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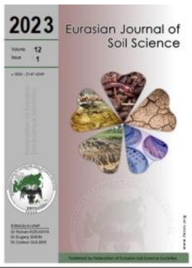

Pores distribution influences the soil microorganism's response to changes in temperature and moisture

Efraín Francisco Visconti-Moreno *, Ibonne Geaneth Valenzuela-Balcázar

Universidad Francisco de Paula Santander, Faculty of Agricultural and Environmental Sciences. Research group on Environment and Life – GIAV, Cucuta, Colombia

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Author(s)

E.F.Visconti-Moreno *
I.G.Valenzuela-Balcázar

* Corresponding author

Abstract

Microorganisms are an essential fraction of soil organic matter, which presence and activity depend directly on soil physical conditions. This study aimed to address the effect of soil temperature and moisture under contrasting macroporosity conditions on soil biological properties. Soil physical-chemical characterization implicated the collection of composite samples and undisturbed surface soil samples (0 to 10 cm). Also, samples of undisturbed surface soil were extracted in 40 polyvinyl chloride cylinders of 18 cm diameter and 20 cm height for the arrangement of soil mesocosm as the experimental units of a completely randomized experiment with a 2x2x3 factorial arrangement. The experiment duration was 21 days, and the soil biological properties measured were microbial biomass (MB) and soil respiration (SR). Macroporosity showed a significant effect on MB, which indicates that aeration pore influences the number of microorganisms in the soil; for the SR, the macroporosity had a not significant effect. The temperature at the ranges established in the experiment did not significantly affect MB, whereas a highly significant effect of temperature over SR was observed. A highly significant effect of soil moisture was observed on MB and SR. Macroporosity, moisture, and temperature are determining factors in the presence of soil microorganisms, both directly and through the interaction between them. Herein the microorganisms have a wide range of thermal adaptation, and the effect of soil temperature can boost soil microorganisms. In turn, it was observed that the microorganisms present are significantly sensitive to the moisture deficit in soil.

Keywords: Microbial biomass, soil respiration, biological degradation, physical properties, climate change.

Introduction

Conserving the soil as the best habitat for organisms that occupy it is a role that corresponds fundamentally to soil microorganisms since they are responsible for the main biogeochemical processes through which the flow of energy and matter occurs; in terrestrial ecosystems (Pulleman et al., 2012; Mujtar et al., 2019).

Brevik et al. (2015) reported that microorganisms make up an important fraction of soil organic matter (SOM), together with the macro and mesofauna of the soil, and the roots, which constitute the living biomass of soils. Soil microorganisms are responsible for decomposing and transforming organic waste in soils. Through the intense activity of numerous and diverse microorganisms, SOM decomposes, transforms, and stabilizes the soil organic carbon (SOC) (Macías and Camps-Arbestain, 2010; Pulleman et al., 2012).

Soil microbial activity is considered to be an ecological indicator of fundamental importance since, on the one hand, it represents the level of biological activity involving the labile component of SOM and, on the other, it

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integrates the factors of the environment with the soil use and management (Zagal et al., 2002). Indeed different use and management systems on the same soil can differentially affect soil microorganisms, thus modulating the ecosystem services provided by these organisms (Di Ciocco et al., 2014); consequently, it is necessary to know the behavior of the microorganisms in each situation.

Soil management practices are decisive since the agricultural use of soils generally causes a drastic decrease in the total microbial biomass of soils, together with a decrease in the total SOC. The latter is because the decomposition of SOM by microorganisms is strongly affected by the soil's chemical and physical conditions (Kaurin et al., 2018). For example, soil temperature, water content, and aeration are physical conditions that directly influence the activity of microorganisms. For this reason, soil management practices, such as tillage, irrigation and drainage, use of fire, and incorporation of organic fertilizer, can modify soil microorganism communities and affect soil quality (Brevik et al., 2015).

Soil microorganisms' activity will be determined by their sensitivity to temperature, the availability of substrates, their interactions with surface processes and other environmental factors such as soil moisture, and possible adaptations of microbial physiology (Schindlbacher et al., 2011). According to the IPCC (2007), climate change is expected to substantially impact soil moisture and temperature conditions with greater frequency and duration due to droughts. Furthermore, since soil warming is occurring, changes have been observed in the composition of the soil microbial community. The latter, in terms of an increase or decrease in the abundance of fungi. Also, because of an increase or decrease in the abundance of gram-positive or gram-negative bacteria (Rinnan et al., 2008). Also, Kaurin et al. (2018) mentioned that climate models project a 5 to 15% decrease in soil water content in the topsoil (10 cm) by the end of the century. It can mean that microbial communities and the biogeochemical cycles they control will be affected by extreme changes in soil water content. That is because soil microbial communities are susceptible to changes in soil moisture (Morugán-Coronado et al., 2019).

Scientists have increased their interest in the understanding of how drought can impact soil microbes. In this direction Siebielec et al. (2020) studied the impact of water stress on soil microbial activity and diversity. Their results proves the greater susceptibility of microbial communities to drought in sandy soils and the important role of exogenous organic matter in protecting microbial activity in drought periods. Also, Borowik and Wyszkowska (2016) proved that soil microbe's activity depends on the soil moisture level in dependence with the grain-size distribution of soil. They demonstrated that both excessively dry and wet soil create unfavorable conditions that may deplete the biomass of microorganisms. Since soil aeration pores (macroporosity) are a physical characteristic that can be modified by use and management practices (Bronick and Lal, 2005) and is directly involved with the water-air relationships necessary to favor the survival of soil microorganisms (Dexter, 2004). Ishak et al. (2016) studied the interactions between soil moisture and soil microbial activity at different soil compaction conditions, finding that microbial activity was higher in uncompact soils and decreased as soil compaction increased.

The effect of changes in soil temperature and moisture under contrasting aeration conditions on soil microorganisms must be studied. This research aims to evaluate the effect of the soil aeration pores (macroporosity), the soil temperature, and moisture content on the presence of microorganisms in agricultural soil in Norte de Santander, Colombia.

Material and Methods

Study site and soil sampling

The soil selected for this study is located in the Astilleros village of El Zulia municipality in Norte de Santander, Colombia. In an oil palm field 20 years old, with geographic coordinates of reference: 8º 12` 17" N and 72º 32` 52" W and 84 m above sea level altitude. The soil is classified as Fluventic Dystrudepts (Soil Survey Staff, 2010) under a humid tropical forest with an average annual temperature of 27.3 ºC and a mean annual rainfall of 2000 mm (IGAC, 2006a).

A soil sampling was carried out by tracing an imaginary cross of 50 meters on each side to mark five points (intersection and ends of the cross) to achieve soil physical-chemical characterization. At each point, a composite soil sample was collected consisting of five sub-samples of surface soil (0 to 10 cm depth), also arranged on the ends (04) and intersection (01) of a 2-meter-long cross (Valadares-Pereira et al., 2017). At these same five points, ten undisturbed surface soil samples (two at each point) were extracted in metallic cylinders of 5 cm in diameter and 5 cm in height for physical analysis. Also, samples of undisturbed surface soil (0 to 15 cm depth) were extracted in 40 polyvinyl chloride (PVC) cylinders of 18 cm in diameter and 20 cm in height (eight at each point) for the arrangement of experimental units (Schindlbacher et al., 2011; Lubbers et al., 2017).

Experimental Design

The evaluation was carried out through a completely randomized experiment with a 2x2x3 factorial arrangement with 3 repetitions, representing 36 experimental units. The experimental units consisted of soil and microorganism mesocosm, conformed by undisturbed soil extracted at a depth of 15 cm in the PVC cylinders indicated above (Figure 1). The duration of the experiment was 21 days, and the factors were: macroporosity (two levels), soil temperature (two levels), and soil moisture (three levels), as presented in Table 1.

A: cylinder buried up to 15 cm deep with 5 cm edge. B: extraction of the cylinder with an undisturbed soil sample. C: cylinder prepared with canvas and mesh in its lower part.

Figure 1. Images of the mesocosm design (experimental units) and construction process, with undisturbed soil at 15 cm depth in PVC cylinders of 18 cm in diameter and 20 cm in height.

Table 1. Organization of treatments to evaluate the effect of macroporosity, soil temperature and soil moisture on the presence of microorganisms.

Macroporosity	Temperature	Moisture
Compacted soil with macroposority <8%	Low temperature 16 - 20 ºC	<20% FC[b]
		FC[a]
		>80% Sat. [c]
	High temperature 36 - 40 ºC	<20% FC[b]
		FC[a]
		>80% Sat. [c]
Well aerated soil with macroporosity >10%	Low temperature 16 - 20 ºC	<20% FC[b]
		FC[a]
		>80% Sat. [c]
	High temperature 36 - 40 ºC	<20% FC[b]
		FC[a]
		>80% Sat. [c]

a: soil moisture at field capacity (FC), b: soil moisture less than 20% of field capacity (<20% FC), c: above 80% of soil saturation (>80% Sat.).

The soil was compacted with a hydraulic press for the treatments with aeration at the limiting level (macroporosity <8%) (Figure 2). The treatments with the non-limiting aeration level (macroporosity> 10%) were left with the natural aeration of the soil without disturbance. During the 21 days of the experiment, to achieve the low temperature (16 – 20 ^{0}C), a room with refrigeration was used, and for the high temperature in another room, the heat was generated with incandescent bulbs to raise the soil temperature (36 – 40 ^{0}C). Thermometers were used for daily monitoring of soil temperature in the experimental units. Distilled water was applied when daily measurements determined it to achieve soil moisture at the three established levels, using a Delta T Devices brand dielectric sensor.

D: preparation of treatments with aeration <8% E: soil temperature monitoring with a Hg thermometer, F: soil moisture monitoring with a dielectric sensor.

Figure 2. Images of the control process of the levels of each factor evaluated.

Soil Physical-chemical characterization.

In order to assess the general conditions offered by the soil to microorganisms in their first 10 cm of depth, the main chemical properties were determined: pH and electrical conductivity in soil/water suspension (1: 1), and the cation exchange capacity by the 1N ammonium acetate method, pH 7 (IGAC, 2006b). In addition, the acid digestion with potassium dichromate oxidation method determined the oxidizable soil organic carbon content (Lozano et al., 2005). Also, the following soil physical properties were measured: texture with the agitation and sedimentation method of modified Bouyoucos, total porosity and aeration pores (macroporosity) using the tension table method with undisturbed samples in metallic cylinders, and the bulk density in the same metallic cylinders of 5 cm in diameter and 5 cm in height, the moisture content at saturation and field capacity was measured in the field with the dielectric sensor, (Pla, 1983; 2010).

Measurement of the presence of soil microorganisms

Considering that the experimental units of undisturbed surface soil without vegetation constitute mesocosms of the soil with the microorganisms that inhabit it (Lubbers et al., 2017), the effect of the macroporosity, the soil temperature, and soil moisture was evaluated in each experimental unit, through indirect measurement of the presence of microorganisms in the soil, through soil microbial biomass (MB) and soil respiration (SR) determinations.

CO_2 emission can measure the presence of microorganisms in the soil due to their respiration. Therefore, at the end of the 21 days of the experiment, an alkali trap was placed in each experimental unit and covered with a hermetic chamber for 24 hours, thus achieving the measurement of soil respiration (SR) according to the static absorption in NaOH method (Anderson, 1982; Lozano et al. 2005).

At the end of the SR measurement, a 200g soil sample from 0 to 10 cm deep was extracted in each experimental unit. These samples were used to measure in the laboratory the carbon of the microbial biomass using the induced respiration method, which is an indirect way of measuring the microbial biomass; as a function of a microbial metabolic response (Dalal, 1998) as a result of adding an easily degradable substrate such as glucose. It is presumed that the respiratory activity of microorganisms is equivalent to the MB present in the soil (Jenkinson and Ladd, 1981; Anderson and Domsch, 1989).

Statistical analysis

The results were tabulated with Microsoft's Excel software to perform the descriptive statistical analysis. Then with the statistical program Minitab18, the statistical assumptions were reviewed, and an analysis of variance was carried out, which allowed interpretation of the relationship of the soil microorganism with the physical conditions: temperature, moisture, and macroporosity.

Results and Discussion

Soil chemical and physical characteristics

In general, the chemical properties analyzed showed the typical condition of a Dystrudept (Table 2), a strongly acid reaction, a low cation exchange capacity, medium organic carbon content, and a non-saline condition (IGAC, 2006b).

Table 2. Chemical characteristics of the surface soil from 0 to 10 cm deep (n=5).

pH	[a] EC, dS m^{-1}	[b] SOC, g kg^{-1}	[c] CEC, $cmol_c$ kg^{-1}
5.07 (±0.21)	0.31(±0.11)	14.0(±0.38)	11.84(±1.91)

a: electric conductivity (EC), b: soil organic carbon (SOC), c: cation exchange capacity (CEC)

The soil physical analysis has revealed (Table 3) that sand is the predominant mineral particle, and the textural class is sandy clay loam. In addition, an ideal bulk density consistent with the textural class (USDA, 1999) is observed as an appropriate total porosity and a favorable macroporosity (aeration pore space), which is interpreted as good physical conditions for the growth of plants and microorganisms (Dexter, 2004; Pla, 2010).

Table 3. Physical characteristics of the surface soil from 0 to 10 cm deep (n = 5).

Sand, g kg^{-1}	Clay, g kg^{-1}	Silt, g kg^{-1}	[a] Bd, Mg m^{-3}	Total Porosity, % v v^{-1}	Macroporosity, % v v^{-1}	[b] Moisture at FC, % v v^{-1}
604.3 (±76.4)	256.5 (±3.57)	139.2 (±5.29)	1.35 (±0.05)	47 (±4.18)	13.93 (±2.79)	29.07 (±5.86)

a: bulk density (Bd), b: field capacity (FC)

Effect of macroporosity, soil temperature and moisture

In order to evaluate the effect of the factors: macroporosity, soil temperate, and soil moisture, we carried out a three-way analysis of variance to the data recorded on MB and SR in the experiment (Table 4), revealing a significant effect of the macroporosity, which indicates that soil aeration pore space influences the quantity of microorganisms in the soil. However, for the SR, the macroporosity had a not significant effect.

Table 4. Statistical effects of soil macroporosity, soil temperature, and soil moisture on microbial biomass and soil respiration (3-way ANOVA with 95% confidence level).

Source of Variance	Microbial Biomass	Soil Respiration
Factor 1: Macroporosity	Significant*	Not significant
Factor 2: Soil Temperature	Not significant	Highly significant***
Factor 3: Soil moisture	Highly significant***	Highly significant***
Factor 1 x Factor 2	Not significant	Not significant
Factor 1 x Factor 3	Significant*	Not significant
Factor 2 x Factor 3	Significant*	Significant*
Factor 1 x Factor 2 x Factor 3	Significant*	Not significant

*p value<0,05 ; ***p value<0,001

It was found that the temperature in the ranges established in the experiment did not significantly affect the MB, suggesting the existence of adaptation mechanisms of microorganisms to changes in soil temperature, as Malcolm et al. (2008) indicated. On the other hand, in our experiment, we observed a highly significant effect of temperature over SR (Table 4), which coincides with Liua et al. (2018), who pointed out that the response of microbial respiration to changes in soil temperature has reported an exponential increase in SR with increasing soil temperature. As expected, a highly significant effect of soil moisture was observed on MB and SR due to the direct influence of soil moisture on the survival of microorganisms (Iglesias, 2008; Wang et al., 2019). Either excessively dry or wet soil conditions decrease the MB, by creating stress on most aerobic bacteria and fungi (Borowik and Wyszkowska, 2016).

When evaluating the effect of double or triple interactions of the studied factors over MB, we found significant effects for three interactions, which show that the response of microorganisms is due to possible adaptations of microbial physiology, as well as interactions with surface processes and environmental factors such as temperature (Schindlbacher et al., 2011). However, the interaction of soil temperature and soil moisture was the only one with a significant effect on the SR.

It was observed that the MB is significantly lower in the compacted soil with macroporosity <8% (Table 5), confirming that soil microbial presence depends on the pore structure and soil compaction conditions (Moráis-Lima do Nascimento et al., 2016). The variation in soil temperature from 16 ^{0}C to 40 ^{0}C did not cause a significant difference in the total amount of microorganisms present in the soil (MB). However, it did generate a significant difference in their activity, with high temperatures generating a significant increase in SR. Soil moisture is a very influential factor in soil microorganisms (Table 5). MB and SR are significantly lower when the soil has less moisture.

Table 5. Microbial biomass and soil respiration according to each factor after 21 days of experiment in the soil mesocosms with microorganisms.

Variable /Factor	Macoporosity		Soil Temperature		Soil moisture		
	<8%	>10%	16 – 20 ^{0}C	36 - 40 ^{0}C	<20% FC	FC	>80% Sat
	n= 18	n= 18	n= 18	n= 18	n= 12	n= 12	n= 12
Microbial Biomass	50.64 a^x	66.70 b	62.70	54.64	25.37 a	77.11 b	73.54 b
(mg C kg^{-1})	(±34.78)	(±28.29)	(±34.60)	(±30.25)	(±14.09)	(±16.82)	(±31.84)
Soil respiration	168.40	212.20	106.79 a	273.77 b	90.86 a	223.82b	256.16 b
(mg CO_2 m^{-2} h^{-1})	(±150.80)	(±143.40)	(±81.70)	(±151.30)	(±44.10)	(±173.70)	(±140.10)

x: comparison of means was made by Fisher LSD (95%); different letters indicate a significant difference at p<0,05.

Discussion

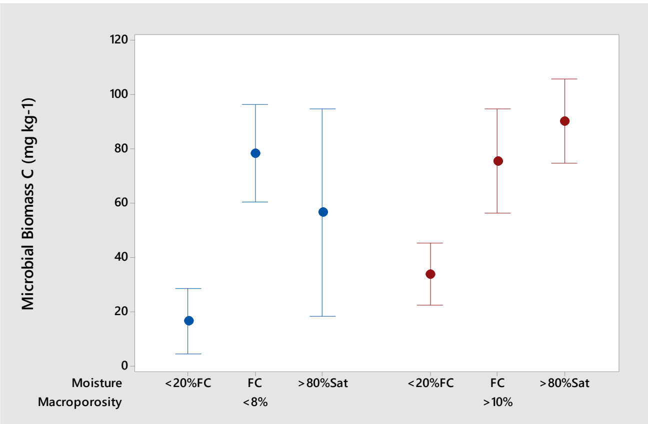
In agreement with other studies (Frey et al., 2009), reduced soil macroporosity can cause a decrease in MB due to O_2 depletion by aerobic microorganisms and CO_2 increase in the soil atmosphere. Nevertheless, the CO_2 evolved seems to stay trapped in the compacted soil since we found an insignificant effect of macroporosity on the SR. It may also correspond with the anaerobic respiration in compacted soils (Liu et al., 2018). So, the relationships between soil compaction and the growth characteristics of microorganisms are complex (Cui and Holden, 2015).

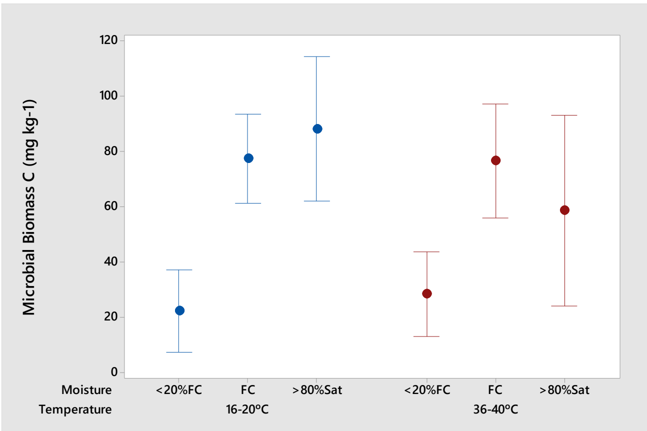
Similar interpretation was made by Ishak et al. (2016), who found that soils with low compaction contain more soil pores predominated with macropores that enhance soil capacity to retain soil water and provide soil oxygen diffusion, thereby increasing soil respiration. But in the compacted soils low microbial activity was observed, which is presumably because at higher levels of compaction and high moisture content, water is taking up all available pore space and creating anaerobic conditions.

Based on Luia et al. (2018) approach, the hypothesis is that the acclimatization or adaptation to different climates by soil microorganisms determines their growth and respiration response to temperature. Therefore, the optimum temperature should be positively correlated with ambient temperature. The study site presents maximum air temperatures of up to 35ºC as the annual average, so this may be the reason why our results show that the variability in temperature keeps the microbial biomass similar, whereas higher temperatures increase its metabolism, generating more respiration in correspondence with many studies that reported a significant increase of SR when soil temperature ascends (Bárcenas -Moreno et al., 2009; Lipson et al., 2009).

Regarding the interaction of macroporosity and moisture on soil microorganisms (Figure 3), we observed that when aeration is limiting (macroporosity <8%), there is a greater MB with the soil moisture at field capacity (FC). On the other hand, if the soil aeration is satisfactory (macroporosity >10%), there is a higher MB when the soil moisture is near saturation. The air-water ratio in soil explains it. In other words, when a limitation on soil aeration appears, microorganisms are affected in their survival in conditions of moisture close to saturation, but if the soil aeration is high, they can thrive in water excess.

Regarding the interaction of temperature and soil moisture on the soil MB (Figure 4), we observe that when the temperature is low, there is a higher MB with soil moisture near saturation, and when the temperature is high, there is a higher MB with the moisture at field capacity (FC). To understand this, we must consider that the temperature may influence the renewal of soil air because the air expansion within the pore space and the tendency of warm air to move upward may boost some air exchange between soil and atmosphere (Jury and Horton, 2004). In addition, besides soil, water affects aeration, so aerobic activity decreases as soil becomes wetter and eventually saturated due to restricted O_2 diffusion (Voroney and Heck, 2015). On the other hand, the thermal properties of water must be involved in boosting MB at cold soil temperature with water content near saturation.





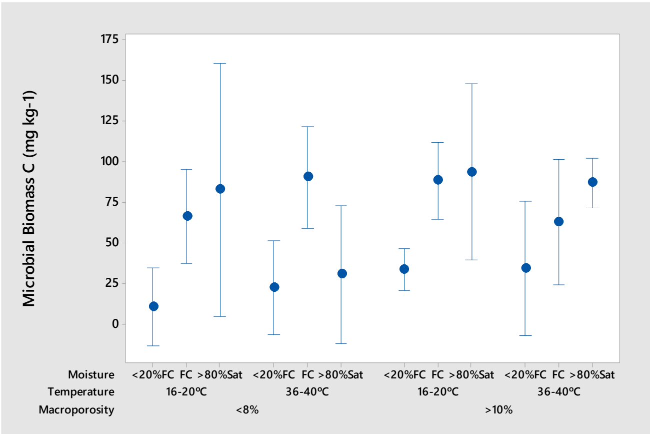
FC: field capacity, Sat: saturation. Intervals are the standard deviation.

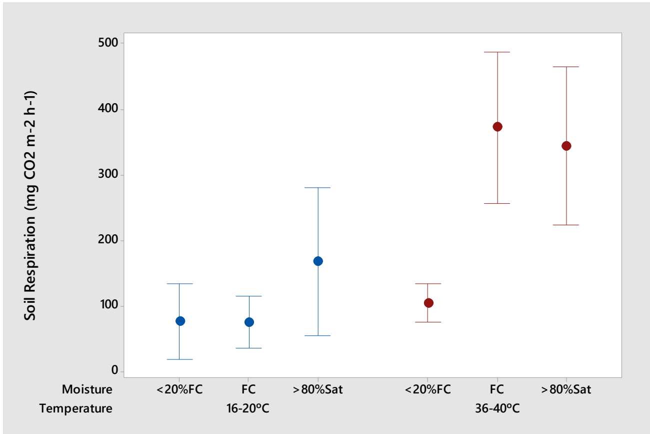
Figure 3. Effect of the interaction between macroporosity and soil moisture on microbial biomass after 21 days of experiment in the soil mesocosms with microorganisms.

Figure 4. Effect of soil moisture and temperature interaction on microbial biomass after 21 days of experiment in the soil mesocosms with microorganisms.

The analysis of the effect of the triple interaction of factors (Figure 5) allowed the finding that the combination of factors that favored the highest total MB is when the soil has high macroporosity, low temperature, and soil moisture from field capacity to saturation. Demonstrating that a higher macroporosity is necessary for suitable moisture conditions to allow aeration; therefore increasing the availability of O_2 for microorganisms (Dexter, 2004; Voroney and Heck, 2015). While the most limiting condition for the soil MB is limiting aeration with dry soil in any temperature condition.

For the interaction of soil temperature and soil moisture on SR (Figure 6), it was found that the highest SR occurred when the soil temperature was high and the soil moisture was ideal or near saturation. It expresses that these conditions accelerated the microbial activity of soil. In contrast, low temperature with moisture at field capacity or dry soil is the most limiting condition for the microbial activity of the soil and generates an SR decrease.





FC: field capacity, Sat: saturation. Intervals are the standard deviation

Figure 5. Effect of the triple interaction of factors on microbial biomass after 21 days of experiment in the soil mesocosms with microorganisms

Figure 6. Effect of soil moisture and temperature interaction on soil respiration after 21 days of experiment in the soil mesocosms with microorganisms

In the experiment, it was observed that water content had a highly significant effect on the MB and SR, which indicates that soil water content is decisive for the soil microorganism's survival. Field capacity or a condition near saturation appears to be suitable for microorganisms, coinciding with the various studies that have indicated this (Harris, 1981; Barros et al., 1995; Prado and Airoldi, 1999; Chen et al., 2007). However, the marked effect of the scarcity of soil water on microorganism's survival found in this study is also due to the absence of growing plants since these, through their exudates, can help in the survival of microorganisms (Chen et al., 2007).

The temperature significantly affects SR, but on MB, the effect of temperature is conditioned by the soil water content. It implies that temperature alone does not alter the presence of microorganisms in this soil but indeed increases their activity level, which has also been reported in other studies (Barcenas-Moreno et al., 2009; Vimal et al., 2017; Liu et al., 2018). It is imperative to highlight that soil moisture deficit seriously affects microorganisms at temperatures above 36ºC. Therefore, in high temperatures conditions ideal water content in soil is necessary to promote MB.

Conclusion

This study confirms the need to bear in mind the distribution of soil's pore space, the state of water content and temperature, to favor the survival of soil microorganisms. The microorganisms present in the studied soil have a wide range of thermal adaptation, and the increase in soil temperature is confirmed as a factor that intensifies the activity of soil microorganisms. In turn, it was observed that the microorganisms present are significantly sensitive to the moisture deficit in soil.

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