoparasitism shown by Trichoderma sp. was a host specific (Pythium oligandrum) (Benhamou et al., 1999). The complex group of extracellular enzymes has been reported to be a key factor in pathogen cell wall lysis during mycoparasitism (Verma et al., 2007).

The microorganisms in biodegradation of toxic compounds

Torres (2003) indicates that bioremediation practices consist mainly of the use of different organisms (plants, yeasts, fungi, and bacteria) to neutralize toxic substances, or transforming them into less toxic substances or making them harmless to the environment and human health. One of the most used bio-correctional measures is the use of microorganisms for soil decontamination (ecosystem service) and is based on the absorption of organic substances by these microorganisms, which they use as the carbon source needed for growth and energy for their metabolic functions.

The bacteria were found to be a group of bacteria mainly from the genus *Pseudomonas* which degrade the hydrocarbon 3-phenoxybenzoic in soils (Halden *et al.*, 1999), and *Sphingomonas wittichii* RW1 which under anaerobic conditions is capable of transforming the metabolite 2,7-dichlorobenzene producing the metabolites 4-chloroethanol and 1,2,3,4-tetrachlorodibenzo.

The best known bacterial genus in terms of efficiency in the degradation of petroleum fuels are *Pseudomonas, Acinetobacter, Agrobacterium, Flavobacterium, Arthrobacter* (Torres, 2003), *Aeromonas, Corynebacterium* and *Bacillus*. Of these, *Pseudomonas, Agrobacterium,* and *Bacillus* are also characterized for having the ability to fix atmospheric N (Lugtenberg *et al.,* 2001).

The AMF increased tolerance to metals in most of their host plants (van Der Heijden, 1998). *Glomus mosseae* BEG-132 captured between 470 and 680 μ g g⁻¹ of Cu (based on dry weight) and increased tolerance to As and Cu (Sánchez *et al.*, 2004).

Hernández et al. (2003) evaluated the behavior of free living atmospheric nitrogen fixing bacteria populations (ANFB) and hydrocarbonoclastic ANFB (HC's) in soils contaminated by fuels such as kerosene. The presence of kerosene did not drastically affect populations of ANFB and HC's-ANFB, and after evaluating atmospheric N fixation, it was found that the bacteria could perform this function. The largest populations were: for ANFB $(410 \times 10^4 \text{ CFU g}^{-1} \text{ root})$ in the rhizoplane in a concentration of 2500 mg kg⁻¹ kerosene and HC's-ANFB- $(299 \times 10^4 \text{ CFU g}^{-1} \text{ soil})$ in the rhizosphere in a concentration 500 mg kg⁻¹ kerosene [CFU-colony forming units]. These results showed that HC's-ANFB can be an option for bioremediation of kerosene contaminated soil and its application will induce the incorporation of N into these soils.

The microbiota in soil formation

The earthworm participates in ecosystem services such as soil formation, regulation and supply of water by means of mechanical activity within the soil due to its ability to move, creating structures that affect aeration and water infiltration (galleries), degradation of organic material and its incorporation into soil. Part of this degradation is due to the digestion that takes place in their digestive tract and with the production of manure (excretas) as part of the biogenic structure, for which they are also called ecosystem engineers (Brown et al., 2001, Lavelle et al., 2006).

There are three functional groups of earthworms which based on their feeding style and habitat contribute in one way or another to ecosystem services: the epigeous (litter inhabitants, consumers of decaying organic matter, dorsoventrally flattened and pigmented); the endogenous (inhabitants of ground, not pigmented, consuming land and subdivided into poly-, meso- and oligo-humic (Lavelle and Spain, 2001); and anecic (ground dwellers and consumers of leaves) forming galleries (Brown et al., 2001; Brito-Vega et al., 2006). These behaviors usually lead to a stimulation of plant growth (Whalen and Parmelee, 1999; Hallaire et al., 2000; Eriksen-Hamel and Whalen, 2007). For example, Eriksen-Hamel and Whalen (2007) analyzed two species of earthworms, the endogenous Aporrectodea caliginosa which was dominant in the field and the anecic Lumbricus terrestris which barely survived field conditions in the crop, and found that the N-total in soybeans increased 25% with the increase of the earthworm population (100 to 500 individuals m⁻²).

Organic matter

Soil organic matter (SOM) is constituted of many diverse components with different states of decomposition, which vary depending on the quality of material, during mineralization (sugars, amino acids, hemicellulose, cellulose, and lignin) and humification. During the process of decomposition, organic matter is enhanced by the participation of soil organisms that ingest and transform a mixture of organic substrates and inorganic soil (micro- and macro-organisms). At the end of this process, part of the final product is absorbed by plant roots or other organisms. The organisms are involved at different levels of the trophic system, including earthworms that participate favorably in changes of N from the topsoil; some feed on microbes (microbivores), organic matter in decomposition (detritivores), or a mixture of microbivores - detritivores (Domínguez et al., 2009). It is still uncertain as to what trophic level earthworms should be located, given that they may use different feeding strategies, from selective and nonselective mechanisms, plus they have the ability to obtain energy from both living and dead carbon sources (Rodríguez-Echeverria, 2009).

The activity of earthworms in the organic matter

The decomposition of organic matter occurs in two distinct phases in relation to the activity of earthworms: 1) active phase, where the worms process organic matter, alter the physical and chemical properties, and the microbial composition (Lores *et al.*, 2006); and 2) the maturation phase, where microorganisms take over in the decomposition of organic material previously processed by earthworms (Domínguez *et al.*, 2009).

Earthworms are involved in the decomposition, and transformation organic matter through processes that occur in their digestive system. The processes include modification of microbial and diversity, the modification of microfauna populations, the homogenization of the substrate and the intrinsic processes of digestion and assimilation, including also the production of mucus, which are a source of easily assimilated nutrients for microorganisms (Domínguez *et al.*, 2009). These microorganisms produce extracellular enzymes that degrade cellulose and certain phenolic compounds, increasing the degradation of ingested material (Salzman, 2005).

The mineralization of nutrients is performed by the metabolic activity of bacteria and fungi. But this metabolic activity is influenced by soil fauna that lives in interaction with microorganisms, and also by various interactions that determine the transfer of nutrients through the system. In this sense, the excreta of earthworms play an important role in decomposition, because they contain nutrients and microorganisms that are different from those contained in the organic material before ingestion (Domínguez *et al.*, 2009).

CONCLUSION

The concept of ecosystem services enables the analysis of the link between ecosystem functioning and human welfare. The activity of soil biota may decrease or increase the productivity of ecosystems. Negative effects can cause a considerable decrease in plant productivity (pests) or increase the positive effects (beneficial organisms.) Each organism may have a different influence on soil processes and plant production, and the abundance or biomass can reach thresholds, both positive and negative on the ecosystems services provided to humanity.

REFERENCES

- Abbott, L. K., Gazey C. 1994. An ecological view of the formation of VA mycorrhizas. Plant Soil. 159:69-78.
- Alarcón, A. 2007. Micorriza arbuscular. In: Microbiología agrícola. (Ids): Ferrera-Cerrato, R., Alarcón, A. Trillas, México. pp. 568.
- Almeida-Leñero L., Nava M., Ramos A., Ordoñez M. de J., Jujnovsky J. 2007. Servicios

ecosistématicos en la cuenca del río Magdalena, Distrito Federal, México. Gaceta Ecológica. Número especial 84-85: 53-64.

- Balvanera, P., Cotler H. 2007. Acercamiento al estudio de los servicios ecosistématicos. Gaceta Ecologica. 84-85:8-15.
- Barrer, S. E. 2009. El uso de hongos micorrizicos arbusculares como una alternativa para la agricultura. Facultad de Ciencias Agropecuarias. 7:124-132.
- Benhamou, N., Rey P., Picard K., Tirilly Y. 1999. Ultrastructural and cytochemical aspects of the interaction between the mycoparasite Pythium oligandrum, and soilborne plant pathogens, Phytopathology 89:506–517.
- Boyd, J. W., H. S. Banzhaf. 2005. Ecosystem services and government: the need for a new way of judging nature's value. Resources. 158:16-19.
- Brito-Vega, H. Espinosa-Victoria D., Figueroa-Sandoval B., Patrón-Ibarra J.C. 2006.
 Diversidad de lombrices de tierra con labranza de conservación y convencional. Terra latinoamericana. 24: 99-108.
- Brown, G.G., Fragoso C., Barois I., Rojas P., Patrón C.J., Bueno J., Moreno G.A., Lavelle P., Ordaz V., Rodríguez C. 2001. Diversidad y rol funcional de la macrofauna edáfica en los ecosistemas tropicales mexicanos. Acta Zoologica Mexicana. 1:79-110.
- Brunner K., Montero M., Mach R.L., Peterbauer C.K., Kubicek C.P. 2003. Expression of the ech42 (endochitinase) gene of Trichoderma starvation atroviride under carbon is antagonized via a BrlA-like cis-acting element. FEMS Microbiology Letters. 218:259-264.
- Brussaard, L. 1998. Soil fauna, guilds, functional groups and ecosystem processes. Applied Soil Ecology 9:123-135.
- Brussaard, L. 1999. On the mechanisms of interactions between earthworms and plants. Pedobiologia 43:880-885.
- Cook, R.J. 1993. Making greater use of introduced microorganisms for biological control of plant pathogens. Annual Review of Phytopathology 31: 53–80.

- Domínguez, J., Aire, M., Gómez-Brandón, M. 2009. El papel de las lombrices de tierra en la descomposición de la materia orgánica y el ciclo de nutrientes. Ecosistemas. 18:20-31.
- González-Chávez, M. C. A., Gutiérrez-Castorena M. C., Wright, S. 2004. Hongos micorrízicos arbusculares en la agregación del suelo y su estabilidad. Terra Latinoamericana. 22:507-514.
- Hernández, A. E., Ferrera-Cerrato, R., Rodríguez V. R. 2003. Bacterias de vida libre fijadoras de nitrógeno atmosférico en rizósfera de frijol contaminada con queroseno. TERRA Latinoamericana. 21: 81-89.
- Jenkins, M., Scherr, S. J., Inbar, M. 2004. Markets for biodiversity services: potential roles and challenges. Environment. 46: 32-42.
- Jenkins, M., Scherr, S. J., Inbar, M. 2004. Markets for biodiversity services: potential roles and challenges. Environment 46: 32-42.
- Jones, M., Smith, S. 2004. Exploring functional defitions mycorrhizas: are mycorrhizas always mutualism? Canandia Journal of Botany. 82:1089-1109.
- Kloepper, J. 1994. Plant growth-promotiong rhizobacteria (other systems). In Okon J (Id.) *Azospirillum*. CRC. Boca Raton, FL. EEUU. pp 137-167.
- Lara, A., Echeverría, C. 2007. Conclusiones del Congreso Internacional de los servicios Ecosistémicos en los Neotrópicos: Estado del arte y desafíos futuros. Bosques. 28:10-12.
- Lavelle, P., A. Spain. 2001. Soil ecology. Kluwer. Amsterdam, The Netherlands.
- Lavelle, P., D. Bignell, M. Lepage. 1997. Soil function in a changing world: the role of invertebrate ecosystem engineers. European Journal of Soil Biology. 33: 159-193.
- Lavelle, P., Decaëns, T., Aubert, M., Barot, S., Blouin, M., Bureau, F., Margerie, F., Mora, P., Rossi, J. P. 2006. Soil invertebrates and ecosystem services. European Journal of Soil Biology. 42: 3-15.
- Lavelle, P., E. Blanchart, A. Martin, A.V. Spain, S. Martin. 1992. Impact of soil fauna on the properties of soils in the humid tropics. pp. 157-185. *In:* R. Lal, P.A. Sanchez (eds.).

Myths and science of soils in the tropics Special Publication 29. Soil Science Society of America. Madison, WI, USA.

- Lovera, M., Cuenca, G. 2007. Diversity of arbuscular mycorrhizal fungi (AMF) and soil mycorrhizal potential of natural savanna savannah disturbed the great plains, Venezuela. Interciencia. 32: 108-114.
- Lugtenberg, B., Dekkers L., Bloemberg G. 2001. Molecular determinants of rhizosphere colonization by *Pseudomonas*. Annual Review of Phytopathology. 39:461-90.
- Mantilla-Paredes, A. J. Cardona, G. I., Peña-Venegas, C. P., Murcia, U., Rodríguez, M., Zambrano, M. M. 2009. Distribución de bacterias potencialmente fijadoras de nitrógeno y su relación con parámetros fisicoquímicos en suelos con tres coberturas vegetales en el sur de la Amazonia colombiana. Revista de Biologia Tropical. 57: 915-927.
- Olalde P. V., Aguilera, G. L. I. 1998. Microorganismos y biodiversidad. Terra Latinoamericana. 3: 289-292.
- Pankhurst, C.E., Doube, B. M., Gupta, V.V.S.R., Grace, P.R. 1997. Soil Biota: Management in sustainable farming systems. CSIRO. East Melbourne. pp. 262.
- Peña, H. B., Reyes, I. 2007. Aislamiento y evaluación de bacterias fijadoras de nitrógeno y disolventes de fosfatos en la promoción de crecimiento de la lechuga (*Lactuca sativa L*). Interciencia. 32:560-565.
- Philippot, L., Germon, J.C.. 2005. Contribution of bacterial to initial input and cycling of nitrogen in soils. *In* Buscot, F., and Varma, A. (Ids.). Microorganisms in soils: roles in genesis and functions. Springer, Nueva York, EEUU. pp. 159-176.
- Quétier, F. Tapella, E., Conti, G., Cáceres, D., Díaz, S. 2007. Servicios ecosistématicos y actores sociales. Aspectos conceptuales y metodológicos para un estudio interdisciplinario. Gaceta ecológica. 84-85:17-26.
- Reyes, I., Valery, A. 2007. Efecto de la fertilidad del suelo sobre la microbiota y la promoción del crecimiento del maíz (*Zea mays L.*) con *Azotobacter* spp. Bioagro. 3:117-126.

- Reyes, I., Valery, A., Valduz, Z. 2006. Phosphatesolubilization and colonization of maize rhizosphere by wild and genetically modified strains of *Penicillium rugulosum*. Microbiology Ecology. 44:39-48.
- Rodríguez-Echeverria, S. 2009. Organismos del suelo: la dimensión invisible de las invasiones por plantas no nativas. *Ecosistemas* 18:32-43.
- Salzman, J. 2005. The promise and perils of payments for ecosystem services. International Journal of Innovation and Sustainable Development 1:5-20.
- Sánchez, V. G., Carrillo, G. R., Martínez, G. A., González, Ch. Ma.C. 2004. Tolerancia adaptativa de hongos micorrízicos arbusculares al crecer en sustratos contaminados con As y Cu. Revista internacional de Contaminación Ambiental. 20:147-158.
- Smith, S. Read, D. 1997. Mycorrhizal Symbiosis. 2 ed. Londres: Academic Press Limited, p.605.
- Torres, R. D. 2003. El papel de los microorganismos en la biodegración de compuestos tóxicos. Ecosistemas. 2:1-5.

- van Der Heijden, M. 1998. Different arbuscular mycorrhizal fungal species are potential determinants of plant community structure. Ecology. 79: 2082-2091.
- Van Eekeren, N. 2010. Grassland management soil biota and ecosystem. Wageningen University, Wageningen. English. Thesis. p. 264.
- Yedidia, I., Benhamou, N., Chet, I. 1999. Induction of defense responses in cucumber plants (*Cucumis sativus* L.) by the biocontrol agent *Trichoderma* harzianum, Applied Environmental Microbiology. 65:1061–1070.
- Zehr, J.P., Jenkins, B.D., Short, S.M., Steward, G.F. 2003. Nitrogenase gene diversity and microbial community structure: a cross-system comparison. Environental. Microbiology. 5: 539-554.
- Zeilinger, S., Galhaup, C., Payer, K., Woo, S.L., Mach, R.L., Fekete, C., Lorito, M., Kubicek, C.P. 1999. Chitinase gene expression during mycoparasitic interaction of *Trichoderma harzianum* with its host, Fungal Genet. Fungal Genetics of Biology. 26:131–140.

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