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Soil Bacterial Community Associated With High Potato Production and Minimal Water Use

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In agriculture, water consumption for crop production represents 69% of all water use. Precision irrigation systems based on available soil water have been developed to improve crop production, reducing water use. Besides the improvements in irrigation management, a better resolution of the optimal water level is required, and revealing the impact of soil matric potential on the soil microbial community may help. Here, the effect of four soil matric potential treatments (−15 kPa, −25 kPa, −30 kPa, and −45 kPa) was evaluated on the soil microbial community across three potato cultivars and two soil types (silt and sand). The results confirmed the soil matric potential with −25 kPa as the optimal irrigation level, which promoted high potato production using the minimal water use. The irrigation levels affected the composition, predicted functionality, and the ecological network of soil bacterial community. Water excess (−15 kPa) and deficit (−30 and −45 kPa) promoted an increase in microbial interaction and alpha-diversity. The results suggested higher Positive/Negative ratio for phyla *Proteobacteria*, *Actinobacteria*, and *Acidobacteria* in optimal irrigation level (−25 kPa) than other irrigation levels. Also, correlation analyses revealed an interesting association between the irrigation levels, potato production, and bacterial functionality, especially in the carbon cycle (fixation and emission). Therefore, this study proposed important associations between the soil bacterial community and water management, focusing on high potato production and minimal water use. The advancement of this knowledge may lead to a more comprehensive assessment of the optimal irrigation levels of others crop production systems. Furthermore, the inclusion of biological mechanisms, especially microbial interactions, in agriculture studies has the potential to contribute to the development of water management practices conducive to both increasing crop yield and maintaining a sustainable soil environment.

Keywords: precision irrigation, microbial interaction, soil matric potential, crop production, soil health, water use

INTRODUCTION

Reducing water consumption is one of the most critical challenges facing the twenty-first century (Cosgrove and Loucks, 2015). Based on the parameters of population growth, economic growth, consumption patterns (diet, bio-energy, and demand), global production and trade pattern, and technological development, it has been estimated that in 2050, the population in the world will be

around 8–10 billion, increasing by 180% agricultural water use in the worst case scenario (Ercin and Hoekstra, 2014). Given that agriculture is responsible for 69% of the global water use, this will have a significant impact on the world's water resources (Frenken and Gillet, 2012). Thus, there are remarkable ongoing efforts to improve irrigation strategies while maintaining food production and reducing adverse environmental impact (Bajželj et al., 2014). Accordingly, accurate methods have been developed to monitor water in the soil system. The adsorbed soil water content can be characterized by the total potential (i.e., energy per unit volume [Pa]), or Ψ_T (Groenevelt et al., 2004) which corresponds to the sum of four potentials: matric potential (Ψ_m); osmotic, or solute potential (Ψ_s); the gravitational potential (Ψ_Z); and pressure potential (Ψ_A), where only the matric and solute potentials affect plant absorbance (Kirkham, 2005). Thus, the optimal irrigation level for different crops is mostly assumed and based on the water matric potential (Caron et al., 2017).

Although current irrigation strategies have considerably improved crop production, methods to improve their efficiency are strongly desirable. One possible solution is to integrate soil water management with other environmental components, such as the soil microbial community. The soil has been classified as one of the most diverse ecosystems on Earth (Thompson et al., 2017). It has been verified that the microbial community plays an essential role in the soil environment system; that is acting on the biogeochemical cycles, such as those of nitrogen (Prosser and Nicol, 2008), sulfur (Zecchin et al., 2017), and carbon (Meyer et al., 2017). The soil microbial community also plays significant roles in plant nutrition. Castrillo et al. (2017) demonstrated that there is a direct correlation between the rhizosphere microbial community, the phosphorus uptake by plants, and the plant immunity to nutritional-stress events. Moreover, it has been suggested there is a correlation between the quality of irrigation water and the soil microbial functionality and stability (Frenk et al., 2018); however, the effect of water management on the soil microbial community remains unclear.

The available soil water may drive the structural, functionality and interaction of the soil microbial community, and this correlation may improve the use of water by plants. In this study, the effect of four targeted matric potential levels (−15, −25, −30, and −45 kPa) on the soil microbial community (composition, predicted functionality, and microbial interaction) was explored using three potato cultivars and two soil types (silt and sand). Potatoes, which are sensitive to dry soil conditions (Dalla Costa et al., 1997) and saturated soil conditions (Jackson and Colmer, 2005), require timely irrigation and thus, there is a requirement to assess a potential correlation between soil matric potential, soil microbial community, and crop production. In particular, the hypothesis tested was that, despite soil type and potato cultivars, (i) the water management affects soil bacterial structure, functionality, and co-occurrence patterns; (ii) the soil bacterial co-occurrence patterns and functionality have a potential association with potato yields; and (iii) the irrigation level which promotes the best potato yields is associated with the highest soil microbial diversity. This research represents a stepping stone toward the integration of microbial community

dynamics into the development of comprehensive irrigation strategies.

MATERIALS AND METHODS

Soil Preparation and Characterization

The soils were obtained from potato fields located at Peribonka city (silt soil; 48°45'37.07" N and 72°1'24.84" W), and Dolbeau-Mistassini city (sandy soil; 48°51'31.04" N and 72°11'50.49" W). Both soils were collected at 20 cm topsoil, homogenized and placed into the pots (not sieved). The soils were classified as Sandy soil (0% clay, 8.16% silt, 91.84% sand, 3.13% C_{org} , and pH 5.01) and Silt loam soil (0.08% clay, 58.16% silt, 41.76% sand, 2.73% C_{org} , and pH 5.35), considering the USDA Soil Taxonomy (Soil Survey Staff, 1999). The retention curve of each soil is available at **Figure S1**. The retention curve correlates the soil matric potential values and the water content of each soil, indicating their, respectively, Field Capacity (0.0938 m^3/m^3 for sand soil, and 0.2735 m^3/m^3 for silt soil) and Wilting point (0.053 m^3/m^3 for sandy soil, and 0.065 m^3/m^3 for silt soil). The water retention curve was obtained by the van Genuchten equation (van Genuchten, 1980),

$$\text{Water content } (\theta) = \theta_r + \frac{\theta_s - \theta_r}{[1 + (\alpha |\psi|)^n]^{1-1/n}} \quad (1)$$

Where, θ_r is the saturated water content ($m^3 m^{-3}$), θ_s is the residual water content ($m^3 m^{-3}$), α is related to the inverse of air entry suction (m^{-1}), ψ is the soil matric potential in module, and n is the pore-size distribution.

Irrigation Experiment

The experimental work was conducted in a greenhouse located at the Laval University campus (Québec, QC, Canada). Potatoes were cultivated in 72 pots (60 × 40 × 60 cm), using three replicates of four soil matric potential, two types of soils and three potato cultivars. The water management treatment was classified into different levels of soil water matric potential mean, namely and ~ −15, −25, −30, and −45 kPa. The levels of soil water matric potential were chosen based on the previous study focused on irrigation levels and potato production (see Wang et al., 2007). For sand soil the matric potential levels corresponded to 0.0846 (−15 kPa), 0.0757 (−25 kPa), 0.0731 (−30 kPa), and 0.0685 (−45 kPa) m^3/m^3 of water content. For silt soil the matric potential levels corresponded to 0.2549 (−15 kPa), 0.2328 (−25 kPa), 0.2256 (−30 kPa), and 0.2104 (−45 kPa) m^3/m^3 of water content. Thus, the irrigation level of −25 kPa showed 11% (sand soil) and 9% (silt soil) less water content than the irrigation level of −15 kPa.

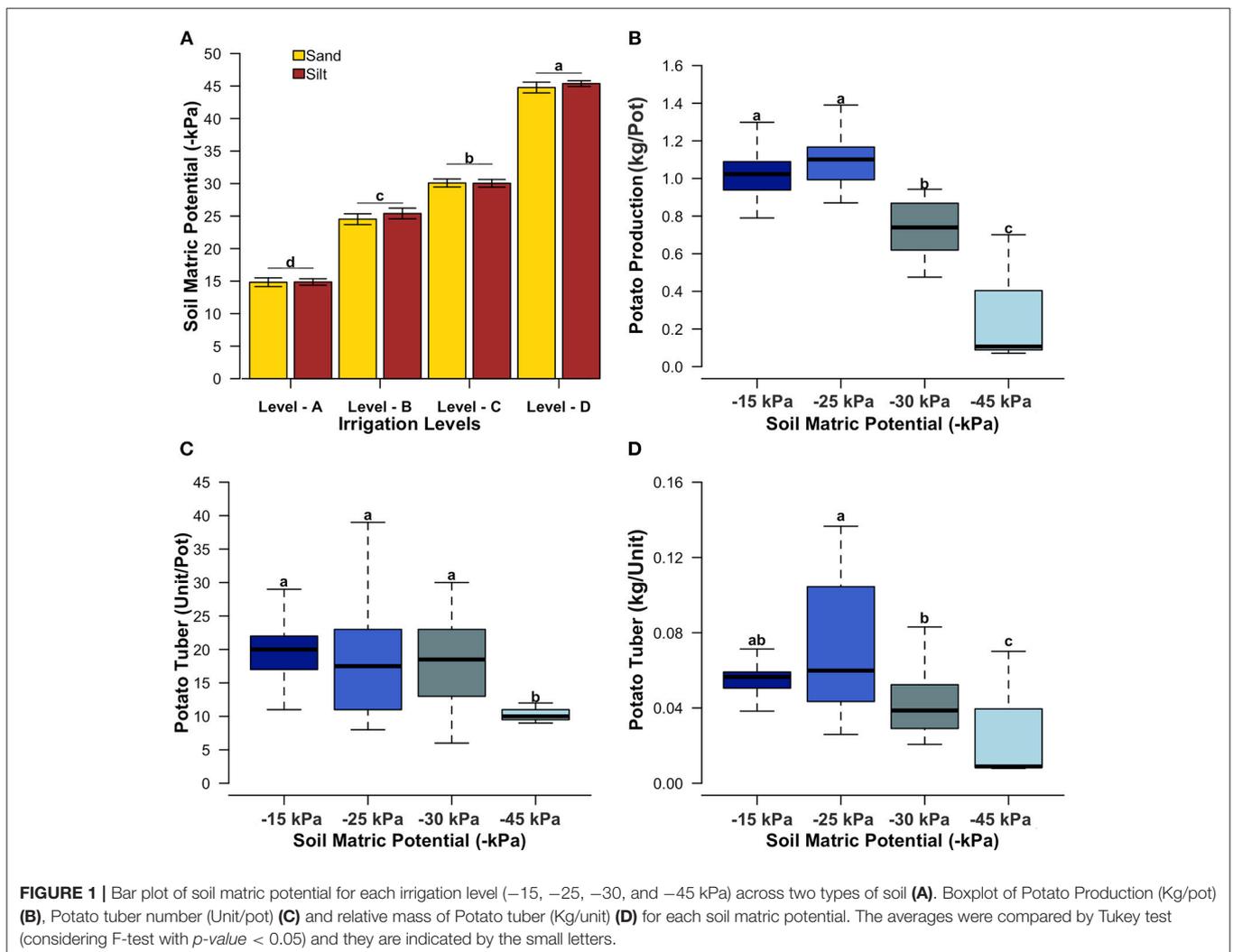
Eight irrigation supply lines allowed to control irrigation at the subplot level independently. The soil matric potential at a depth of 15 cm was measured at 2-min intervals with a datalogger, and the sub-plot level mean values (3 reps × 3 varieties) were calculated. Irrigation was manually initiated when the predefined thresholds were reached, and irrigation durations were adjusted throughout the growing season to avoid leaching

following the procedure described in L  tourneau et al. (2015). The three potato cultivars used were Goldrush (most cultivated mid-season variety in Quebec), Envol (popular early variety), and Red Maria (mid-late to late variety), which are expected to show similar physiological response across irrigation variance (FPPTQ, 2016). After the development of potato plants (30 days), the water experiment went on for 90 days, until harvest. During the experiment, it was used rainfall water ($\text{pH} \approx 7$ and $\text{EC} \approx 180 \mu\text{S cm}^{-1}$) for irrigation, and the mean temperature in greenhouse was 24°C . No fertilizer was coupled into the water supply. Potato tuber number and fresh biomass were measured for each pot. The soil samples were taken from each pot (0–10 cm depth) at the end of the experimental period for downstream elemental concentrations analyses by X-ray fluorescence spectrometer, available nutrients analyses by Mehlich III and DNA extraction.

DNA Extraction and 16S Sequencing

For total DNA extraction and 16S sequencing, we followed the protocol available from the Earth Microbiome Project (EMP; www.earthmicrobiome.org). The total DNA was obtained from

0.25 g of soil using the PowerSoil DNA Isolation kit (MoBio, Carlsbad, USA) according to the manufacturer's instructions. Quality of extracted DNA was visualized by electrophoresis at 0.8 % agarose gel. The sequence of prokaryotes (bacteria and archaea) were obtained by the primers 515F-806R, targeting the V3–V4 region of the 16S SSU rRNA (Caporaso et al., 2011). The DNA library was performed using the Nextera XT Library Prep kit[®] with sequences of 300 base pairs. The products were quantified using the Quant-iT PicoGreen dsDNA Assay Kit[®] (ThermoFisher/Invitrogen cat. no. P11496; follow manufacturer's instructions) for equimolar pool tuning and sequenced using the MiSeq PE Cluster v3 cBot kit[®] (2 × 300 bp) on the Illumina MiSeq2500[®] platform (IRDA, Quebec, Canada). A total of 5.2 million sequences were obtained. The bioinformatics analyses were performed in *Qiime* (Caporaso et al., 2010), following the protocols for *Illumina 16S analyses* available at <http://qiime.org>. The reads were joined into paired-end sequences, and filtered by the quality and chimeric sequences. The sequences filtered were binned into operational taxonomic units (OTU) using Sumaclus method at 97% identity (Kopylova et al., 2016).



The taxonomic classification was based on SILVA's ribosomal database-123 (Quast et al., 2013). We removed the singleton and Archaea sequences. The OTU table was rarefied at 54,535 sequences/sample depth.

Statistical Analyses

The statistical analyses were performed in R.3.4.3 (Sasaki et al., 2005). Firstly, we confirmed the differences in irrigation levels (−15, −25, −30, and −45 kPa) by ANOVA-test followed by Tukey test (confidence level of 95%) using package 'laercio'. We evaluated the elemental (X-ray) and chemical (Mehlich III) composition of soil types (silt and sand) by principal component analysis (PCA) after the irrigation experiment. We standardized the soil types composition data by Hellinger, and the PCA was performed using the packages "FactoMineR" and "factoextra." The results of potato experiment, such as potato production (Kg/pot), potato tuber number (unit/pot), and relative mass per potato tuber (Kg/unit), were compared by ANOVA-test and ranked by Tukey test, considering $p < 0.05$. The coefficient of variation (CV) was lower than 32% indicating no transformation necessity (Box and Cox, 1964).

We performed the bacterial functionality prediction using the method and package 'Tax4Fun' (Aßhauer et al., 2015). The Tax4fun produced the KO table (KO codes per samples), which we standardized by percentage of row. Using the package "PathView" and KO table, we evaluated the relative

abundance of each gene predicted across nitrogen metabolism (KEGG map 00910), sulfur metabolism (KEGG map 00920), methane metabolism (KEGG map 00680), and carbon fixation pathways in prokaryotes (KEGG map 00720). The microbial association network using the package "SpiecEasi" (Kurtz et al., 2015). Microbial co-occurrence patterns were inferred using the covariance selection method and Stability Approach to Regularization Selection (StARS) as bootstrap. The microbial association network was based on the minimum occurrence of 40% of treatment samples, as indicated by Faust and Raes (2012). The SPIEC-EASI package produced the nodes and edges list, which were used in Gephi 0.9.2 (Bastian et al., 2009) to build the network plots. The topological properties of each network analysis, such as the number of interactions, the minimum distance between nodes (Newman, 2003), modularity (Newman, 2006), and Positive/Negative ratio (Ma, 2018), were performed using the package "igraph" (Csardi and Nepusz, 2006). Positive/Negative ratio (P/N) is obtained by the Equation (2), where P/N higher than 1 indicates low competition, and lower than 1 indicates high competition of microbial community (Ma, 2018).

$$\frac{P}{N} \text{ ratio} = \frac{\text{Number of positive edges}}{\text{Number of negative edges}} \quad (2)$$

The first step of correlation analyses between irrigation levels, soil type and potato variety on the total structure of the soil bacterial community (OTU table) were performed using 'vegan' package. Here, we used permutation MANOVA (PERMANOVA; Anderson, 2017) with the three-way correlation formula,

$$\text{dist (OTU table)} \sim (\text{potato production} + \text{potato tuber number}) \times (\text{irrigation levels} + \text{potato cultivar}) \quad (3)$$

These correlations were performed using "Bray-Curtis" as a microbial distance (*dist*), 9999 permutations, and no constrain permutation groups. The second step of PERMANOVA correlations was performed using the formula using two-way factorial design,

$$\text{dist (OTU table)} \sim (\text{potato production} + \text{potato tuber number}) \times (\text{irrigation levels} + \text{potato cultivar}) \quad (4)$$

Here, we used 'Bray-Curtis' as the microbial distance (*dist*), 9999 permutations. These correlations aimed to verified one-way correlations such as microbial tables related with potato experiment results (production and tuber number), and also two-ways correlations such as microbial tables related with irrigation levels \times potato production. At this second step, the objective of the analysis was more focused on the microbial community. Thus, soil types were used as a constraint permutation group. The microbial tables used were OTU table (complete, and filtered by phyla and class), KO table (obtained from Tax4fun method), and co-occurrence nodes (OTU table filtered by nodes

TABLE 1 | Averages and standard deviation (s.d.) of the soil chemical composition for silt and sand soils.

Chemistry composition	Sand soil		Silt soil	
	Mean (mg/Kg of soil)	s.d.	Mean (mg/Kg of soil)	s.d.
Ni	0.20 b	0.03	0.27 a	0.01
Cr	0.25 a	0.01	0.21 b	0.01
Pb	0.87 a	0.01	0.68 b	0.05
Cu	0.45 b	0.05	1.02 a	0.02
Zn	3.13 b	0.23	4.99 a	0.33
Na	37.97 b	0.30	39.67 a	0.40
S	16.08 b	1.99	30.28 a	0.42
P	186.70 a	7.01	58.03 b	3.28
K	41.09 b	9.66	119.85 a	5.90
Ca	864.30 a	151.83	673.54 a	26.83
Mg	45.39 a	7.36	42.54 a	1.74
Al	1663.60 b	13.24	1861.55 a	33.74
B	40.87 a	0.16	40.64 a	0.21
Fe	124.16 a	1.75	95.19 b	2.13
Mn	8.78 a	0.17	8.18 a	0.53
Cd	0.04 a	0.01	0.04 a	0.00
Co	0.06 a	0.02	0.09 a	0.00
Si	745.40 a	7.55	719.00 b	6.56
Ti	0.87 a	0.02	0.79 a	0.07
As	0.01 a	0.10	0.09 a	0.06

The letters indicates the significant variation for each element, considering Tukey test and ANOVA-test ($p < 0.05$)

with interaction in network analysis). The alpha diversity was evaluated by Shannon index (H' ; equation 5), which were compared by ANOVA-test and ranked by Tukey test (confidence level of 95%)

$$H' = - \sum_{i=1}^R p_i \ln p_i \quad (5)$$

The Shapiro-Wilk normality test was performed using package 'vegan' (Oksanen et al., 2013). Normal distribution of alpha diversity values was obtained after interquartile range transformation.

RESULTS

The Irrigation Affected the Total Potato Production

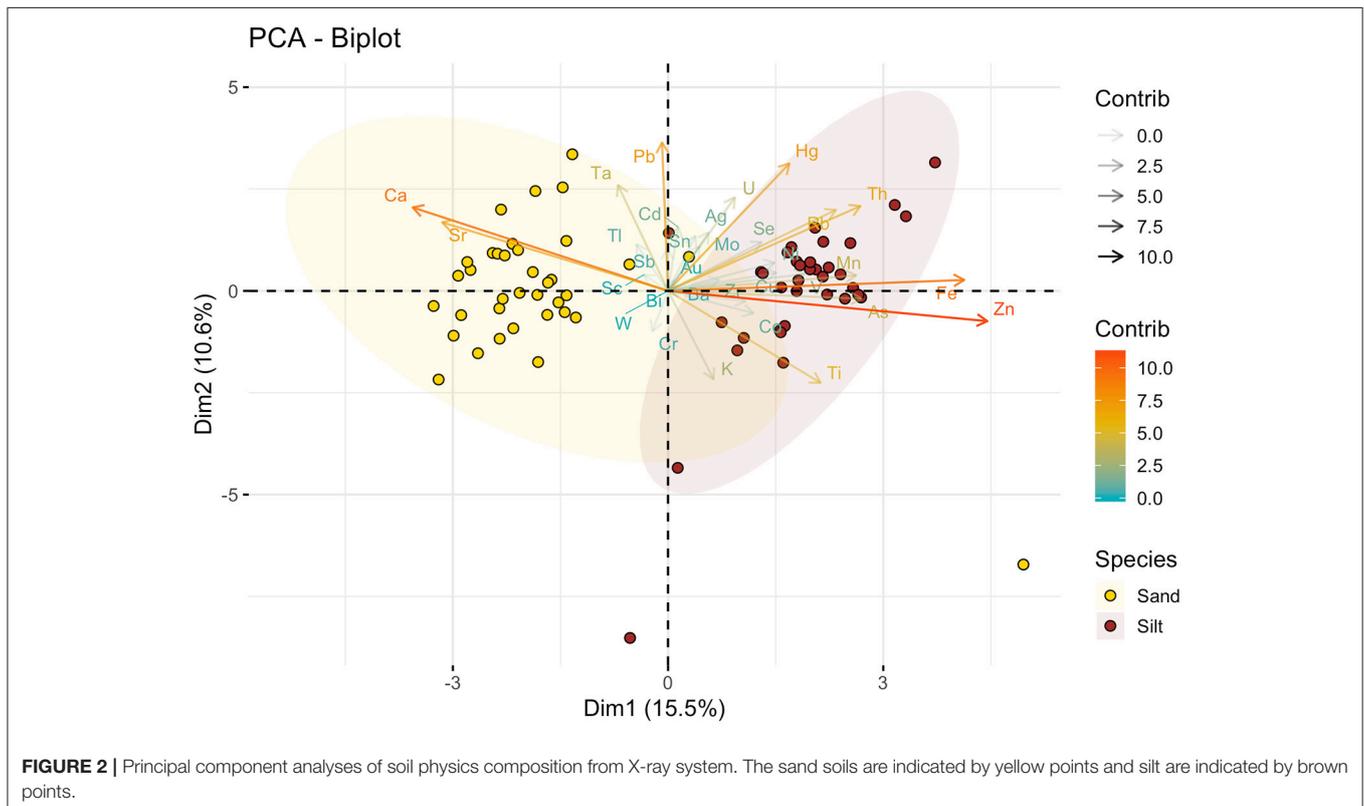
The values of soil matric potentials were confirmed around -15 , -25 , -30 , and -45 kPa for the irrigation levels A, B, C, and D, respectively (Figure 1A), showing a significant difference (ANOVA, p -value < 0.05). The elemental composition and available nutrients of each soil type are indicated in Figure 2 and Table 1, respectively. In general, the two soil types showed significant variances in the elemental composition, and it was not observed differences in the soil matric potentials between soil types, as expected (Figure 1A). In Figure 1B, we observed

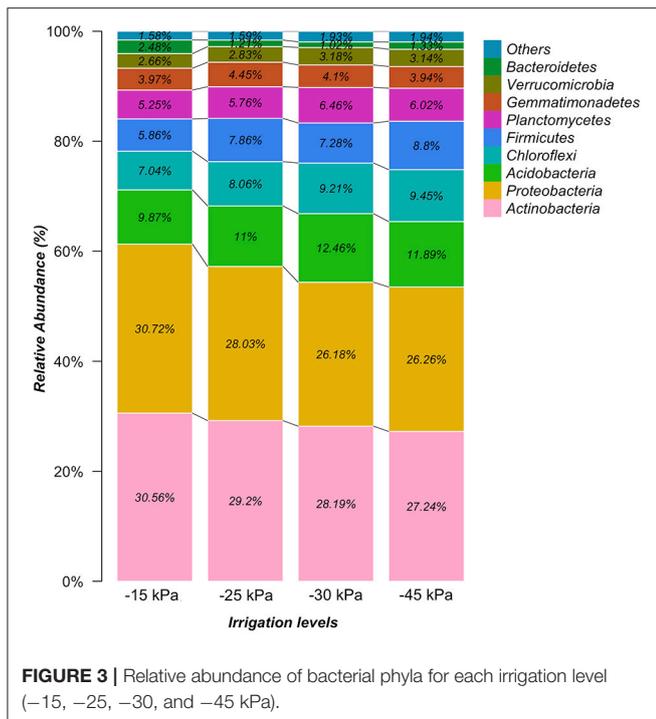
that the total potato production (Kg/pot) was affected by the irrigation levels. While the soil matric potentials of -15 (44.27 t/ha) and -25 kPa (44.95 t/ha) presented the highest potato mean yield, treatments with -30 (30.72 t/ha) and -45 kPa (12.21 t/ha) showed a significant reduction in the potato mean yield (ANOVA, $p < 0.05$). Furthermore, it was not observed a significant difference in potato production (ANOVA, p -value > 0.05) for soil types and potato cultivars (Figures S2A,C).

The number of potato tuber per pot was similar across the soil matric potentials -15 , -25 , and -30 kPa, showing significant reduction only for -45 kPa (Figure 1C). As indicated in Figures S3B,D, the number of potato tuber was significantly different across the soil type (sand $>$ silt), and potato cultivars (Goldrush $>$ Red Maria $>$ Envöl). We also verified the relative mass per potato tuber (Kg/unit) which showed a significant variance across the soil matric potential (Figure 1D), with highest values for -25 kPa. The irrigation level with -15 kPa showed an intermediate average of relative mass per potato tuber between the irrigation levels -25 and -30 kPa.

Taxonomic Composition, Predicted Functionality, and Microbial Interactions Across Irrigation Levels

In general, the irrigation levels affected the taxonomic composition of the soil bacterial community. In Figure 3, there is a clear trend of decreasing the relative abundance of phyla *Actinobacteria* and *Proteobacteria* from -15 to -45 kPa. Also in general, it was observed a trend of increasing of phyla





Acidobacteria, *Firmicutes*, and *Chloroflexi* from –15 to –45 kPa. Retrieved OTU were classified into 704 bacterial genera across the soil samples (Table S1). We observed that *Bacillus* (average of 4.9%), *Arthrobacter* (average of 4.5%), *Streptomyces* (average of 4.3%), *Bradyrhizobium* (average of 3.3%), and *Variibacter* (average of 3.2%) were the five most abundant genera classified. In general, we observed an effect of the irrigation levels on the genera composition, such as *Bacillus* (increasing pattern) and *Arthrobacter* (decrease pattern) from –15 to –45 kPa. Also, we verified the soil bacterial alpha diversity (by Shannon index). As the values of the alpha diversity from –45 kPa did not follow a normal distribution (Shapiro–Wilk test, $p < 0.01$) we transformed the data by interquartile range. The alpha diversity indicated unexpected results for each irrigation level (Figure 4). The irrigation levels with higher potato production (–15 and –25 kPa) showed the lowest alpha diversity. On the other hand, irrigation levels of –30 and –45 kPa showed high alpha diversity.

We tested four metabolic paths, those of nitrogen, sulfur, methane, and carbon fixation for prokaryotes, aiming to verify the impacts of irrigation levels on the potential functionality of soil bacterial community. The results obtained for each metabolic paths are indicated in the Supplemental Material (Figures S3–6). Overall, the soil matric potential affected the occurrence of predicted genes in soil. As indicated in Figure 5, more than 50% of the gene *ccsB* (K15233)—belonging to carbon fixation in prokaryotes—was predicted for the irrigation level –25 kPa, while no prediction was found in –45 kPa. For nitrogen metabolism, the genes *amoABC* (K10944, K10945, and K10946) were predicted to be less abundant in irrigation level with –45 kPa (21%) compared with the other treatments. Also for the irrigation level –45 kPa, it was observed higher prediction for

genes related to the reduction process, such as 27% of the gene *cysNCD* (K00955 and K00957) in sulfur metabolism, and 78% of genes *mtaA* (K14080) and *mtbB* (K16178) encoding methyltransferases involved in methanogenesis.

The soil microbial co-occurrence patterns also showed a significant variation across soil matric potential. The network graphs are presented in Figure 6, and their analyses are indicated in Table 2. Overall, we observed that the irrigation level with –25 kPa promoted the lowest quantity of edges specifying pairwise covariation of OTU (10,193), with lower average connections per node (average degree of 9.97). We also observed that this irrigation level showed the highest Positive/Negative ratio, with the highest minimum distance between the nodes (minimum spanning tree of 3.10), and highest modularity (0.42). On the other hand, the irrigation level with –45 kPa presented the highest number of edges (13,044). We also observed that the irrigation level with –45 kPa presented a bacterial network with the highest node connectivity (Average degree of 12.13), and lowest Positive/Negative ratio (1.62). The irrigation levels of –15 and –30 kPa showed similar ecological network topology.

We verified the composition of phyla displaying connectivity in ecological networks and also evaluated their Positive/Negative ratio across the irrigation levels (Table 3). The three phyla *Proteobacteria*, *Actinobacteria*, and *Acidobacteria* displaying the highest levels of connectivity showed the highest Positive/Negative ratio at irrigation level at –25 kPa. This irrigation level also showed the highest Positive/Negative ratio for *Bacteroidetes* (2.08) and *Verrucomicrobia* (2.44); and lowest Positive/Negative ratio for *Armatimonadetes* (1.03) and *Nitrospirae* (1.83). We also observed others patterns in phyla interactions, such as *Firmicutes* Positive/Negative ratio reduced from –15 kPa (4.59) to –45 kPa (2.22).

Correlation Between Soil Bacterial Community, Irrigation Levels, and Potato Production

The first step of correlation analyses aimed to verify the effect of irrigation levels, soil type and potato variety on the total structure of soil bacterial community. The PERMANOVA analysis indicated that soil types (sand and silt), water management treatment and potato variety showed a significant correlation with soil bacterial community. In Figure 7 we observed that the soil type explained 44.95% of the soil microbial community variation, while irrigation levels and potato cultivar explained 4.69 and 2.31%, respectively. We also observed two-way correlations, where irrigation level \times soil type (3.1%), and irrigation level \times potato cultivar (2.31%) were also explained by the variation in soil microbial community. The second step of analyses aimed to correlate the potato tuber number (unit/pot) and potato production (Kg/pot) with taxonomic composition (OTU table), predicted functionality (KO table), and also microbial interactions nodes (OTU table filtered by network nodes). In overall in Table 4, we observed that the potato tuber number showed a correlation with all microbial tables (taxonomic, functionality, and interaction). Besides, the correlation between potato tuber number and each microbial

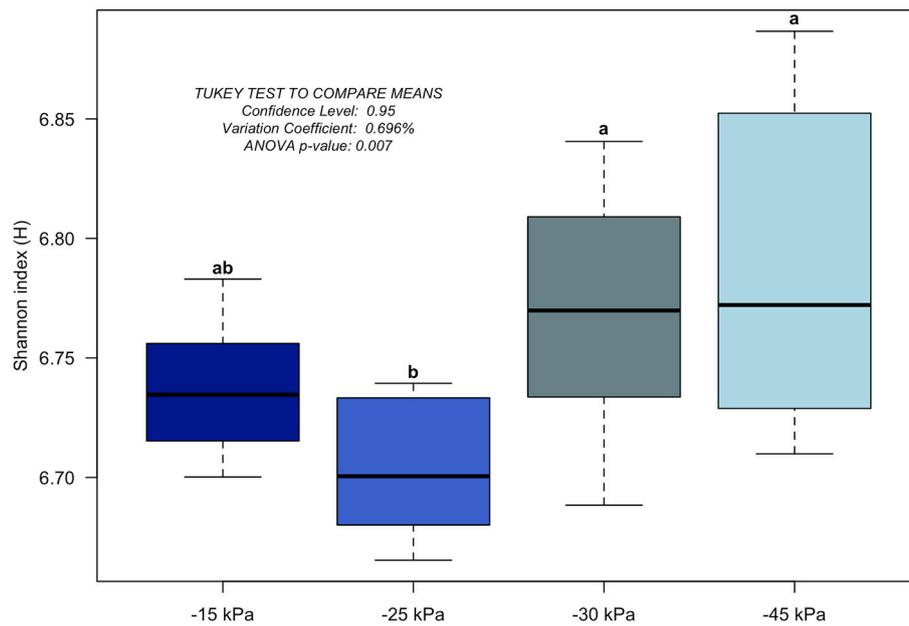


FIGURE 4 | Boxplot of alpha-diversity by Shannon index for each irrigation level (–15, –25, –30, and –45 kPa). The averages were compared by ANOVA and Tukey test (considering p -value < 0.05) and they are indicated by the small letters.

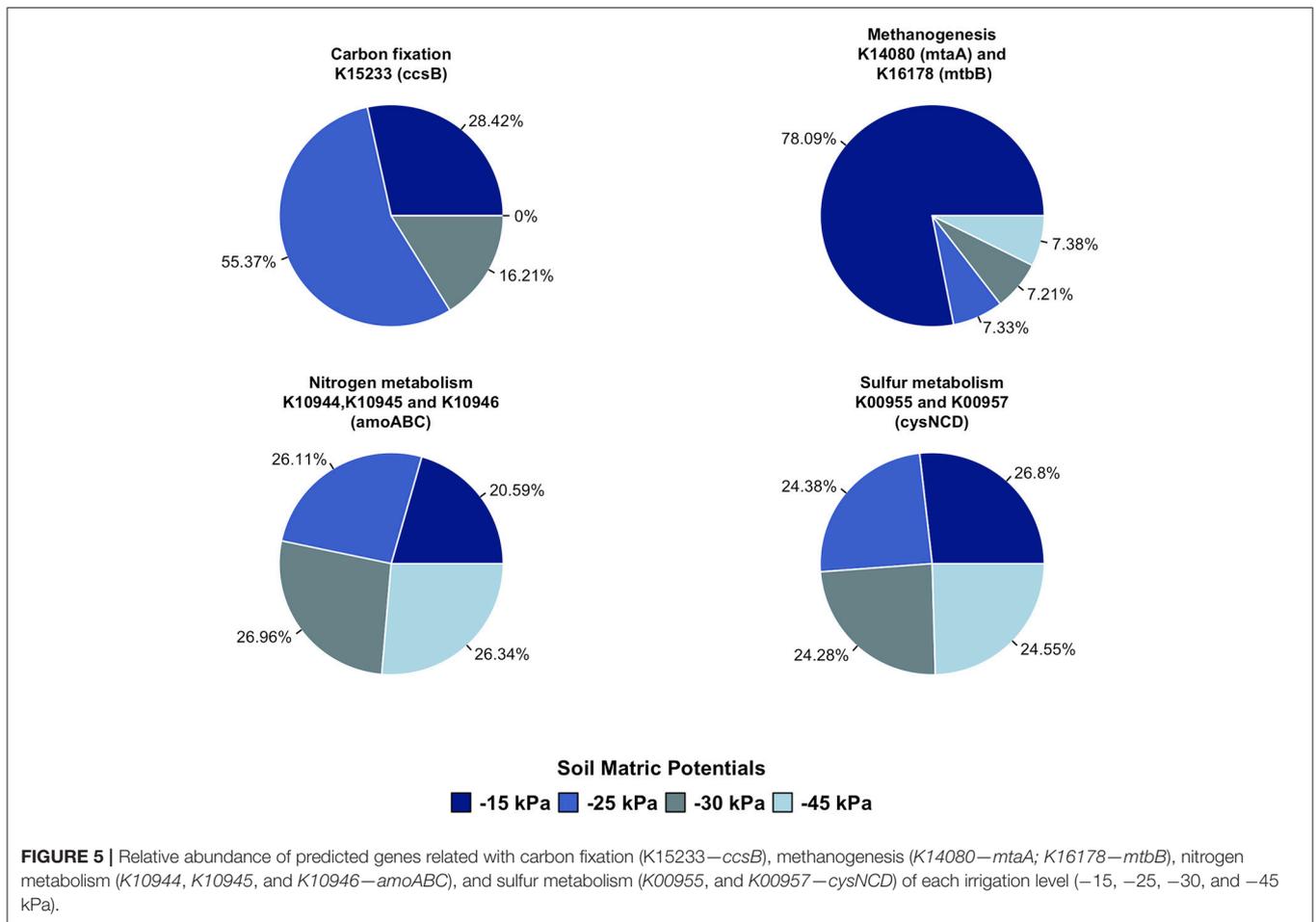
tables were similar, such as 15.2% for taxonomic composition, 15.6% for co-occurrence table, and 14.1% for predicted functionality table. The PERMANOVA analyses indicated that the phyla *Firmicutes* (20.75%), *Gemmatimonadetes* (25.80%), and *Chloroflexi* (20.75%) were the phyla with the highest correlation with potato tuber number. At the class level, *Thermoleophilia* (19.46%) and *Bacilli* (19.79%) were more correlated with potato tuber number. For the correlation between predicted functionality and potato tuber number, we verified the highest and lowest correlation in the Sulfur cycle (15.16%) than Carbon fixation (12.23%), respectively.

Interestingly, it was not observed a significant one-way correlation between microbial tables \times potato production, with an exception for carbon fixation (5.42%) and sulfur cycle (5.64%). However, we observed a significant correlation in a two-way correlation using the factorial design of *microbial tables* \sim (*irrigation* \times *potato production*). This two-way correlation indicated a stronger correlation (18.73%) between predicted functionality and irrigation \times potato production. Also, the carbon fixation explained 20.44% of the variation on the correlation irrigation \times potato production. The co-occurrence table (nodes selected in network analysis) showed a higher correlation with irrigation \times potato production (13.92%) than taxonomic composition table (12.87%), which present all OTU's. We also observed *Firmicutes* and *Proteobacteria* was the phyla with the highest correlation with irrigation: potato production. *Gammaproteobacteria* (13.9%), *Chloroflexi* (13.71%), and *Thermoleophilia* (13%) were the three classes with the highest correlation with irrigation: potato production. Three-way correlations with the factorial design irrigation levels \times potato variety \times potato tuber number showed no significant correlation ($p > 0.05$) with microbial tables.

DISCUSSION

Reducing water use is among the most challenging issue in irrigated agriculture, and one way to contribute to this challenge is to integrate soil microbial ecology knowledge to fine-tune irrigation strategies. This study evaluated the effect of four irrigation levels (–15, –25, –30, and –45 kPa) on potato productivity and soil microbial community across three potato cultivars and two soil types (silt and sand). The irrigation levels affected the potato production (Kg/pot), suggesting the soil matric potential –25 kPa as the optimal irrigation level for potato plants. Comparing the irrigation levels from –15 to –25 kPa, we estimate an increase of 680.74 Kg of potato per ha, and reduction of \sim 10% in the soil water content. Thus, irrigation levels higher than –25 kPa, such as –15 kPa, have excessive irrigation, and lower than –25 kPa, such as –30 and –45 kPa, deficient irrigation. The absence of difference in potato production (Kg/pot) of –25 and –15 kPa demonstrated that high production could be reached with the minimal use of water. Our experiment also indicated that the soil matric potential –25 kPa resulted in best values for the relative mass of potato tuber (Kg/unit of potato accordingly). Thus, we compared the soil microbial community at –25 kPa with other soil matric potentials aiming to reveal soil microbial indicators associated with potato production, and to improve their irrigation management efficiently.

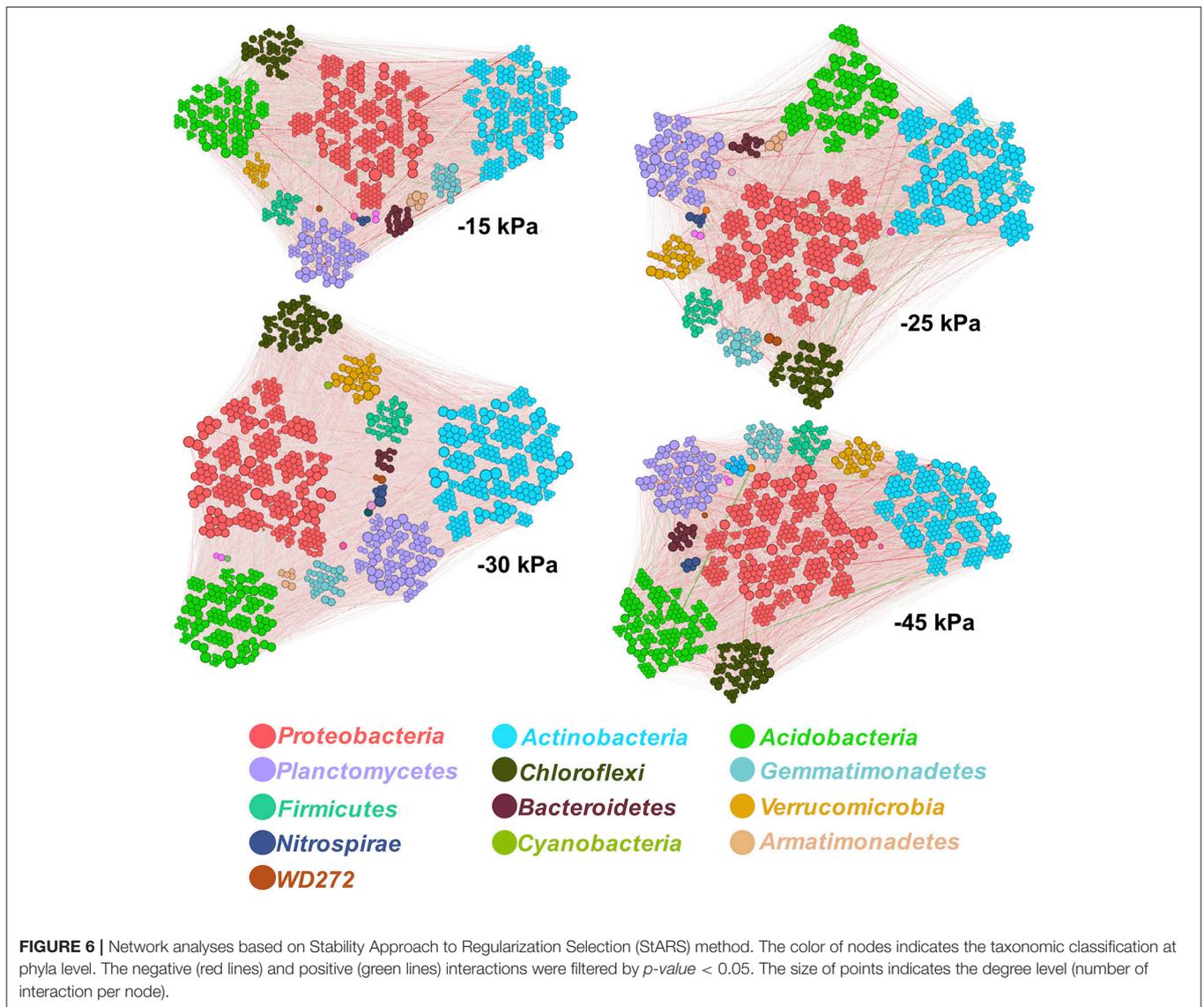
The first set of questions was addressed to the effect of irrigation levels on soil bacterial composition, functionality, and interaction. Five most abundant bacterial phyla (such as *Proteobacteria*, *Actinobacteria*, *Acidobacteria*, *Firmicutes*, and *Chloroflexi*) shift in response to soil water content. As reviewed by Naylor and Coleman-Derr (2018), the bacterial community has been presented evolutionary survival strategies under drought



stress. These strategies are related to three aspects in general: morphological resistance (e.g., sporulation activity), life strategy (e.g., oligotroph or copiotroph), and interaction with plants (e.g., plants recruitment). Thus, the increases of Firmicutes phyla, as well as genus *Bacillus* (Firmicutes phylum), in samples with low quantity of water (−45 kPa) can be explained by their sporulation capacity (Vos et al., 2009). Copiotroph is microorganisms that grown fast and requires a rich environment, especially related to carbon (Ho et al., 2017). Irrigation selects copiotroph microorganisms (Hartmann et al., 2017). The *Proteobacteria* is classified as copiotroph group (Fierer et al., 2007), explaining their reduction under drought condition (−45 kPa). In opposite point, the *Acidobacteria* has been classified as oligotrophic (i.e., microorganisms with slow growth and poor environment adapted) (Ho et al., 2017), explaining their increase in treatments with low quantity of water (−45 kPa). Plants under drought stress increase the exudation of organic carbon (Henry et al., 2007), recruiting specific groups of soil microorganisms (Naylor and Coleman-Derr, 2018). The high occurrence of the genus *Bradyrhizobium* (*Proteobacteria* phyla) at the −30 kPa treatment could be related to microbial recruitment of potato under drought stress. By similar strategy, different microbial groups may be selected by plants under different irrigation levels, such

as the phyla *Actinobacteria*, as well as the genus *Arthrobacter* (*Actinobacteria* phyla) showing higher abundance at −15 kPa.

The carbon cycle has been associated to plant response to drought systems, especially with the plant exudation, and microbial recruitment (Naylor and Coleman-Derr, 2018). The predicted functionality indicated interesting variation at predicted genes related to carbon fixation and emission. The gene *ccsB*, predicted in 55% of the samples with the irrigation level of −25 kPa, is related to the production of *citryl-CoA synthetase* enzyme (Aoshima et al., 2004). The gene *ccsB* acts on the reduction of the citrate cycle (Arnon-Buchanan cycle) where the CO₂ is fixated into the microbial cells. These findings suggest that the microbial community in −25 kPa (i.e., optimal water level) is more related to carbon fixation than in the other irrigation levels. For the other genes predicted, the genes *mtaA* [coenzyme M methyltransferase—EC:2.1.1.246] (Sauer and Thauer, 1999), and *mtbB* [protein Co-methyltransferase—EC:2.1.1.249] (Soares et al., 2005) are both related with methanogenesis. The prediction of genes was strongly related to −15 kPa (i.e., excessive irrigation), suggesting a possible reduction in the oxygen and emission of CH₄. It is important to note that this study not aimed to verify gas emission, but suggests that an optimal irrigation level may be associated with



carbon cycle (such as high carbon fixation and low carbon emission). Besides the slight variation across the treatments, the prediction of genes related to the sulfur and nitrogen metabolic paths indicates a variation between the irrigation level with excess available water (−15 kPa) and the other levels. The genes *cysNCD* [bifunctional enzyme CysN/CysC—EC:2.7.7.4 2.7.1.25 and sulfate adenylyltransferase subunit 2—EC:2.7.7.4] (Leyh et al., 1992) are related to sulfate reduction producing hydrogen sulfide (H₂S). This gene has been found in soils with low oxygen levels, such as wetlands (Pester et al., 2012), reinforcing the results associated with excessive irrigation (−15 kPa). Also, the genes *amoABC* [ammonia monooxygenase—EC:1.14.18.3 1.14.99.39] (Norton et al., 2002) related to oxidation of ammonium (NH₄⁺) producing nitrite (NO₂⁻) were predicted to be slightly less prevalent in irrigation level with −15 kPa than in the other treatments. The ammonium oxidation may occur under either aerobic or anaerobic conditions (i.e., anammox)

(Van de Graaf et al., 1995); however, the gene relates to ammonia monooxygenase under aerobic conditions (Norton et al., 2002), agreeing with the lower prediction in the treatment with excessive water available (−15 kPa).

The potential microbial interaction, based on co-occurrence or covariation, has been suggested as a promising indicator of system stability and quality. Karimi et al. (2017) observed a variation from 10 to 50% in the connections linked with system perturbation induced by changes in environmental conditions, affecting the local community. Overall, perturbed systems show lower connections (edges) than no-perturbed systems. For example, urban air (polluted) showed 40% fewer connections than rural air (no polluted) (Karimi et al., 2016). This pattern has also been observed in soil systems by different land uses, where crop soils have shown lower connections than natural forest soils (Lupatini et al., 2014). Thus, it was expected that irrigation levels which promote excess or deficit of available soil

TABLE 2 | Topological parameters of network analysis of each irrigation level.

Network attributes	Irrigation levels			
	−15 kPa	−25 kPa	−30 kPa	−45 kPa
Nodes ^a	991	1,025	1,054	1,073
Edges ^b	11,523	10,193	12,768	13,044
Int. Positives ^c	7,323	6,793	8,136	8,074
Int. Negatives ^d	4,200	3,401	4,632	4,970
Positive/Negative ratio ^e	1.74	2.00	1.76	1.62
Average Degree ^f	11.55	9.97	12.11	12.13
Average Path length ^g	2.36	3.10	2.25	2.53
Network diameter ^h	11	13	11	13
Modularity ⁱ	0.39	0.42	0.26	0.36
Members ^j				
Avg. Clustering Coef. ^j	0.05	0.04	0.04	0.04
Avg. Betweenness ^k	688.75	745.78	774.74	786.94

^aOTU's with at least one connection obtained by the co-occurrence analysis;

^bNumber of connections between the OTU's;

^cNumber of the positive connections, which may reflect facilitative interactions among microorganisms (Ma, 2018);

^dNumber of negative connections, which may reflect inhibitive interactions among microorganisms (Ma, 2018);

^eThe positive/Negative ratio indicates the level of competition of the microbial community (Ma, 2018). P/N ratio higher than 1 indicates low competition, and lower than 1 indicates high competition;

^fAverage of the number of connections per node;

^gThe small distance based on edges to connect all nodes in the network;

^hThe distance between the most extended nodes presented in the network (Newman, 2003);

ⁱIndicates the proportion of connections inside groups (identified by the algorithm) in the relations of connections with other groups. The groups are indicated as members (Newman, 2006);

^jIndicates the degree of each node in the network tend to cluster together;

^kThe measure of the centrality of the network, indicating the shortest path from nodes marginal located at the network to nodes in the center of the network.

water (considered as perturbed systems) would be related with system disturbance, showing lower connections than a system with an optimal level of available soil water (considered as a stable system). However, the results suggested the opposite, where the potato system with optimal irrigation level (−25 kPa) showed the lowest number of connections. Other topological properties observed for the irrigation level of −25 kPa were highest positive: negative ratio, the highest distance between groups of nodes (average path length), and densely connection inside of each group of nodes (modularity). The positive: negative ratio >1 indicates more quantities of promotion between the nodes (Xiao et al., 2017). Besides, the positive: negative ratio was higher than 1 for all of the irrigation levels, the irrigation level with less quantity of available water (−45 kPa) showed the lower positive: negative ratio. This result was also observed at phyla level. Then, we suggest that an optimal irrigation level (such as −25 kPa) it is not merely limited to the irrigation level supporting highest crop production but also a level where the microbial community shows higher promotion (positive interaction) between the nodes with densely intern interaction. On the other hand, the excess or water deficit (such as −15, −30, and −45 kPa) may promote more competition between the microbial community, increasing the total connections (edges).

The high number of connections may be related with a response of the microbial community to tolerate the water excess or deficit, such as an increase in the production of secondary metabolites (Braga et al., 2016). Thus, we suggest for irrigation levels in crop systems that the increase in the total connections may be related to water disturbance. These variations on the taxonomic composition, predicted functionality, and potential microbial interactions associated with irrigation levels confirms our first hypothesis.

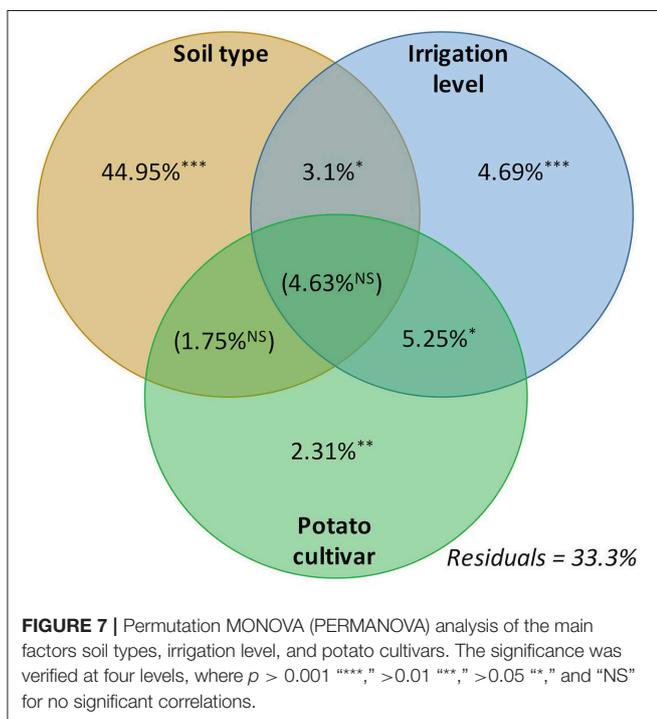
The second set of questions were addressed to evaluate the correlation between irrigation levels, soil type, and potato cultivar with soil bacterial community. The results confirmed that the difference in soil composition was strongly correlated with the structure of the soil bacterial community, suggesting that each soil type was a different source of soil bacterial community. Interestingly, the irrigation level was the only variable showing a significant one-way correlation (bacterial community ~ irrigation level), and also two-way interactions with soil type (bacterial community ~ irrigation level × soil type) and potato cultivar (bacterial community ~ irrigation level × potato cultivar). This result suggested that the soil bacterial community is not only affected by the available quantity of water but also by an effect that water may promote on the soil and potato cultivar. It has been observed that variation on the water supply affects the soil microbial community in natural (Taketani et al., 2017) and crop (Bastida et al., 2017) systems. Our first set of correlations confirmed an effect of soil matric potentials on soil bacterial community, and also reveal an effect of irrigation levels inside of other factors (soil type and potato cultivars). Nevertheless, there are still many unanswered questions about the association between crop plants and soil microbial communities across different environmental conditions, including systems with water excess or deficit.

The second group of correlations analyses was addressed to potato yield, where we evaluated the correlation between the production (i.e., potato production and potato tuber number) with microbial composition, predicted functionality, and co-occurrence nodes. Overall, the results suggested that soil microbial community (composition, predicted functionality, and co-occurrence nodes) are one-way correlated with the potato tuber number, but two-way correlated with potato production and irrigation levels (i.e., irrigation level × potato production). The two-way correlation suggested that only when the variation in potato production is associated with irrigation level information by the factorial design, they present a significant correlation with bacterial community variances. The results also suggested that the potato tuber number was more correlated with taxonomic table (OTU table) and co-occurrence nodes, while the potato production was more two-way correlated with predicted biogeochemistry cycles, mainly the carbon cycle. The phylum *Gemmatimonadetes* showed the highest correlation with potato tuber number. This phylum has been already identified in soil cultivated with potato (Liu et al., 2014), and their distribution has been related to soil moisture (DeBruyn et al., 2011). Besides the small variation of *Gemmatimonadetes* relative abundance across the irrigation levels, the −45 kPa

TABLE 3 | Relative abundance (percentage) and Positive/Negative ratio* at phylum level for the nodes of each network analysis.

Phyla	Irrigation levels			
	–15 kPa	–25 kPa	–30 kPa	–45 kPa
<i>Proteobacteria</i>	32.84% (1.59)	31.99% (2.08)	31.98% (1.68)	32.19% (1.85)
<i>Actinobacteria</i>	26.73% (1.67)	25.78% (1.83)	25.12% (1.62)	24.12% (1.56)
<i>Acidobacteria</i>	13.81% (1.81)	15.12% (2.21)	15.15% (1.89)	15.16% (2.17)
<i>Planctomycetes</i>	8.91% (1.73)	9.11% (1.59)	9.41% (1.75)	8.41% (1.71)
<i>Chloroflexi</i>	5.91% (1.88)	5.91% (1.72)	6.30% (1.77)	6.38% (2.44)
<i>Gemmatimonadetes</i>	3.20% (2.95)	3.29% (2.18)	3.01% (1.53)	3.05% (2.37)
<i>Firmicutes</i>	2.90% (4.59)	3.78% (2.70)	3.86% (2.30)	3.88% (2.22)
<i>Bacteroidetes</i>	1.70% (1.55)	1.16% (2.08)	0.85% (1.28)	1.39% (1.4)
<i>Verrucomicrobia</i>	2.70% (2.26)	2.71% (2.44)	3.01% (1.62)	3.23% (1.90)
<i>Armatimonadetes</i>	0.70% (1.65)	0.48% (1.03)	0.56% (2.36)	0.46% (1.85)
<i>Nitrospirae</i>	0.40% (3.6)	0.48% (1.83)	0.56% (2.26)	0.83% (2.27)
WD272	0.20% (3)	0.19% (2)	0.19% (3.5)	0.90% (2)
<i>Cyanobacteria</i>	–	–	1.80% (2.17)	–

*Positive/Negative ratio is a division between the positive and negative connections of each network analysis. Positive/Negative ratio higher than 1 indicates low competition, and lower than 1 indicates high competition of microbial community (Ma, 2018).



showed the lowest *Gemmatimonadetes* relative abundance and also the lowest potato tuber number (unit/pot). These findings suggest that the *Gemmatimonadetes* occurrence may be associated with potato tuber formation. For potato production, we suggest a different and more complex interaction where the bacterial community correlated may be better classified by functionality, such as carbon cycle (fixation and emission), than their taxonomic affiliation. Further, the irrigation level would promote or reduce the bacterial functionality, which may

regulate the potato production in this system. It is important to note that these general suggestions are one of the other explanations that could justify the link between microbial predicted functionality, irrigation levels, and potato production. Besides some questions remain about this link, we confirmed our second hypothesis suggesting that the soil bacterial interaction and functionality have a potential association with potato yields.

The third hypothesis tested was whether the irrigation level with the highest production is the same as the highest bacterial diversity. The microbial diversity has been considered as one of the most important indexes of soil quality (Brussaard et al., 2007). The high microbial diversity has benefits for the cropping system, e.g., the crop rotation improving the soil microbial diversity and promoting disease suppressive capacity in soil (Peralta et al., 2018). Thus, we expected that the irrigation level with higher production would also show a higher soil bacterial diversity. However, the irrigation levels –25 and –15 kPa, which showed the highest potato production also showed the lowest alpha-diversity. It is crucial to note that this result did not disqualify the microbial soil diversity as an excellent soil quality indicator. This result suggested that, in crop systems, the alpha-diversity of the bacterial community may also indicate water stress (excess or deficit), also affecting the potato production. For this fact, we propose a similar explanation used for the potential microbial interactions, where the excess or deficit of water may increase the connections of soil bacterial community, producing secondary metabolites and also opening different niches in the system. Thus, the opening of new niches would be a collateral effect of the microbial community interactions aiming to tolerate the water stress. This unexpected absence of linkage between alpha diversity and productivity might be more important in the field (e.g., the impact on long-term productivity), which also could include other variables such as microbial

TABLE 4 | PERMANOVA analysis between potato tuber number, potato production, and irrigation: production with the microbial tables taxonomic composition (OTU table), predicted functionality (KO table), and microbial interaction (OTU table filtered by nodes).

Microbial tables	Tuber number (unit/pot)	Production (kg/pot)	Irrigation x Production (kg/pot)
Taxonomic composition (OTU table)^a	15.16%	–	12.87%
Actinobacteria	14.28%	–	11.79%
<i>Actinobacteria</i>	12.29%	–	11.12%
<i>Thermoleophilla</i>	19.46%	–	13.00%
Proteobacteria	11.35%	–	13.00%
<i>Alphaproteobacteria</i>	10.25%	–	–
<i>Betaproteobacteria</i>	15.05%	–	12.64%
<i>Gammaproteobacteria</i>	12.00%	–	13.90%
<i>Deltaproteobacteria</i>	10.79%	–	9.67%
Acidobacteria	13.45%	–	11.90%
<i>Acidobacteria</i>	13.03%	–	–
Firmicutes	20.75%	–	14.35%
<i>Bacilli</i>	19.79%	–	14.64%
Planctomycetes	14.24%	–	11.00%
<i>Planctomycetacia</i>	14.37%	–	10.93%
Gemmatimonadetes			
<i>Gemmatimonadetes</i>	25.80%	–	12.31%
Verrucomicrobia	14.98%	–	–
<i>Spartobacteria</i>	17.09%	–	–
Chloroflexi	17.62%	–	12.48%
<i>Chloroflexi</i>	15.45%	–	13.71%
Predicted Functionality^b	14.10%	–	18.73%
<i>Carbon fixation</i>	12.23%	5.42%	20.44%
<i>Methane cycle</i>	14.36%	–	18.11%
<i>Sulfur cycle</i>	15.16%	5.64%	17.19%
<i>Nitrogen cycle</i>	13.86%	–	18.02%
Co-occurrence table (Nodes table)^c	15.59%	–	13.92%

^aOTU table that assigned using SILVA's ribosomal database–123 (Quast et al., 2013), and rarified at 54,535 sequences/sample depth;

^bKO table containing the functionality prediction composition obtained by the method and package "Tax4Fun" (Abzhauer et al., 2015);

^cOTU table filtered by the nodes identified in network analysis based on covariance selection method and Stability Approach to Regularization Selection (StARS) as bootstrap. In taxonomic composition (OTU table), the phyla are in bold followed by class.

distribution (beta diversity). Irrigation level with high potato production showed lower alpha-diversity, refuting our third hypothesis.

The present study was designed to determine the effect of irrigation levels on soil bacterial community, focusing on a high potato yield with minimal water use. These experiments confirmed that the water matric potential of -25 kPa as an optimal irrigation level for potato production, and also revealed unexpected patterns of soil bacterial community. The most apparent finding to emerge from this study is that the water excess or deficit promotes an increase in total microbial interaction, and also in bacterial alpha-diversity, which may be used in further studies to identify irrigation levels with optimal water use. It is important to emphasize that as the water was the only factor that varied in the experiment for two soil types and three potato cultivars, any possible variation among other soil parameters are a consequence of the water matric potential. The correlations revealed associations between the irrigation levels, potato production, and bacterial functionality,

especially in carbon fixation. These associations raised questions more specific for soil microbial community in crop systems. The advancement of this knowledge may lead to a more comprehensive assessment of the optimal irrigation levels of various crop production systems. Furthermore, the inclusion of ecological studies in field agriculture has the potential to contribute to the development of water management practices conducive to both increasing crop yield and maintaining a sustainable soil environment.

DATA ACCESSIBILITY

Fastq files, OTU table, and raw environmental data will be available for download from <https://doi.org/10.6084/m9.figshare.6840533>. The fastq files containing the genomic sequence (DNA) will also be available at European Nucleotide Archive (ENA; <https://www.ebi.ac.uk/ena/>), study number PRJEB27037.

AUTHOR CONTRIBUTIONS

TG, SG, and AR conceived the presented idea. SG conceived the original idea of irrigations levels on potato cultivars. J-PM and GL carried out the irrigation experiment. TG and PC performed the bioinformatic and statistical analysis. AR encouraged TG to investigate network analysis and supervised the findings of this work. All authors discussed the results and contributed to the final manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fenvs.2018.00161/full#supplementary-material>

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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