CENTRO DE INVESTIGACIÓN Y DE ESTUDIOS AVANZADOS
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DEPARTAMENTO DE BIOTECNOLOGÍA Y BIOINGENIERÍA

"Análisis del efecto de diferentes prácticas agrícolas sobre la población microbiana".

Tesis que presenta:

M. en C. Laurette Shona Learita Prince

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Dr. Luc Dendooven

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"Analysis of effect of different agricultural practices on microbial populations".

Doctoral thesis by:

Laurette Shona Learita Prince

FOR THE DEGREE OF DOCTOR OF SCIENCE

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Advisors:

Dr. Luc Dendooven

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Resumen

La agricultura en el Valle del Yaqui, Sonora depende principalmente del riego ya que es una región árida con escasas lluvias. Es indispensable implementar prácticas agrícolas que permitan el uso eficiente del agua en estos agroecosistemas. El objetivo del presente trabajo fue evaluar el efecto de combinar diferentes métodos de siembra (suelo húmedo y seco) con las diferentes prácticas agrícolas (convencional y de conservación) sobre la estructura de la comunidad bacteriana presente en los suelos del campo experimental Norman E. Borlaug (CENEB).

Las colectas de suelos se realizaron en cuatro tiempos después de la siembra del trigo, las parcelas estuvieron sometidas a diferentes prácticas agrícolas (convencional y de conservación) y diferentes tipos de siembra (húmedo y seco). Las muestras de suelo se mantuvieron en bolsas selladas hasta el momento de su análisis. En el laboratorio se realizó la caracterización fisicoquímica de los suelos y extracción de DNA metagenómico. Se evaluó la estructura de las comunidades bacterianas en las diferentes muestras mediante la secuenciación del gen 16S rRNA usando la plataforma Illumina Miseq.

El contenido de agua y la conductividad electrolítica fueron significativamente afectados por la practica agrícola y el tipo de siembra a través del tiempo. Los filos abundantes fueron Proteobacteria, Acidobacteria y Actinobacteria y *Steroidobacter*, *Bacillus, Kaistobacter*, *Flavisolibacter*, *Acinetobacter* y *Rubrobacter* fueron los géneros abundantes en este estudio. La estructura de la comunidad bacteriana estuvo afectada por el contenido de agua en las muestras de suelo. *Streptomyces* y *Balneimonas* fueron abundantes en los suelos con siembra en seco, *Streptomyces* fue abundante en las muestras con labranza convencional y *Balneimonas* fue abundante en las muestras con práctica de conservación. *Acinetobacte*r fue el grupo abundante en suelos con siembra en húmedo y agricultura de conservación. Actinobacteria, Nitrospirae, *Rhodoplanes* y [Thermi] fueron abundantes en suelos bajo agricultura de conservación y siembra en suelo húmedo, y *Cellvibrio*, *Flavisolibacter*, *Pontibacter* y Proteobacteria fueron los grupos abundantes en suelos con práctica agrícola convencional. El índice de Shannon demuestra mayor diversidad de especies en suelos con práctica convencional que en suelos con prácticas de conservación. El contenido de agua en el suelo fue el principal factor que determinó la estructura de la comunidad bacteriana. El efecto del contenido de agua en el suelo no fue evidente a nivel de filo sin embargo el efecto es evidente a cuando se analiza la población bacteriana a nivel de género.

Abstract

Agriculture in the Yaqui Valley, Sonora relies heavily on irrigation as it is an arid region characterized by limited rainfall. It is essential to implement agricultural practices that maximize water use efficiency in these agroecosystems. The aim of this study was to identify the effect of combining dry and wet sowing irrigation methods with contrasting tillage practices (conventional practices and conservation agriculture) on bacterial community structure in soils from the Norman E. Borlaug experimental field (CENEB).

Soil samples were collected on four occasions after wheat was sown in permanent and conventionally tilled beds under wet and dry sowing at CENEB. Soils were characterized and the bacterial communities were identified with Illumina MiSeq sequencing where the 16S rRNA gene was targeted.

Water content and electrolytic conductivity were significantly affected by the tillage and sowing practices over time. The most abundant phyla in this study were Proteobacteria, Acidobacteria and Actinobacteria. Meanwhile, *Steroidobacter*, *Bacillus*, *Kaistobacter*, *Flavisolibacter*, *Acinetobacter* and *Rubrobacter* were the most abundant genera identified in this study. The bacterial community structure was affected by soil water content. *Streptomyces* and *Balneimonas* were enriched in dry sowed soil, the first in conventionally tilled beds and the latter in permanent beds, while *Acinetobacter* in wet sowed soil under conservation agriculture. Actinobacteria, Nitrospirae, *Rhodoplanes* and [Thermi] were enriched in soil under conservation agriculture in wet sowed soil, and *Cellvibrio*, *Flavisolibacter*, *Pontibacter* and Proteobacteria in soil under conventional tillage practices. Shannon index indicated that there was a high species diversity in both conventional practices and conservation agriculture.

Soil water content was the principal factor shaping the bacterial community structure. While the three most dominant phyla were affected by the difference in water content in the tillage practices under dry and wet sowing, it was at the genera level that these fluctuations were more obvious.

1. Introduction

1.1. Importance of agriculture in Mexico

The agricultural sector plays an important role in the socioeconomic growth and development of any country (Meijerink and Roza 2007; Bezemer and Headey 2008; FAO 2013):

- It provides nourishment for humans and livestock
- It generates employment
- It contributes to the national revenue
- It stimulates international trade and foreign exchange
- It is the main source of raw material for major industries
- It is a key element to ensure food security in a country

Mexico is known for its great biodiversity and produces close to 200 agricultural goods on approximately 22.1 million hectares of land (Seminis 2018). In 2018, the agricultural sector generated almost 4% of the Gross Domestic Product in the country and created over 6 million jobs (SFA, SAGARPA 2011; SAGARPA, SIAP 2018; World Bank 2019). Mexico ranked 13th worldwide in crop production and is a major exporter of cucumbers, tomatoes, avocados, lemons and peppers; while crops such as oats, corn, sorghum, wheat and chrysanthemum are produced on a large scale, nationally (SAGARPA, SIAP, 2018).

Wheat (*Triticum* sp.) is one of the most consumed grains worldwide, close to 60% is used for human consumption (OCDE 2011). It therefore plays an important role in food security, as it is an affordable source of protein and carbohydrates (Balkovič et al. 2014). Wheat is the second most produced grain in the world and the third most important grain in Mexico (OCDE 2011). The leading wheat producing states are Sonora, Baja California, Guanajuato, Sinaloa, Michoacán, Chihuahua, Zacatecas and Tlaxcala, accounting for almost 90% of the national wheat production of which approximately 50% is grown in the state of Sonora (FIRA 2015; SIAP 2016). The Yaqui Valley is a major wheat belt in Sonora. The region is characterized by an arid climate, so wheat cultivation heavily relies on irrigation (Verhulst et al. 2011; Márquez et al. 2014; Mondani et al. 2019). With the increasing water scarcity in the region, improving

the efficiency of irrigation water use in agricultural systems is a necessary precaution to mitigate the situation. It is of utmost importance to adopt more sustainable agricultural and sowing practices in the Yaqui Valley to maximize the performance of the irrigation systems and enhance the response of crops to water application, ultimately improving soil quality in the region.

1.2. The role of soil in agriculture

Soil is a major component of the biosphere and is vital for crop production (Doran and Zeiss 2000). Soil quality is a critical element for agricultural development since it promotes the health of flora and fauna (Doran and Parkin 1994). The Soil Science Society of America (SSSA) defined soil quality as the ability of a soil to function whether it is within the boundaries of a natural or managed ecosystem, which suggests that the main functions of a healthy soil are (Karlen et al. 1997):

- To sustain biological activity, diversity and productivity
- To regulate the flow of water and solutes
- To filter, buffer, degrade, immobilize and, detoxify organic and inorganic compounds of natural and anthropogenic origin
- To store and recycle nutrients and other elements in the ecosystem

Soil quality, i.e. the ability of a soil to function, can be monitored through physical, chemical and biological properties in a soil (Shukla et al. 2006). Soil properties such as texture, water holding capacity, infiltration rate, root depth, pH, total nitrogen, electrolytic conductivity, nutrients availability, organic carbon, the amount of extractable nitrogen, phosphorous and potassium, can serve as indicators for soil quality assessment (Wienhold et al. 2004; Gil-Sotres et al. 2005; Laishram et al. 2011).

1.2.1. Negative impacts of agriculture on soil

Agriculture may have direct and indirect effects on soil quality; the extent of which depend on climate, terrain, soil type (mother rock), agricultural practices and the size of the terrain (Zalidis et al. 2002). For instance, conventional tillage practices, which rely heavily on soil tillage, prompt soil alteration due to the use of heavy machinery causing compaction, and the excessive use of fertilizers and pesticides (Thierfelder and Wall 2009; Wang et al. 2018). Likewise, other factors such as erosion, atmospheric pollution, and salinization cause deterioration of soil quality (Wienhold et al. 2004). Over time, alteration of agricultural soils leads to degradation, consequently leading to loss of organic matter and, crop and microbial diversity (Yin et al. 2010; Homburg and Sandor 2011; Sun et al. 2015).

1.3. Importance of soil microorganisms in agriculture

The rhizosphere is the narrow zone of soil rich in both organic and inorganic nutrients where microorganisms such as bacteria, fungi, archaea, protozoa, nematodes, algae and micro-arthropods interact with plant roots (Philippot et al. 2013; Garcia and Kao-Kniffin 2018). Since microbes actively participate in C, N, P and S biochemical cycles, factors such as the quantity, diversity and activity of microbial biomass can serve as indicators of soil quality (Gil-Sotres et al. 2005).

Root-associated microorganisms, such as endomycorrhizal and ectomycorrhizal fungi, nitrogen fixing bacteria and plant growth promoting rhizobacteria (PGPR) are beneficial to plants, and play an important role in sustaining soil ecosystem as the following (Raaijmakers et al. 2007; Zhao et al. 2014):

- Recycling of nutrients in soil
- Transformation of C, N, P and S
- Degradation of xenobiotic organic compounds and immobilization of heavy metals
- Forming and maintain soil structure
- Improving soil drainage and aeration
- Control of plant pests and pathogens

From an agronomic standpoint, the symbiotic relationship between microbial biomass and plants represents higher crop yield and lower production costs (Huang et al. 2014). Plant-microorganism relationships increase plant growth rates, make plants more tolerant to both biotic and abiotic stress and enhance plant resistance against diseases (Bakker et al. 2015).

Not all rhizosphere microorganisms are beneficial to plants, some are pathogens, the most common belonging to fungi, nematodes and oomycetes, such as *Rhizoctonia solani*, *Thielaviopsis basicola*, *Pratylechus penetrans*, *Fusarium solani* f. sp. *phaseoli*, *Pythium ultimum*, *Plasmodiophora brassicae*, *Plasmopara halstedii*, etc. (Raaijmakers et al. 2007; Bálint et al. 2014).

Pathogens cause deleterious effects on plants such as stunted growth, root discoloration, wilting, necrosis and distortion of leaves and roots (Schippers et al. 1987). For example, the fungus *Cochliobolus sativu*s causes root rot in cereals like wheat and barley (Mathre et al. 1999).

1.4. Conservation agriculture (CA)

Conservation agriculture is a farming system based on three principles (Govaerts et al. 2009a; Hobbs et al. 2008):

1. Little to no tillage
2. Permanent crop cover
3. Crop rotations (species diversification)

Conservation agriculture improves soil quality as the three techniques minimize soil disturbances, lessen both wind and water erosion, by reducing water runoff and improving water infiltration, and increase microbial activity due to increased soil biomass availability, which ultimately increases the carbon and nitrogen available to plants (Hobbs 2007; Kassam et al. 2009; Berger et al. 2010; Hossain 2013; Habig and Swanepoel 2015). The CA technologies contribute to fuel saving, increased levels of organic matter improving aggregate stability and soil structure, stimulation of carbon fixation, and decreased carbon dioxide emission to the atmosphere (Wall, 2007; Stagnari et al. 2009; Thierfelder et al.

2015; Mafongoya et al. 2016). A major advantage of CA is that it increases water-use efficiency, which is crucial in arid and semi-arid regions where there is water shortage (Hobbs 2007; Li et al. 2011). Soils under CA maintain a more stable temperature and retain moisture since crop residue left on the surface helps to reduce evaporation (Thierfelder and Wall 2009; Erenstein et al. 2012).

1.4.1. Conventional tillage practices vs CA: their impact on agricultural soil

Tillage practices can have a profound effect on soil characteristics and these differences can alter soil microbial community structure (Zhu et al. 2018). For instance, removal of crop residues depletes soil organic matter reducing the amount of C substrate available for soil microorganisms (Shokati and Ahangar 2014). Leaving crop residues in the field and incorporating them in soil brings organic material in direct contact with microorganisms, providing them with C substrate thus accelerating mineralization (Luo et al. 2010). Tillage to incorporate organic material breaks up soil aggregates liberating organic material that favors the growth of copiotrophs, but in the long term depletes soil organic matter (Luo et al. 2010; Wang et al. 2016). Leaving crop residue on the soil surface prevents soil erosion and favors water infiltration but limits availability of organic material in the short term as incorporation of organic material will depend principally on macrofauna activity (Anderson et al. 2017). The lack of organic material affects soil microorganisms directly. Indirectly, the lack of soil organic material alters water content, temperature, gas diffusion and soil structure which are all known to affect soil microorganisms (Kaisermann et al. 2013).

1.5. Importance of water in agriculture

Water is one of the most abundant natural resources on the planet covering 71% of the earth's surface, but unfortunately, only 1.72% of this is available as fresh water for human activities (USGS 2016). Globally, around 70% of the total fresh water is allocated to agriculture (FAO 2017). In Mexico, 77% of fresh water, extracted from aquifers and rivers, is used for agricultural purposes (CONAGUA 2015).

The agricultural sector is a major source of water pollution; agricultural activities cause pollutants such as nitrates, phosphorous, pesticides, sediments, salts, and pathogens to end up in aquifers and major bodies of water (Mateo-Sagasta et al. 2017). The extent of pollution heavily depends on the type of soil and crops grown, the climatic conditions in the region and the agricultural practices employed (Parris 2011).

To address the growing demand for water in agriculture, it is necessary to implement practices that can (FAO 2017):

- Reduce water losses
- Increase water use efficiency
- Increase water productivity

The International Maize and Wheat Improvement Center (CIMMYT, acronym in Spanish) has been experimenting with different agricultural practices to improve yields while maintaining sustainability of the agroecosystems and improving water use efficiency (Sayre and Hobbs 2004; Govaerts et al. 2006; Hobbs et al. 2008; Verhulst et al. 2012). Conservation agriculture is a sustainable agricultural system that not only promotes crop intensification and reduction of production costs but also encourages soil and water conservation (Hobbs 2007; Knowler and Bradshaw 2007; Li et al. 2011; Verhulst et al. 2011).

1.5.1. Drying and rewetting: effect on soil microbial activity

Semi-arid and arid regions are prone to long dry spells with noticeable fluctuations in precipitation during the year (Bailey 1979). Soils in these regions experience sudden changes in moisture contents, which are attributed to irregular rain fall and high evapotranspiration (Fierer and Schimel 2003). Studies have shown that these drying and rewetting events liberate soil organic material, increase microbial activity, and alter soil structure (Denej et al. 2001). The sudden increase in respiration, often referred to as the "Birch effect", alters the nutrient content, e.g. N and P, in soil (Birch 1958; Gordon et al. 2008; Xiang et al. 2008; Thomson et al. 2010). Soil drying has a negative impact on matric and osmotic potential limiting the amount of water available to soil microorganisms (Mavi and Marschner 2012).

This can dehydrate microorganisms resulting from the accumulation of solutes, such as amino acids, carbohydrates and polyols and in extreme cases microbial activity may come to a halt (Kieft et al. 1987; De Nobili et al. 2006; Borken and Matzner 2009; Muhr et al. 2010). Some microorganisms can withstand soil drying by forming endospores and cysts and some bacterial and fungal hyphae are able to survive desiccation by secreting mucilage (De Nobili et al. 2006; Borken and Matzner 2009). Rewetting a dry soil increases water potential, which can cause one of the following responses in microbial biomass (Kieft et al. 1987):

- Cell lysis as a result of the high turgidity
- Elimination of intracellular solutes, as carbon dioxide, by catabolism
- Elimination of intracellular solutes via active or passive transport

Two theories have been proposed to explain the changes brought about by wetting pulses: (1) upon rewetting dry soil, organic matter that was previously unavailable to microorganisms becomes accessible and is mineralized by them; and (2) rewetting dry soil causes a change in the osmotic potential which can lead to microbial cell lysis or/and a release of osmolytes, and hence an increase in substrates available to microorganisms (Fierer and Schimel 2002; Borken and Matzner 2009; Göransson et al. 2013).

1.6. Antecedent of the present study

Researchers at CIMMYT's Norman E. Borlaug experimental station (CENEB, acronym in Spanish), collaborate with farmers in Yaqui Valley to find sustainable ways of improving crop yield and increasing water productivity. Mulvaney et al. (2014) published a work where they compared two sowing/irrigation methods: wet and dry sowing. Wheat growers in the region traditionally use wet sowing, which involves applying a pre-seeding irrigation to the field two to three weeks prior to sowing. In doing so, farmers can remove the first generation of weeds before sowing wheat seeds (Govaerts et al., 2009b). Diversely, dry sowing involves sowing wheat seeds a day or two before irrigating the field. This provides more moisture in the soil for seeds to germinate.

The field experiment consisted of a summer maize-winter wheat rotation grown in a permanent bed system under dry and wet sowing practices. Four seed treatments were applied in the field experiment: a control with no chemicals added; two comprising fungicides mixtures (carboxin + thiram + chlorothalonil and difenoconazole + mefenoxam); a mixture of two fungicides and an insecticide (difenoconazole + mefenoxam + thiamethoxam).

It was observed that seeds germinated under wet sowing regardless of seed treatment. Meanwhile under dry sowing, seeds treated with fungicides generally had a higher rate of germination and emergence than the control. The group suggested that the fungicides used in the seed treatments suppressed a soil pathogen that was only active in dry sowed soil. They also suggested that the extended moist conditions before seeds were planted under wet sowing may have favored beneficial bacteria that would have competed with pathogens present in the wet sowed soil.

2. Justification

Given the water shortage in the Yaqui Valley, it is important to implement agricultural practices that minimize the use of this resource. Combining dry sowing, a method of seed sowing that improves irrigation water use efficiency, with conservation agriculture techniques can offer a viable means to combatting problems related to water scarcity in the valley. However, more knowledge is required to better understand how bacterial community is impacted by dry sowing.

3. Hypothesis

The microbial population in an arid soil used for agriculture will be modified by the application of dry and wet sowing methods, both under conventional tillage practices and conservation agriculture.

4. General objective

To evaluate the effect of dry and wet seed sowing and the different tillage practices under conventional tillage practices and conservation agriculture on soil microbial communities.

4.1. Specific objectives

- To describe the bacterial relative abundance in the soil samples under the two agricultural and irrigation practices.
- To evaluate the changes in bacterial community structure in the soil samples due to the two agricultural and irrigation practices.
- To correlate the physicochemical properties with the bacterial population in the soil samples.
- To determine changes in microbial alpha diversity in the soil samples under the two agricultural and irrigation practices.

5. Materials and methods

5.1. Description of the experimental site

Soil samples were collected at CENEB located in The Yaqui Valley (Lat. 27.33˚ N, long. 109.09˚ W, 38 masl), near Ciudad Obregon in the state of Sonora, Mexico (Mulvaney et al. 2014). The climate at the experimental station is characterized by arid conditions with a mean average temperature of 24.7 ˚C and average rainfall of 384 mm between 1971 to 2000 (Verhulst et al. 2011). According to the World Reference Base Classification System, the soil type at the station is Hyposodic Vertisol (IUSS Working Group WRB 2015).

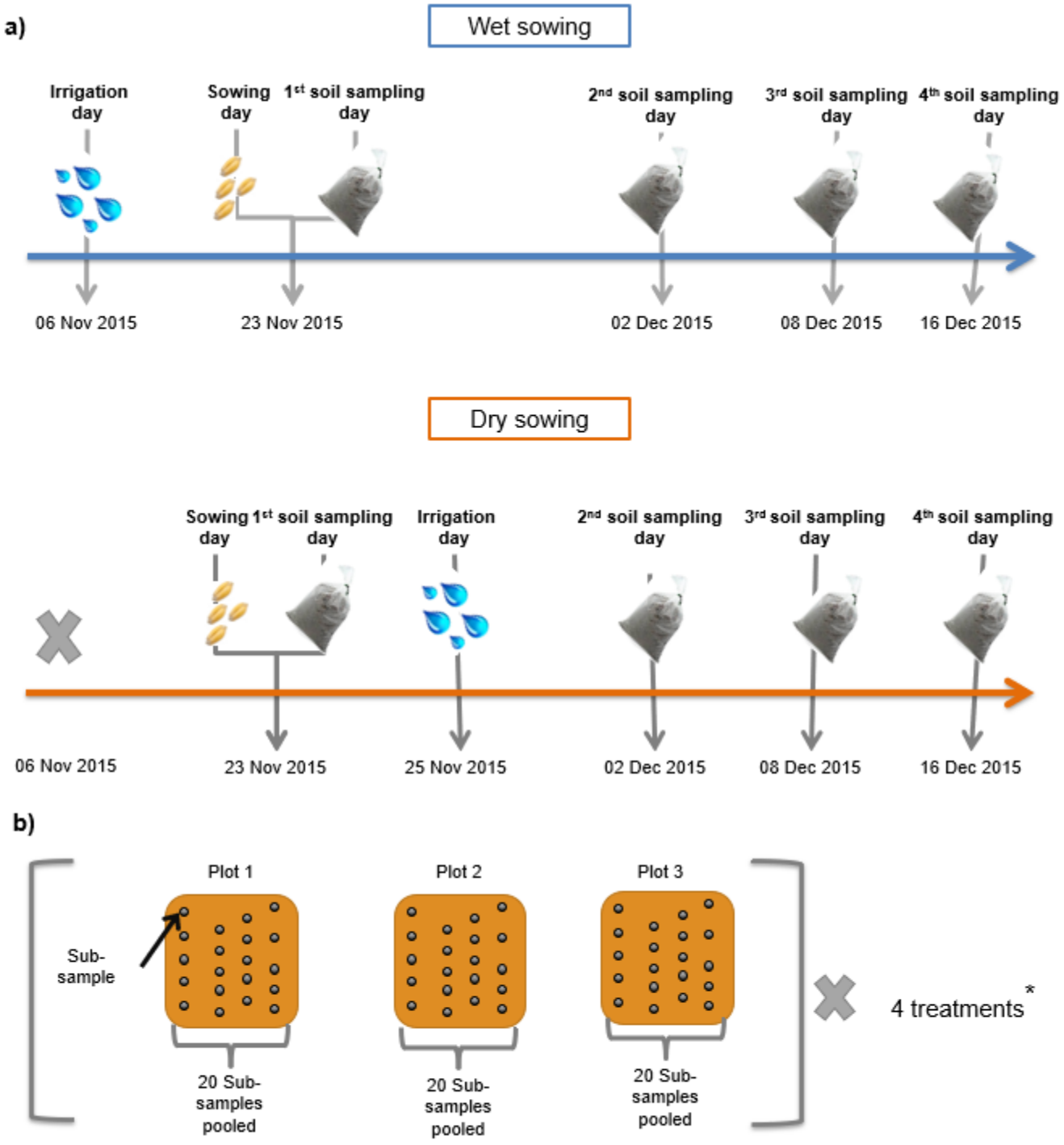
5.2. Field experiment and soil sampling

The field experiment commenced in the winter of 2007-2008 with a maize (*Zea mays*)-durum wheat (*Triticum durum*) rotation. Maize was grown in the summer and wheat in the winter. The experiment was comprised of two tillage treatments: permanents beds (PB) for soils under conservation agriculture, where only the furrows were reshaped each season but the soil on top of the beds was not tilled, and conventionally tilled beds (CB) that were tilled and remade each season. Crop residues were left on the soil surface in PB and incorporated by tillage in CB. The tillage treatments were implemented in 1996 and were divided in treatments with dry and wet sowing.

Sampling for this study was done in 2015. The sub-plot selected for this study had a N management treatment where 240 kg urea-N ha^{-1} was applied on two occasions, 30% at pre-planting and 70% at first node. The sub-plot was divided into four treatments (n = 4): two PB and CB plots each with a wet and dry sowing practice, with three plot replicates. Each plot included four raised beds measuring 0.75 m wide and 10 m long (total plot size 30 m^2), with two wheat rows sown on each bed 24 cm apart.

In wet sowing practice, PB and CB plots were first irrigated on November 6, 2015 and wheat cultivar CIRNO C2008 was sown on November 23 (Figure 1). In dry sowed soil, wheat cultivar CIRNO C2008 was also sown on November 23 and the PB and CB plots were irrigated on November 25.

Soil was sampled from twelve plots comprising two PB and CB treatments with dry and wet sowing practices (n = 2) in triplicate (n = 12). Sampling was done on four occasions: November 23, December 2, 8 and 16 of 2015. Bulk soil, 0-7 cm top layer, was randomly taken from 10 sampling points from the 12 plots and pooled separately so that 12 soil samples of approximately 1 kg were collected on each sampling day. Altogether, 48 samples were obtained, which were air dried before being transported to the Laboratory of Ecology (Cinvestav, Mexico City). Each soil sample was divided into subsamples for physicochemical characterization and DNA extraction, as described below. Subsamples for characterization were stored at room temperature until analyses while those for extraction were kept in refrigeration at -20 °C.



Treatments: Dry sowing, Wet Sowing, Conservation Agriculture, Conventional Tillage Practices.

Figure 1. Irrigation, seed sowing and soil sampling procedures at CENEB, Yaqui Valley.

Seven physicochemical properties were analyzed in each soil subsample: pH, soil water content (WC), electrolytic conductivity (EC), water holding capacity (WHC), soil texture, total organic carbon (TOC) and total nitrogen (TN). The pH was determined in a soil-water suspension using a glass electrode Thomas 1996). Soil water content was determined by the filter-paper method (Fawcett and Collis-George 1967). The saturated soil-paste extract method described by Rhoades et al. (1989) was used to estimate EC of soil samples. Determination of WHC was done using the method described by Cassel and Nielsen (1986). Soil texture was measured utilizing the hydrometer method (Bouyoucos 1962). The Tiessen and Moir (1993) dry oxidation method was followed to measure total organic carbon. The Kjeldahl acid digestion was used to determine TN (Bremner 1996).

5.3. Metagenomic DNA extraction, 16S rRNA gene amplification and Illumina library preparation

Organic material was removed from 0.5 g of each soil sample before DNA extraction following the steps (modified to suit the soil in this study) described by Ceja-Navarro et al. (2010). Soil was added to a 15 mL Falcon™ centrifuge tube containing 10 mL 0.15 M sodium pyrophosphate solution. The contents of the centrifuge tube were shaken for 1 min, left to stand for 10 min, then centrifuged at 6500 rpm for 15 min, after which the supernatant was decanted. Washing was repeated three times. Excess sodium pyrophosphate solution was removed from sedimented soil by adding 10 mL 0.15 M phosphate buffer. The same washing techniques mentioned above were used and were done twice.

Three methods of DNA extraction were used: a combined chemical and thermal shock (freezing to -40 ˚C then thawing to 65 ˚C) lysis described by Valenzuela-Encinas et al. (2008); a chemical lysis utilizing a solution of detergents explained in detail by Hoffman and Winston (1987), and a combined enzymatic and thermal shock (heating from room temperature to 80 ˚C) lysis reported by Sambrook and Russel (2001). A mechanical lysis with sterilized sand, using the FastPrep-24TM 5G instrument, was done in all three methods of extraction to obtain the final supernatant. Proteins and other impurities were removed by a chloroform:isoamyl alcohol extraction, followed by DNA precipitation using Polyethylene Glycol (PEG).

Three centrifuge tubes with washed soil were used in each extraction method, so that 1.5 g of each soil sample was used for each method. Each extraction method was done thrice for each sample, hence, a total of 4.5 g per soil sample was used per extraction method. In all, 13.5 g of each sample (n = 12) was used to extract DNA for each sampling day (n = 4).

Agarose gel electrophoresis was done to evaluate the quality of the extracted DNA from the three methods. Agarose gel, 0.8%, were prepared by mixing agarose with running buffer TAE. SYBR™ Gold was used as the loading dye. The gels were run at 75V for 35 min. The DNA bands were observed in

the MiniBis Pro gel documentation system. After the quality was approved, DNA extracted by the three different methods were pooled by sample for amplification.

For the amplification of the 16S rRNA gene, the following overhang adapters and their sequence-specific primers were used for the variable V3 and V4 regions (Klindworth et al. 2013): forward (5'-TCGTCGGCAGCGTCAGATGTGTATAAGAGACAG-3') and reverse (5'-GTCTCGTGGGCTCGGAGATGTGTATAAGAGACAG-3'). The first round PCR cycles were run under the conditions indicated by Navarro-Noya et al. (2013). The PCR products were detected by electrophoresis on 1.5 % agarose gel. For each sample, 4 amplicons between 500-600 bp were pooled and purified using the Ultra Clean PCR Clean-up kit (MO BIO Laboratories, Ca) as recommended by the manufacturer. To construct each library, a unique pair of index primers was in the second round of PCR. A total of 6 PCR products were pooled per library, tested for quality by reviewing amplicon size, purified and quantified. Purification was done as described above. The purified amplicons were quantified in a NanoDrop™ 3300 (Thermo Scientific NanoDrop) using Quant-iT™ PicoGreen® dsDNA (Invitrogen, Carlsbad, USA), then normalized by pooling purified amplicons in equimolar concentrations of each sample and the final concentration was determined. The libraries were subsequently sequenced on the Illumina MiSeq system by Macrogen, Inc. (DNA Sequencing Service, Seoul, Korea).

5.4. Bioinformatic analysis

5.4.1. Sequence analysis

Sequence quality was assessed with FastQC version 0.11.6 (Andrew et al. 2010). The QIIME pipeline version 1.9.1 was used to process the trimmed bacterial sequences (Caporaso et al. 2010b). Reads with a Phred score < 19 were eliminated from demultiplexed and filtered sequences. A similarity threshold of 97% was applied to generate operational taxonomic units (OTU_{97}) clusters. This was done using the Uclust algorithm to run open reference OTU picking pipeline to compare reads against Greengenes

v13_8 database (Edgar 2010). The representative sequence for each OTU_{97} was aligned with Python nearest alignment space termination (PyNAST) version 1.2.2 at an identity threshold of > 75% and the rest were removed (Caporaso et al. 2010a). The taxonomic composition was assigned with ribosomal database project using the naïve Bayesian rRNA classifier (http://edp.cme.msu.edu/classifier/classifier.jps) for a representative set of sequences selected for each OTU97 (Wang et al. 2007). Biological observations matrices (BIOM) were constructed with the taxonomic assignments for each sample. Reads were rarefied at 3000 per sample to minimize biases due to the large differences among sample counts (Weiss et al. 2017). Alpha diversity indices were calculated with rarefied BIOM tables (Kuczynski et al. 2011). The raw sequences were deposited in the National Center for Biotechnology Information (NCBI) database Sequence Read Archive (SRA) under BioProject PRJNA542494.

5.4.2. Statistical analysis

The statistical analyses were done in R (R Development Core Team 2013). Spearman's rank correlation coefficient was calculated to evaluate the relationship between the abiotic factors. A two-way ANOVA (t2way test in the WRS2 package "A collection of robust statistical methods" (Mair 2018) was used to determine the interactions effects of the tillage practices (PB and CB) and sowing practices (wet and dry sowing) on soil characteristics. Variations in relative abundance of bacterial phyla and genera were explored with principal component analysis (PCA). Constrained analysis of principal coordinates (CAP) tests were used to explore the effect of tillage and sowing treatments on the bacterial phyla and genera and soil characteristics. The effect of the treatments, tillage, and sowing practices, on bacterial phyla and genera was determined with a permutational multivariate analysis of variance (PERMANOVA) using distance matrices test (adonis, method Bray-Curtis, argument strata). The random forest algorithm was used to assess the effect of the tillage practices and sowing irrigation on soil characteristics, alpha diversity, and bacterial phyla and genera over time (Breiman and Cutler 2018). The PCA, CAP and adonis tests were done with the vegan package (Oksanen et al. 2018). The

corrplot package was used to visualize correlation matrices (Wei and Simko 2017). The heatmaps were constructed with the pheatmap package (Kolde 2018).

6. Results

6.1. Soil physicochemical characteristics

The results obtained for the physicochemical analyses are found in Table 1. Soil texture was determined to be clay and the samples had moderately to strongly alkaline pH, ranging from 8.3 to 8.8 (USDA, NRCS 1998). The t2way test indicated that water content (WC) and total C and N were significantly different between the two (Table 1). A random forest test revealed that EC was significantly affected (Table 2) by tillage (p = 0.008) and sowing practices (p = 0.007). Soil moisture content and pH did not show significant changes to tillage (PB or CB) nor sowing (wet or dry sowing) practices.

6.2. Bacterial community structure

6.2.1. Alpha diversity

The rarefaction curves of the OTUs generated at 97% similarity are shown in Figure 2. Analyzing more sequences would still have generated a limited number of new OTUs. The analysis of alpha diversity indices was done using reads rarefied at 3000. The 48 samples generated 144, 000 rarefied reads amounting to 92077 OTUs. The values of Chao1 estimator ranged between 5908 and 12604; Shannon index values varied between 9.093 and 10.701, while the Simpson index values ranged between 0.979 and 0.999 (Table 3).

A two-way ANOVA test was used to determine if there were dissimilarities among the soil samples because of the different treatments in the alpha diversity indices. The three indices were significantly affected by the means of the sampling days (Table 3): Chao 1, p = 0.008; Shannon, p = 0.001 and Simpson, p = 0.009. According to a random forest test, Shannon (p = 0.006) and Simpson (p = 0.004) were significantly affected by the tillage practices (Table 4).

Table 1. Edaphic characteristics of soils sampled at CENEB, Yaqui Valley.

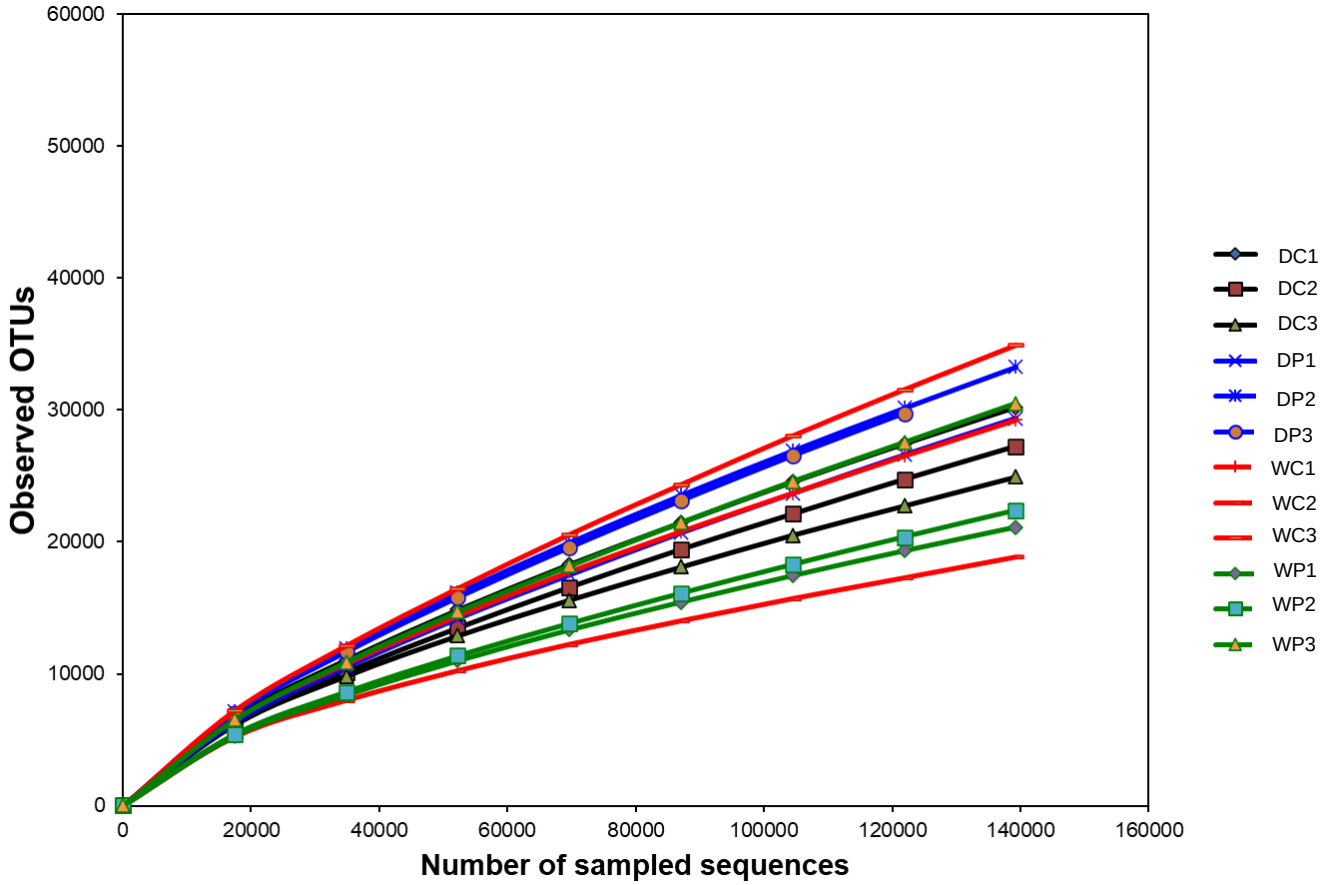
	pH	EC [a]	WC [b]	WHC [c]	TN [d]	TC [e]	Clay	Silt	Sand
Sample		(dS m^{-1})	———	———	———	(g kg^{-1} soil)	———	———	———
1DC	8.4±0.1 [f]	1.21±0.19	165± 7	582± 5	0.78±0.07	9.8± 1.0	440±30	180±20	380±60
2DC	8.5±0.2	1.51±0.13	617±106	588± 24	0.79±0.06	8.7± 0.3	410±10	220±10	370±20
3DC	8.5±0.2	1.38±0.09	234± 8	625± 28	0.66±0.01	10.4±1.1	430±30	200±52	370±30
4DC	8.6±0.1	1.48±0.28	176± 14	612± 7	0.58±0.04	N/A [g]	430± 2	180±20	390±20
1DP	8.4±0.1	1.66±0.41	116± 13	609± 11	0.72±0.03	10.0±0.3	420±19	200±26	380±50
2DP	8.5±0.0	1.76±0.25	695±221	559± 49	0.70±0.03	9.5± 0.3	440±30	190±80	370±50
3DP	8.5±0.1	1.54±0.26	218± 12	611± 40	0.59±0.04	9.2± 0.7	470±20	120±30	410±40
4DP	8.7±0.1	1.35±0.15	155± 11	580± 6	0.60±0.06	N/A	440± 3	150±20	410±10
1WC	8.4±0.1	1.24±0.14	251± 22	559± 33	0.76±0.04	9.8± 0.4	440±20	180±20	380±40
2WC	8.5±0.1	1.67±0.21	120± 57	621± 43	0.74±0.04	8.8± 1.1	430±10	190±20	380±10
3WC	8.4±0.1	1.64±0.28	191± 12	589± 15	0.63±0.05	10.6±1.6	450±20	180±50	370±30
4WC	8.6±0.1	1.52±0.48	118± 4	612± 18	0.60±0.09	N/A	440±20	180±20	380±30
1WP	8.5±0.1	1.65±0.51	242± 41	596± 41	0.72±0.02	10.0±0.5	430±20	200±20	370±20
2WP	8.5±0.0	2.12±0.44	99± 28	564± 21	0.64±0.11	9.4± 0.7	420±20	200±20	380± 1
3WP	8.4±0.1	1.92±0.42	155± 13	646± 41	0.63±0.04	9.8± 0.4	460±20	180±30	360±20
4WP	8.5±0.2	1.83±0.20	106± 14	587± 5	0.54±0.05	N/A	430± 4	170± 7	400± 5
F value	1.69	1.76	24.02	2.48	4.93	12.04	2.84	2.75	3.54
P value	0.181	0.165	<0.001	0.060	0.004	<0.001	0.038	0.043	0.018

[a] EC: Electrolytic Conductivity, [b] WC: Water Content, [c] WHC: Water Holding Capacity, [d] TN: Total Nitrogen, [e] TC: Total Carbon,
[f] Plus and minus standard deviation of the mean, [g] N/A: not available.
1-4: Sampling Days, D: Dry sowing, W: Wet Sowing, C: Conservation Agriculture, P: Conventional Tillage Practices.

Table 2. Effect of tillage and sowing practices on edaphic characteristics of soils sampled at CENEB, Yaqui Valley.

	pH		Water content		Water holding capacity		Electrolytic conductivity		Total carbon		Total nitrogen	
Factor	*F* value	*P* value	*F* value	*P* value	*F* value	*P* value	*F* value	*P* value	*F* value	*P* value	*F* value	*P* value
Tillage practices (TP) [a]	0.80	0.382	1.73	0.206	0.42	0.526	8.41	0.008	0.40	0.537	0.30	0.587
Sowing practices (SP) [b]	0.02	0.889	0.16	0.699	1.06	0.316	8.84	0.007	0.02	0.885	3.44	0.075
Interaction TP*SP	0.18	0.676	0.01	0.959	0.79	0.386	1.02	0.324	0.53	0.479	0.01	0.929

[a] Tillage practices: conventionally tilled and permanent beds, Sowing practices: wet and dry sowing.



1-4: Sampling Days, D: Dry sowing, W: Wet Sowing, C: Conservation Agriculture, P: Conventional Tillage Practices.

Figure 2. Rarefaction curves of bacterial population in soils sampled at CENEB, Yaqui Valley.

Table 3. Alpha diversity of the bacterial communities in soils sampled at CENEB, Yaqui Valley.

	Diversity Index		
Sample	Shannon	Simpson	Chao 1
1DC	10.469	0.999	9383
2DC	10.437	0.999	9302
3DC	10.398	0.997	9789
4DC	10.391	0.998	9359
1DP	10.297	0.998	7529
2DP	10.343	0.998	7615
3DP	10.559	0.999	8637
4DP	10.550	0.999	10509
1WC	10.193	0.998	6848
2WC	10.264	0.998	7179
3WC	10.337	0.998	8243
4WC	9.807	0.99	9370
1WP	10.128	0.998	7002
2WP	10.271	0.998	7578
3WP	10.334	0.998	8019
4WP	10.542	0.999	11593
F value	18.48	4.09	4.20
P value	0.001	0.009	0.008

The indexes were calculated with reads rarefied at 3000 and OTUs = 97% similarity threshold.

Table 4. Effect of tillage and sowing practices on alpha diversity in soils sampled at CENEB, Yaqui Valley.

	Chao1		Shannon		Simpson	
Factor	*F* value	*P* value	*F* value	*P* value	*F* value	*P* value
Tillage practices (AP)	2.57	0.122	9.18	0.006	10.01	0.004
Sowing	0.70	0.412	0.14	0.710	0.39	0.538
Interaction AP*Sowing	1.59	0.219	0.48	0.496	0.21	0.649

6.2.2. Bacterial taxonomy

A total of 37 phyla were identified in the soil samples (Figure 3); the most abundant (> 5%) phylotypes belonging to Proteobacteria (32.16±4.53%), Acidobacteria (19.69±3.11%), Actinobacteria (11.96±2.55%), Bacteroidetes (6.31±%2.05) and Chloroflexi (6.07±1.24%). The most abundant genera (> 1%) determined in this study (Figure 4) were *Steroidobacter* (1.80±0.56%), *Bacillus* (1.66±0.73%), *Kaistobacter* (1.46±0.51%), *Flavisolibacter* (1.27±0.42), *Acinetobacter* (1.08±1.72) and *Rubrobacter* (1.07±0.35).

6.2.3. Effect of soil physicochemical characteristics on bacterial community structure

The Spearman correlation (Figure 5) revealed that the relative abundance of Verrucomicrobia was positively correlated with soil water content ($p < 0.01$) and *Streptomyces* negatively with total N content ($p < 0.001$). The mean relative abundance of Actinobacteria, Bacteroidetes and Proteobacteria was higher in soil from dry sowing compared to wet sowing but lower in Acidobacteria (Fig. 6a). The mean relative abundance of *Acinetobacter* and *Stenotrophomonas* was generally lower in soil from dry sowing compared to wet sowing, and that of *Bacillus* and *Steroidobacter* was higher (Fig. 6b). The physicochemical characteristics caused a clear shift in wet sowing compared to dry sowing in both PB and CB and variations between the plots were smaller in wet sowing than in dry sowing.

6.2.4. Effect of sowing practices on bacterial community structure

The bacterial community structure in soil samples from CB were significantly affected by sowing practices (Table 5) (Phyla $p = 0.002$; Genera, $p = 0.015$). However, the sowing practices had a greater significant effect on bacterial community structure in soils from PB (Phyla and Genera: $p < 0.001$). A PCA was used to confirm the effect of wet and dry sowing on bacterial community structure. Dry and wet sowing practices could be separated and PB and CB were inclined to cluster by sowing practices (Figure 7). This tendency was more obvious at the genera level (Figure 7 c, d) than the phyla level. *Pedobacter* and *Streptomyces* were enriched in dry sowing while *Pseudonocardia* was enriched in wet sowing in soils under CB. In the case of PB, *Balneimonas* and *Thermomonas* were enriched in dry sowing, and *Methylibium* in wet sowing.

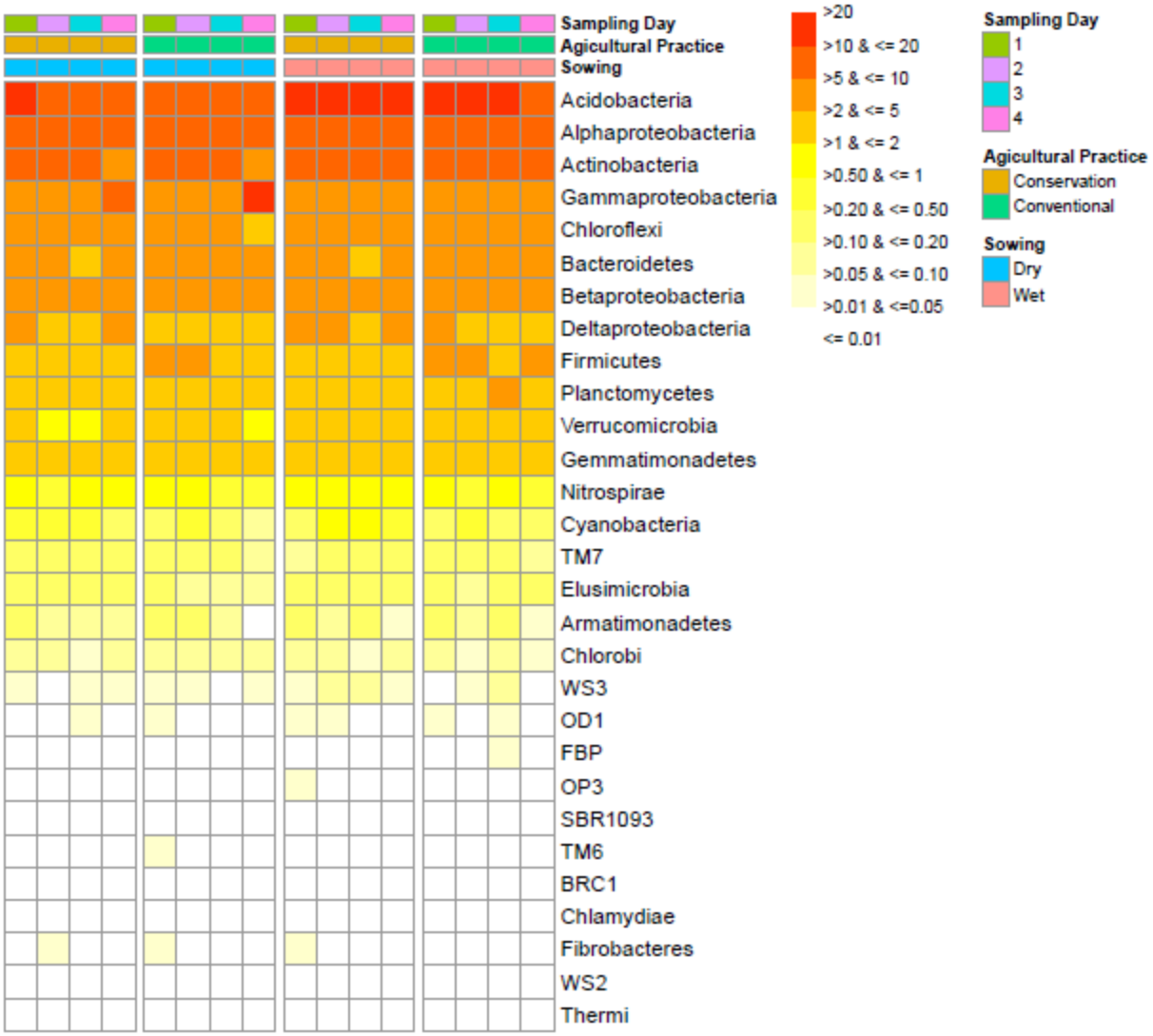


Figure 3. Heatmap of relative abundance (%) of bacterial phyla in soils sampled at CENEB, Yaqui Valley.

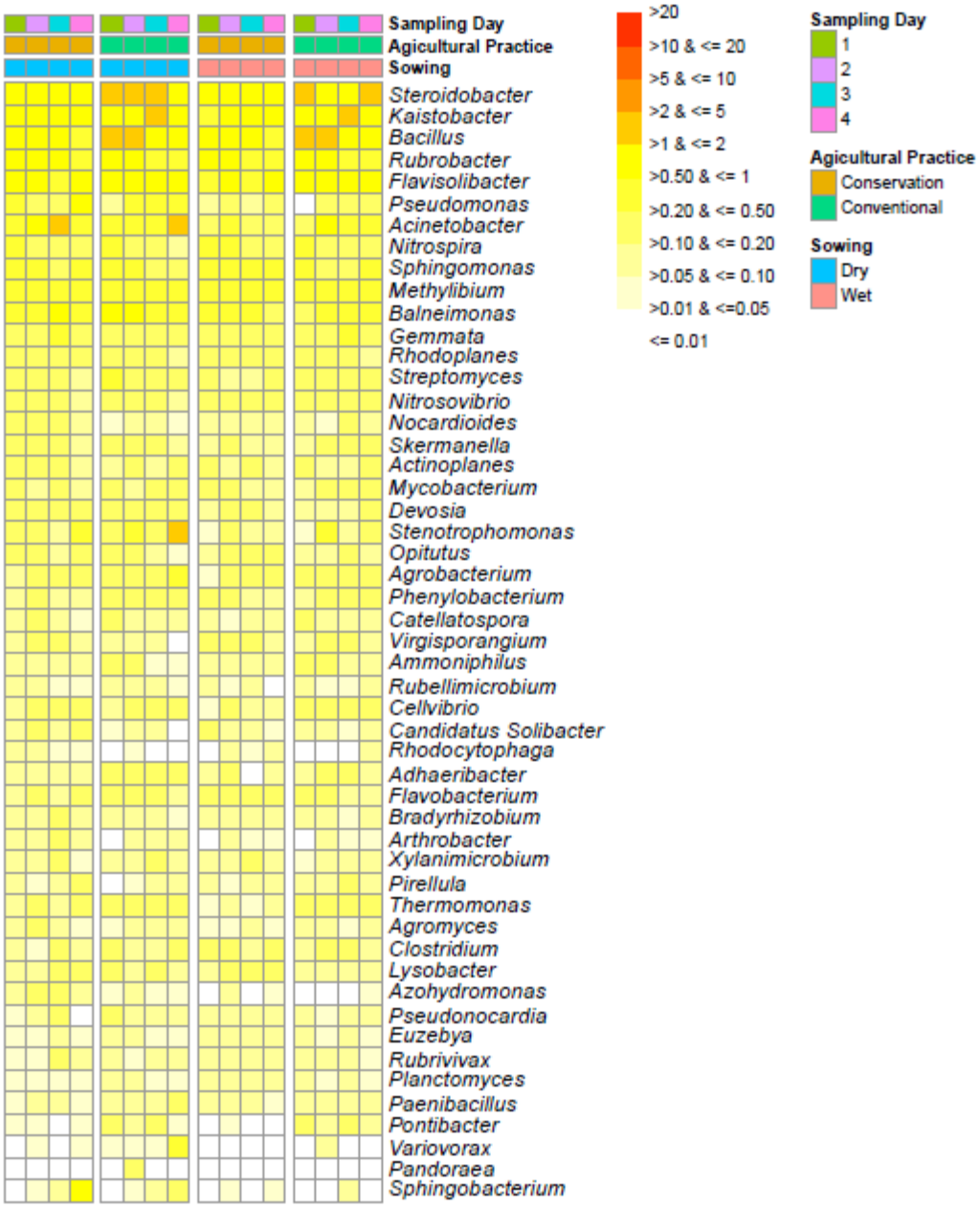


Figure 4. Heatmap of relative abundance (%) of 50 most abundant bacterial genera in soils sampled at CENEB, Yaqui Valley.

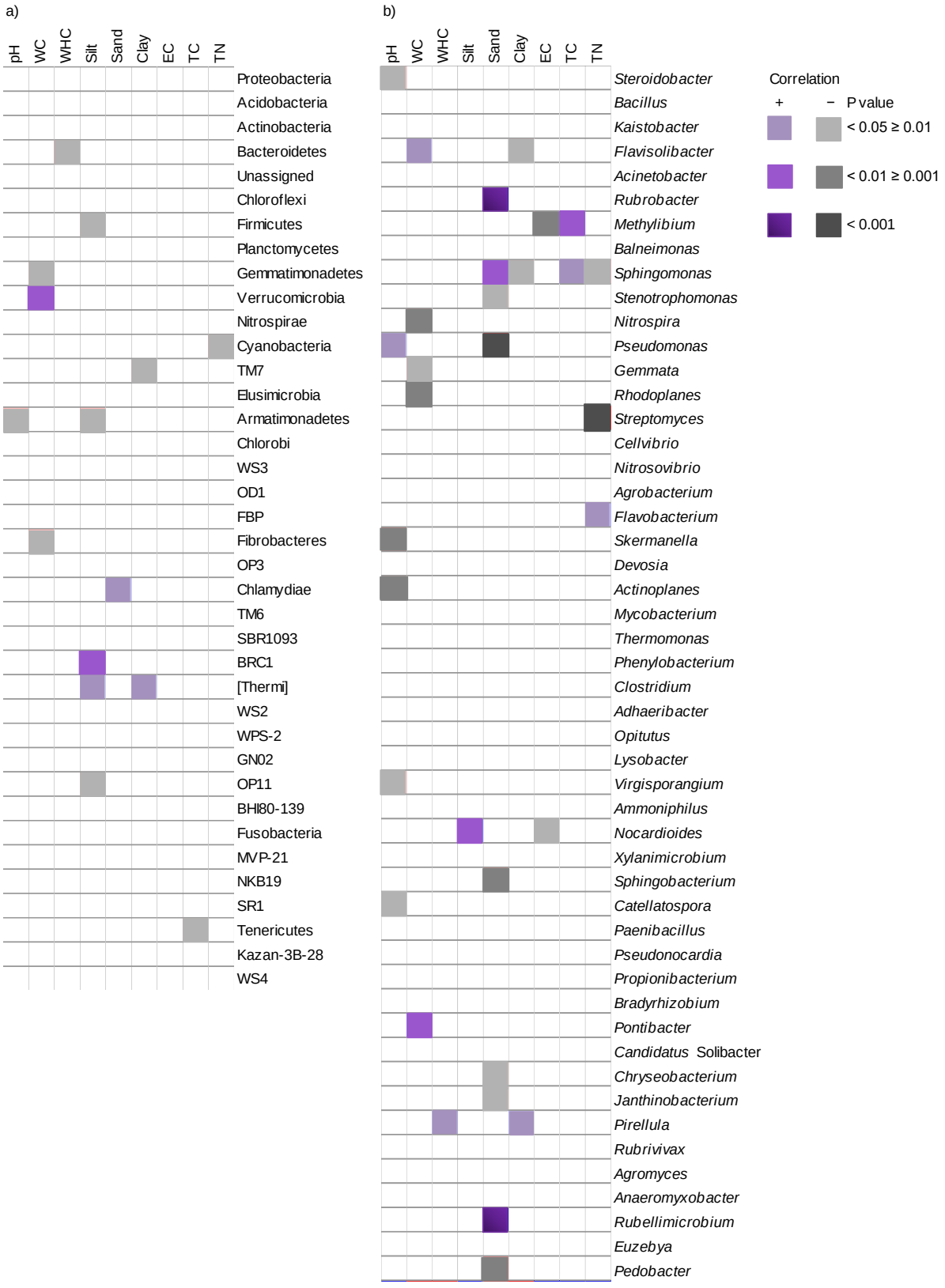


Figure 5. Heatmap of the correlations between relative abundance (%) of the bacterial a) phyla and b) the 50 most abundant genera and edaphic characteristics in soils sampled at CENEB, Yaqui Valley.

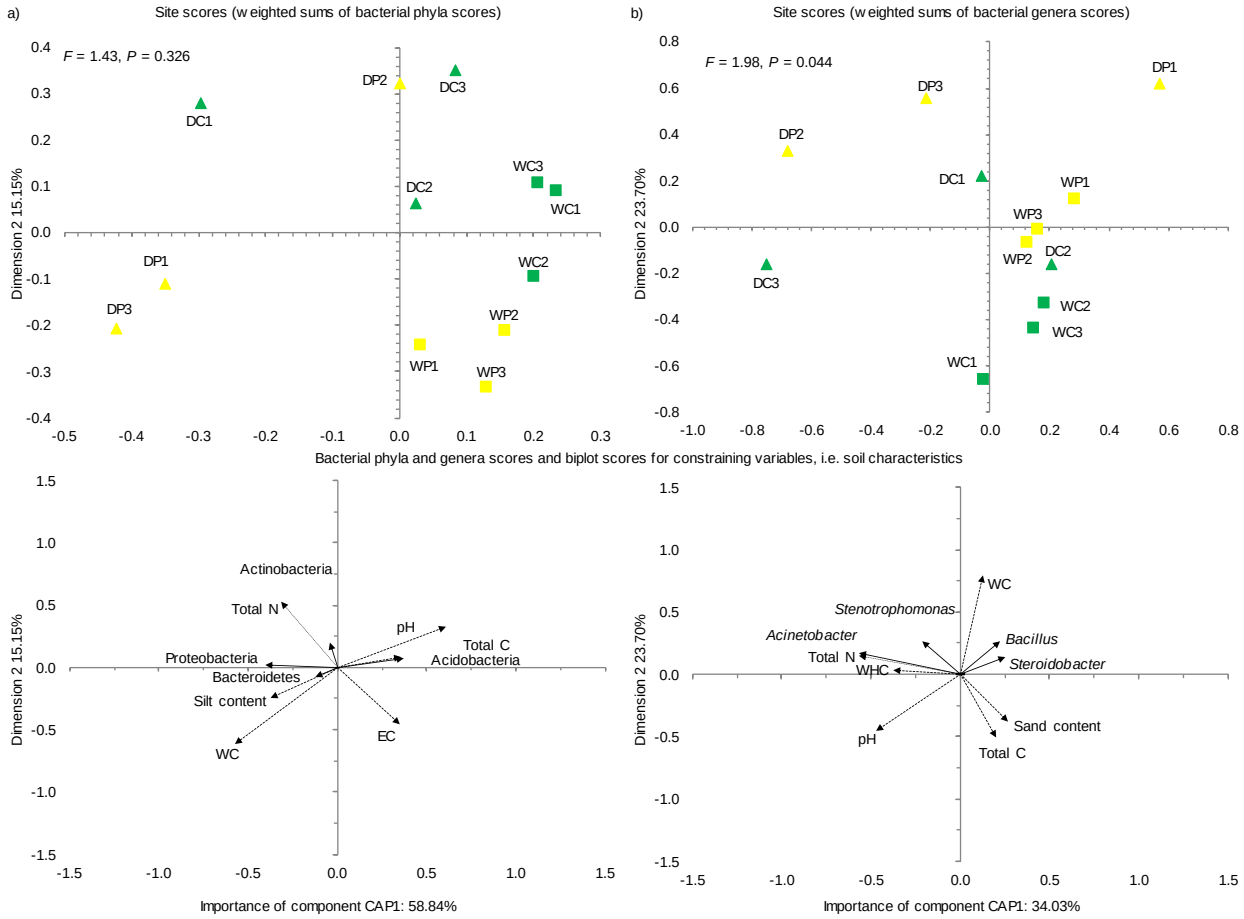
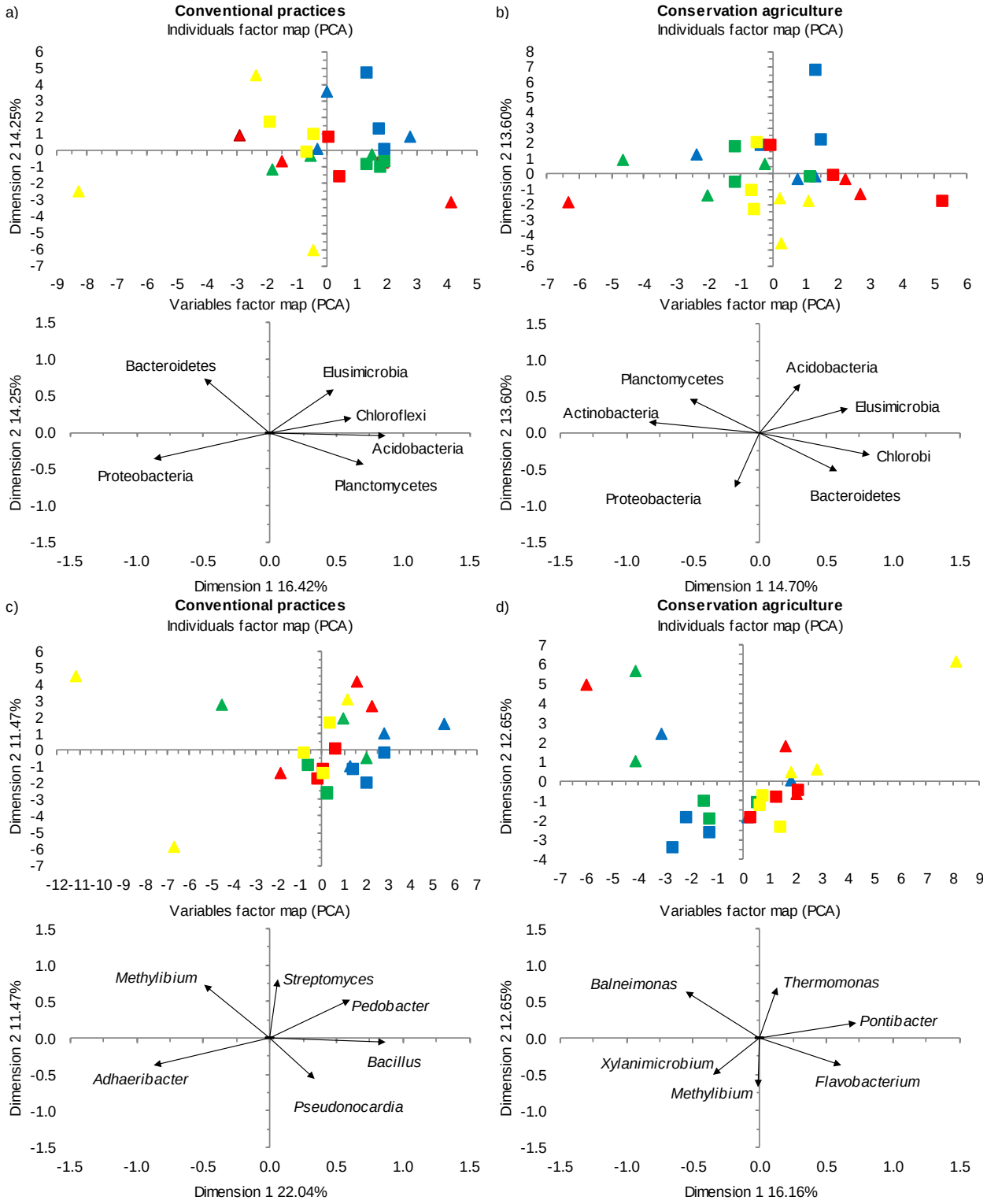


Figure 6. Canonical analysis of principal coordinates (CAP) of the mean relative abundance (%) of a) the bacterial phyla and b) the 50 most abundant bacterial genera and physicochemical characteristics in soils sampled at CENEB, Yaqui Valley.



Sampling day: 1 = Blue, 2 = Red, 3 = Green, 4 = Yellow. Wet sowing: Square. Dry sowing: Triangle.

Figure 7. Principal component analysis (PCA) of bacterial phyla a) and b) and the 50 most abundant bacterial genera c) and d) under conventional tillage practices and conservation agriculture in soils sampled at CENEB, Yaqui Valley.

Table 5. Combined effect of field treatments on bacterial phyla and genera in soil sampled at CENEB, Yaqui Valley.

	Effect of tillage practices on:				Effect of sowing practices on:			
	Wet sowing		Dry sowing		Conservation agriculture		Conventional tillage practices	
	F value	*P* value	*F* value	*P* value	*F* value	*P* value	*F* value	*P* value
Phyla	4.42	0.003	1.58	0.116	4.17	< 0.001	4.25	0.002
Genera	4.57	< 0.001	1.58	0.161	2.36	< 0.001	2.36	0.015

6.2.5. Effect of tillage practices on bacterial community structure

Bacterial community structure was only significantly affected by tillage practices in wet sowing (Table 5), phyla ($p = 0.03$), genera ($p < 0.001$). A PCA (Figure 8) was used to confirm the effect of PB and CB on bacterial community structure in wet sowing and showed that samples from wet sowing grouped by PB and CB. The separation was more accentuated in bacterial genera (Figure 8 c, d) than in phyla. Actinobacteria, Nitrospirae, *Rhodoplanes* and [Thermi] were enriched in PB and *Cellvibrio*, *Flavisolibacter*, *Pontibacter* and Proteobacteria in CB.

6.2.6. Effect of sampling days on bacterial community structure

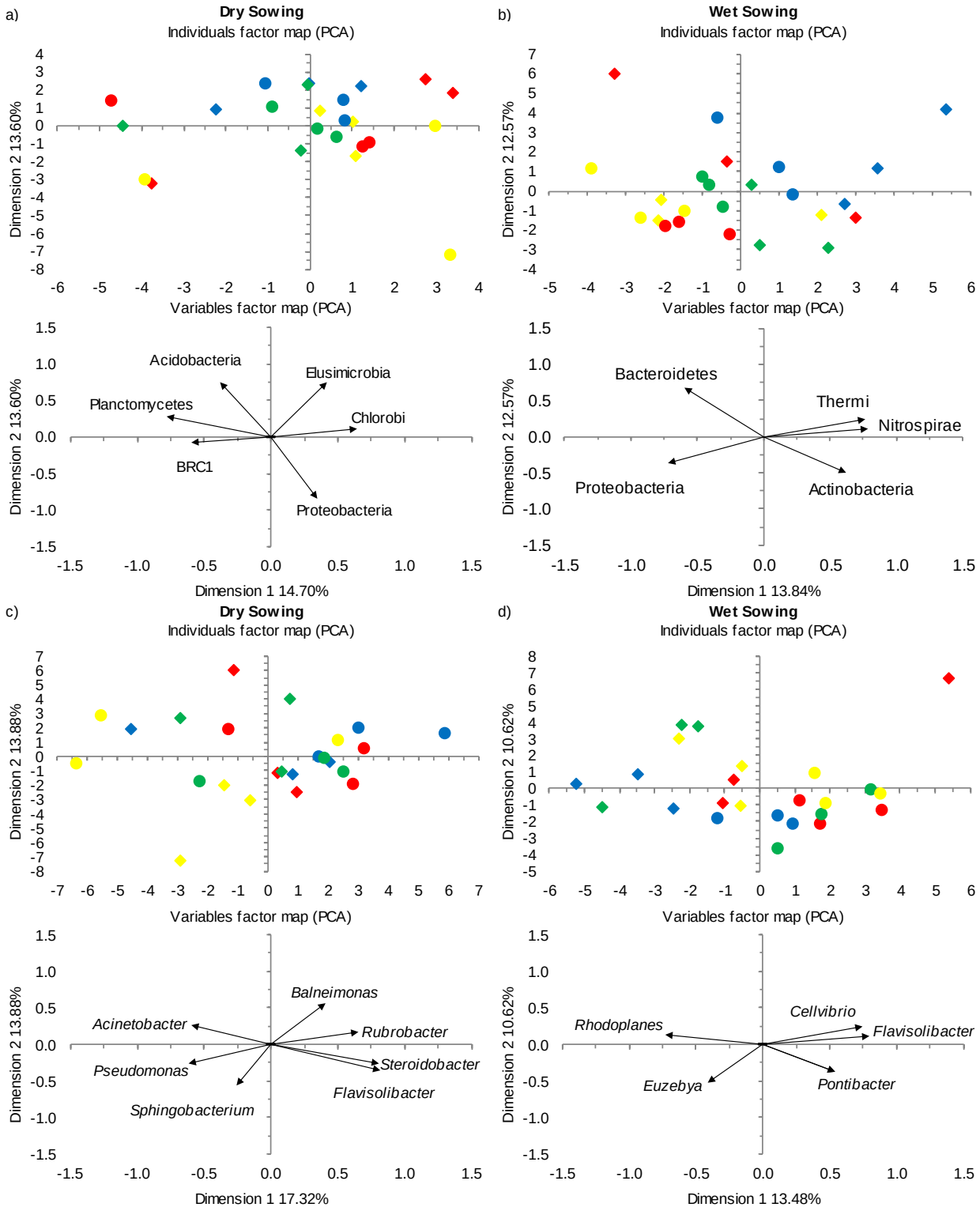
6.2.6.1. Sampling days: how they affect bacterial community structure through the sowing practices

Sowing practices significantly affected bacterial phyla (Table 6) on November 23 ($p = 0.006$), December 8 ($p = 0.002$) and on December 16 ($p = 0.009$). Bacterial genera were significantly affected by dry and wet sowing on November 23 ($p = 0.022$), December 8 ($p < 0.001$) and on December 16 ($p = 0.006$). There was an increase in relative abundance in Acidobacteria, Cyanobacteria, Elusimicrobia, *Nitrosovibrio*,

Nitrospirae and *Virgisporangium* in soil from wet sowing compared to dry sowing, while the realative abundance of Bacteroidetes, *Balneimonas*, *Kaistobacter*, Proteobacteria and WS3 decreased when the mean of the four sampling days was analyzed (Figure 9).

6.2.6.2. Sampling days: how they affect bacterial community structure through the tillage practices

The effect of tillage practices on the bacterial phyla (Table 6) was only significant on 23 November (p = 0.011) and 08 December (p = 0.002), and on 16 December 2015 considering the 50 most abundant genera (p = 0.004). A PCA of the mean relative abundance of the different bacterial phyla and genera from PB and CB separated the different sampling days (Figure 10). For example, Acidobacteria, *Bacillus*, Elusimicrobia, Nitrospirae, *Rubrobacter* and *Steroidobacter* were more abundant on the first sampling day while that of *Acinetobacter* and Proteobacteria were more abundant on the last sampling day.



Sampling day: 1 = Blue, 2 = Red, 3 = Green, 4 = Yellow. Conservation agriculture: Rhombus. Conventional tillage practices: Circle.

Figure 8. Principal component analysis (PCA) of bacterial phyla a) and b) and the 50 most abundant genera c) and d) under wet and dry sowing in soils sampled at CENEB, Yaqui Valley.

Table 6. Effect of tillage and sowing practices on bacterial phyla and genera in soil sampled at CENEB, Yaqui Valley.

	November 23		December 2		December 8		December 16		Mean	
Factor	*F* value	*P* value	*F* value	*P* value	*F* value	*P* value	*F* value	*P* value	*F* value	*P* value
Bacterial phyla										
Tillage practices (TP)	3.04	0.011	0.57	0.730	3.70	0.002	1.70	0.155	2.48	0.081
Sowing practices (SP)	3.56	0.006	1.93	0.101	3.08	0.002	4.18	0.009	6.11	<0.001
Interaction TP*SP	0.92	0.493	0.62	0.688	0.35	0.926	0.84	0.495	0.47	0.801
Bacterial genera										
Tillage practices (TP)	1.57	0.108	1.38	0.153	1.14	0.234	2.61	0.004	2.36	0.011
Sowing practices (SP)	2.01	0.022	1.14	0.306	2.33	<0.001	2.46	0.006	2.33	0.013
Interaction TP*SP	0.56	0.853	0.77	0.735	0.90	0.612	1.63	0.168	0.56	0.855

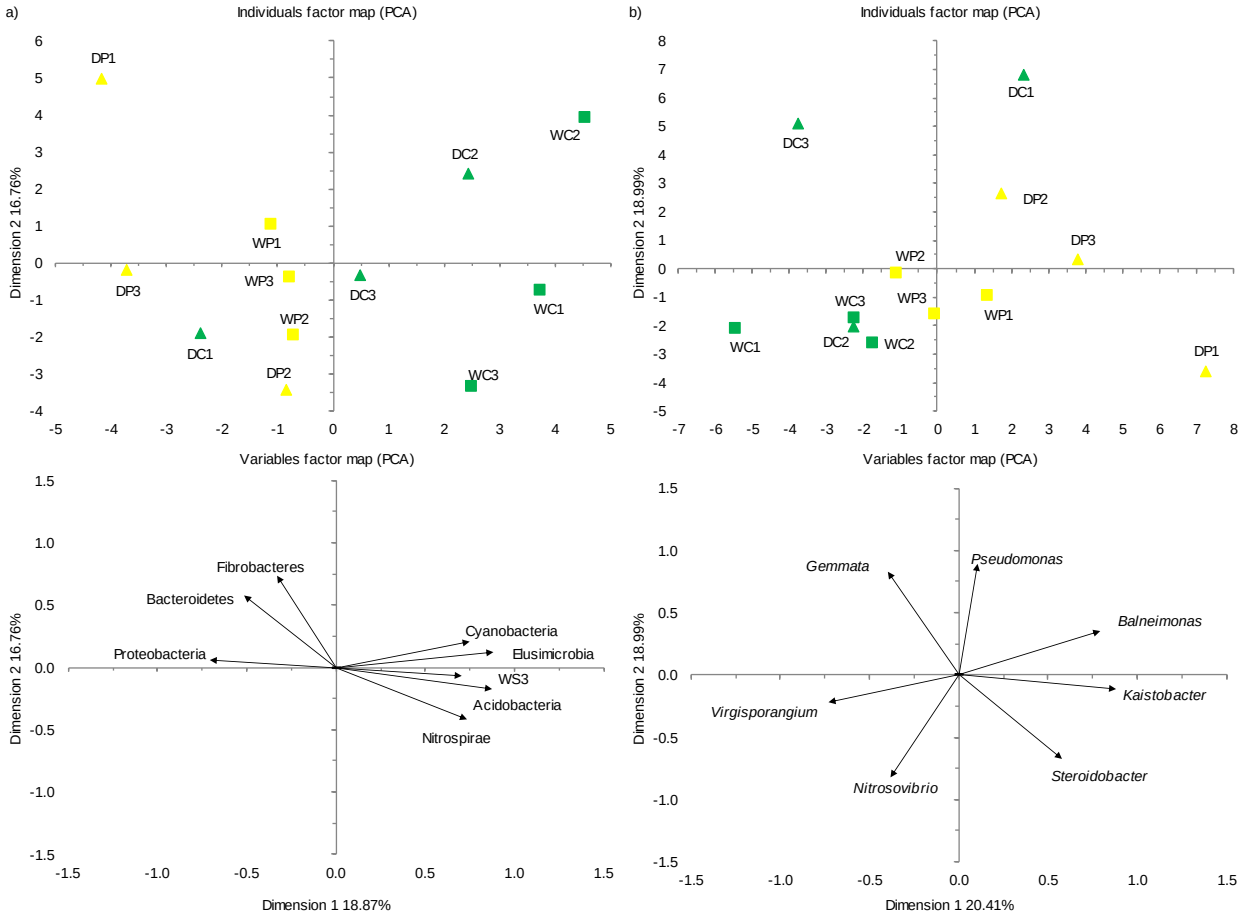


Figure 9. Principal component analysis (PCA) of the mean relative abundance (%) of a) the bacterial phyla and b) the 50 most abundant bacterial genera under the agricultural and sowing practices in soils sampled at CENEB, Yaqui Valley.

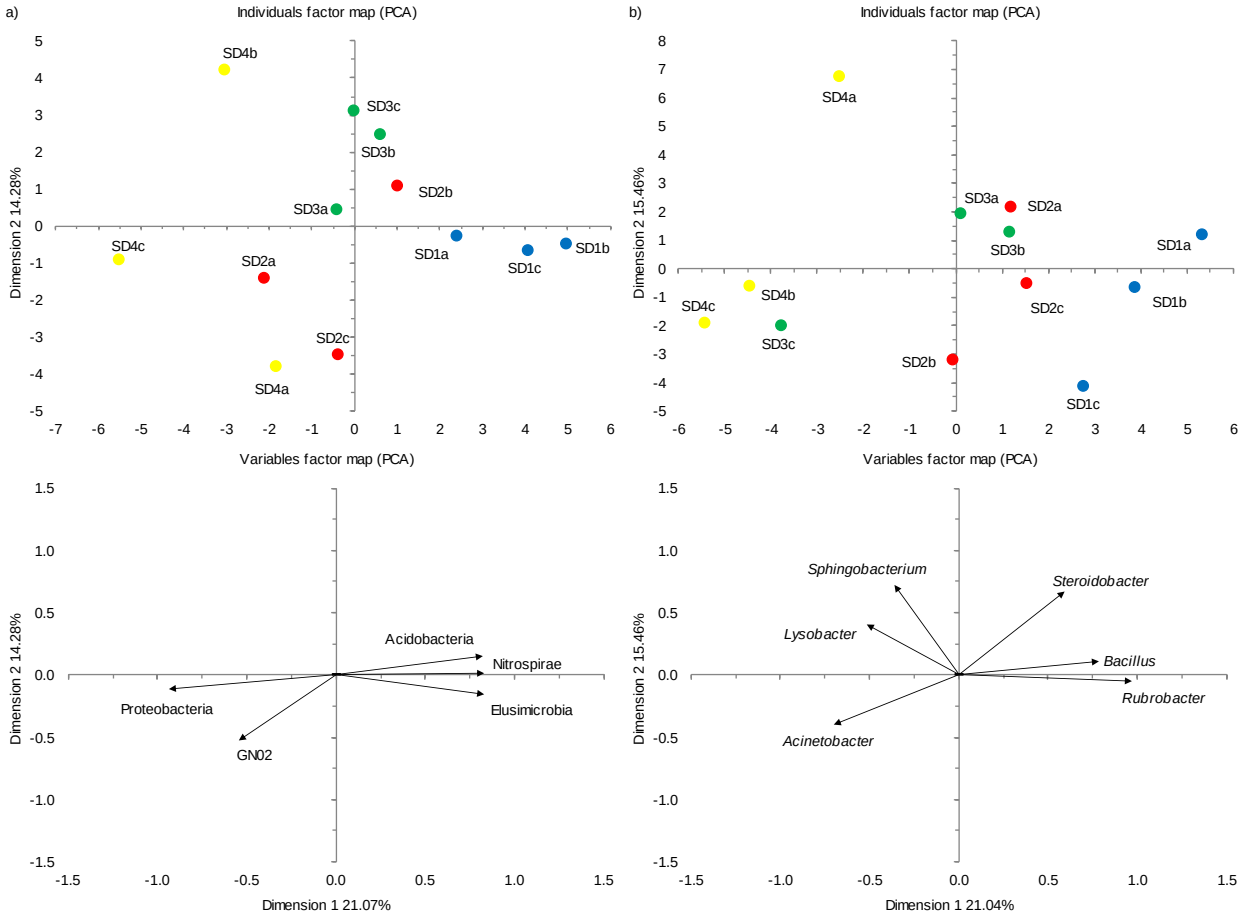


Figure 10. Principal component analysis (PCA) of the mean relative abundance (%) of a) the bacterial phyla and b) the 50 most abundant bacterial genera under the agricultural and sowing practices on the different sampling days (SD) in soils sampled at CENEB, Yaqui Valley.

7. Discussion

Wheat-bacterial interactions were not considered in this study since plant emergence would not have occurred by the first sampling day and there would only have been seedlings with minimal rhizosphere development present on the other three sampling days. The summer maize could have affected the bacterial community at the beginning of the sampling period, as suggested by Alvey et al. (2003). The maize-wheat crop rotation in this study has been ongoing for over 10 years in both tillage practices; therefore, the effect of plant roots on bacterial community structure should be the same in this study (Benitez et al. 2017).

7.1. Soil physicochemical characteristics: how they were affected by sowing practices, tillage practices and sampling

Soils were first irrigated on November 6 in wet sowing, and on November 25 in dry sowing. This difference in application of more than two weeks caused the water content (WC) to be higher in wet sowed soil than in dry sowed on the first sampling day, i.e. on November 23. Variations in soil WC can affect electrolytic conductivity (EC) (Zhang and Wienhold 2002). Rewetting a dry soil prompts an increase in water content, which leads to an increase in water potential, facilitating the diffusion of soluble substrates (Muhr et al. 2010). A decline in EC occurs as these soluble ions usually leach to deeper layers. The opposite happens in soil drying; there is a decrease in water availability, hindering the diffusion of soluble salts. This causes the salts to accumulate, leading to an increase in EC (USDA, NRCS 2011). Overall, wet sowed soils had higher EC values than dry sowed soil.

Electrolytic conductivity is also affected by soil drainage, which can improve the flow of water in soils and induce leaching of soil minerals (Grisso et al. 2009). Soil drainage is affected by tillage. Soil aggregates are disrupted by tillage causing pore size to decrease, which leads to reduced water infiltration (Bescansa et al. 2006; Thierfelder and Wall 2009). Furthermore, heavy machinery operated in CB causes soil compaction, lowering the rate of infiltration in soil (Manyiwa and Dikinya 2014). Aggregate stability is promoted by minimum tillage and leaving crop residue on the soil surface by

averting water runoff and boosting water infiltration (Verhulst et al. 2011). Water infiltration was improved in PB, so drainage was improved, allowing for more leaching of minerals to lower levels of the soil, which resulted in lower EC values (Stagnari et al. 2009).

7.2. Bacterial community structure

7.2.1. Alpha diversity

According to the Shannon index, bacterial diversity was the same in all four treatments. Köberl et al. (2011) reported a Shannon index of 11.21 in soils from an organic farm in an arid region that were amended with rice straw, water hyacinth, wood chips, organic waste, clay, chicken, and cow manure. In this study, plant remains were left on the surface in PB and incorporated during tillage in CB, which might explain why the Shannon index values were in the range to that obtained by Köberl et al. (2011). Bacterial diversity is enhanced by the availability of quality organic matter (Thiele-Bruhn et al. 2012).

7.2.2. The dominant bacterial taxa

The most dominant taxa in this study were Proteobacteria, Acidobacteria and Actinobacteria. They have been reported as the most abundant phyla in arable soil under wheat-maize rotation (Zhao et al. 2014), and in soils under conventional and conservation tillage practices in arid to semi-arid zones (Wang et al. 2016). Many studies have suggested that Proteobacteria, Acidobacteria and Actinobacteria are able to adapt to the harsh conditions, such as long dry spells without rainfall, in arid regions (Blazewicz et al. 2014; Evans and Wallenstein 2012). The three phyla have adapted to the weather at CENEB, which is characterized by arid conditions and sporadic rewetting events. There were no apparent dominant bacterial genera in this study. The relative abundance of *Bacillus*, *Flavisolibacter*, *Kaistobacter* and *Steroidobacter* was high in soils under conventional agricultural practice and an organic milpa system, comparable to PB, in the central highlands of Mexico (Moreno-Espíndola et al. 2018).

7.2.3. Soil physiochemical characteristics and bacterial community structure

Soil pH is said to play a major role in shaping bacterial diversity (Wang et al. 2012). Bacterial diversity may reduce in extreme acidic or alkaline soil (Lauber et al. 2009). The soil in this study, from CENEB, was slightly alkaline and pH had very little effect on the bacterial diversity.

In arid soils, bacterial community structure is strongly influenced by water content (Lennon et al. 2012). Variations in water availability greatly affected the relative abundance of Verrucomicrobia in this study; the phylum was enriched when soil water content was high. Similar findings were reported by Maestre et al. (2015) in their study on the effects of drying and rewetting soils in drylands.

7.2.4. Dry and wet sowing and bacterial community structure

Under prolonged dry conditions, normal functioning of the soil microorganisms is impeded, which may result in cell inactivity (Gordon et al. 2008). However, most microorganisms have developed different coping mechanisms to withstand drought (Fierer and Schimel 2002), for example members of *Bacillus* can form spores, some strains of Cyanobacteria and *Pseudomonas* are able to secrete mucilage and extracellular polymeric substances (Costa et al. 2018). Rewetting a dry soil triggers microbial activity, a phenomenon known as the "Birch effect" (Birch 1958; Yu et al. 2014). The sudden increase in water availability releases organic material as soil structure is disrupted, exposing easily decomposable organic C substrate for microorganisms to metabolize (Huygens et al. 2011; Shi and Marschner 2014). There is also an extra source of organic material from the dead cells of microorganisms that did not survive the dry conditions (Mavi and Marschner 2012). There is an increase in copiotrophs, due to the abrupt availability of the C source (Ho et al. 2017). Meanwhile, oligotrophs are replaced since they favor nutrient deficient conditions (Blazewicz et al. 2014; Naylor and Coleman-Derr 2018). In extended wet conditions, soil becomes waterlogged creating a deficit of O_2 in soil pores and prompting facultative or obligated anaerobes to bloom (Yan et al. 2015). Aerobic microorganisms, that take part in

processes such as nitrification and CH_4 oxidation, are impeded while those involved in anaerobic processes, such as, denitrification and methanogenesis, are favored (Lennon et al. 2012; Moreno-Espíndola et al. 2018).

Soils under wet sowing were irrigated on November 6. There was a rise in microbial activity due to increased respiration and mineralization of the newly available decomposable organic material (Unger et al. 2010), followed by a shift in the bacterial community structure (Miller et al. 2005). On the first sampling day (November 23), Acidobacteria, *Bacillus* and *Rubrobacter* were more abundant than on the other sampling days. Maestre et al. (2015) reported that the relative abundance of Acidobacteria responded opportunistically to rewetting; decreasing in dried soil, but promptly increasing upon rewetting of soil. To protect themselves from abiotic stress factors like desiccation, members of *Bacillus* form spores and stay in a dormant state until conditions, such as increased water and nutrient availability, that favor growth arise (Setlow 2014). The water applied on the first irrigation in wet sowing would have triggered the germination of *Bacillus* spores. Species of the genus *Rubrobacter* are mostly mesophilic, moderately thermophilic, or thermophilic and can therefore endure drought conditions (Chen et al. 2018). Therefore, phylotypes belonging to *Rubrobacter* were favored by an increase in water availability in soil after the first irrigation, as their relative abundance was enriched on the first sampling day.

Irrigation was not applied in the dry sowing treatment until after the first sampling day (November 23), so the microbial activity at that point would have been low. Since wet sowed soil had been irrigated weeks before the first sampling day, it stands to reason that the bacterial community structure in that treatment would be different to that of dry sowed soil. Microbial activity was increased in the dry sowing treatment by the second sampling day as soil was irrigated a week before samples were collected. Due to the difference in irrigation application, similar changes in the bacterial community structure were observed in dry sowing 22 days later than in wet sowed soil. Therefore, dry, and wet sowed soil did not have the same bacterial community structures on the same sampling days. Bacteroidetes and Proteobacteria were more abundant in dry sowing than wet sowing on the first sampling day. These phyla behaved like copiotrophs and were enriched once organic matter became accessible for them to mineralize after soil was rewetted (Fierer et al. 2007). Contrarily, Acidobacteria

and *Acinetobacter* were more abundant in the wet sowing treatment after the first sampling day compared to dry sowing, exhibiting oligotrophic traits (Fierer et al. 2007; Hartmann et al. 2017); available decomposable organic material would have been mineralized by bacteria earlier in wet sowing than in the dry sowed soil.

7.2.5. Tillage practices and bacterial community structure

Wet sowing had a contrasting effect on bacterial community structure in the tillage practices (PB and CB). The burst of respiration after soil was rewetted, the "Birch effect", upon the application of the first irrigation to wet sowed soil on November 6 would have occurred 17 days before the first sampling day. This flush of microbial activity meant that the organic material released during rewetting would have been mineralized by the first sampling day. Therefore, the effect of wet sowing on PB and CB was most likely a result of how crop residue was handled in the field; left on the soil surface in PB and incorporated in soil in CB. Members of Actinobacteria have been said to demonstrate copiotrophic traits (Leff et al. 2015), and should be more abundant in CB where tillage would help to make organic matter more accessible to bacteria compared to no tillage in PB. In this study however, PB had a higher presence of Actinobacteria than CB, hence the phylum was not considered a copiotroph here. Our results were more in line with those reported by Fierer et al. (2007) with Actinobacteria not responding to increased C availability as expected.

Dry sowing did not have a significant effect on the bacterial community structure in the tillage practices. Soil was still dry on the first sampling day (November 23) since irrigation was not yet applied, which suggests that there was little microbial activity in PB and CB, hence bacterial community structure remained stable. By the second sampling day however, there was an obvious change in water availability as dry sowed soil was irrigated (November 25) a week before. It was difficult to notice any effect tillage practices could have on bacterial community structure at that time since the impact of increased water content was so prominent. Irrigation close to the sampling days overshadowed the effect of PB and CB. The effect of the tillage practices in dry sowing treatment was only noticeable after the short-term effect of irrigation on microbial activity had stopped.

7.2.6. Sampling and irrigation days and bacterial community structure

Overall, bacterial community structure was more affected by the rewetting events during irrigation than the tillage practices on the different sampling days. This effect was noted in dry and wet sowed soils, and bacterial community structure was different in the two treatments for at least a month. The relative abundance of *Acinetobacter* was higher on sampling day 4 (December 16) compared to the other three sampling days, indicating that the genus can withstand desiccation. This genus was identified in cultivated desert soil (Marasco et al. 2012), proving that *Acinetobacter* can survive dry conditions by sporulation.

It is interesting to note that *Acinetobacter*, *Bacillus*, *Pseudomonas* and *Streptomyces*, all abundant genera in this study, are plant growth promoting bacteria (PGPB). Plant growth promoting bacteria provide many benefits to plants by: synthesizing siderophores, facilitating the solubilization of minerals such as phosphorous, stimulating plant growth, enhancing plant resistance against biotic and abiotic stresses, secreting antibiotics and other metabolites to suppress the activity and growth of plant pathogens, producing hormones, such as auxins and cytokinins, and other substances that aid in the uptake of nutrients (Beneduzi et al. 2012; Berg and Hallman 2006; Dias et al. 2015).

8. Conclusions

Soil water content played an important role in shaping the bacterial community structure. The effect of the tillage practices, conventional tillage practices and conservation agriculture, on bacterial community was masked by the effect of changes is soil water availability after irrigation. In general, the sowing practices, wet and dry sowing, had a greater effect on bacterial relative abundance than the tillage practices. The effect of dry and wet sowing on abundant bacterial groups was influenced by the time elapsed between irrigation application and the sampling day.

9. References

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