PAPER DETAILS

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Variation in the composition of the microbial community in the rhizosphere of potato plants depending on cropping season, cultivar type, and plant development stage

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Abstract

Changes in the structure of the rhizosphere microbiome are influenced by many factors. In the current investigation, the microbial community composition in the rhizosphere of four potato cultivars was monitored using the soil dilution plating technique on specific media. Tested cultivars were grown for two consecutive cropping seasons. Initial soil samples were collected before planting to assess the initial microbial soil species pool. During the growing period, rhizosphere samples were collected at three timing points. For both cropping seasons, the pH and EC of the rhizosphere varied upon sampling periods but not between cultivars. Bacterial and fungal populations at both cropping seasons and that of actinomycetes at the late-season crop were significantly increased by 35-55%, 14-18% and 17-42%, respectively, in the rhizosphere of all grown potato cultivars as compared to the initial soil stage. The relative abundance of *Pseudomonas* spp., actinomycetes, *Aspergillus* spp., and *Fusarium* spp. populations for all potato cultivars combined were 17.4, 26-64, 51-59 and 10-14% higher at the late-season than at the extra-early cropping season, respectively. For both cropping seasons and all sampled soils combined, the highest abundancies of fungal and actinomycetes communities were recorded at plant senescence and 15 days post-harvest. The total culturable bacteria were more relevant at plant emergence and 15 days post-harvest for the late-season crop and at plant senescence for the extra-early crop. The total culturable bacteria were more abundant in the rhizosphere of cvs. Spunta, Elata and El-Mundo at the late-season crop and that of cvs. Spunta and El-Mundo for the extra-early trial. The highest *Pseudomonas* spp. populations were associated to cvs. Cerata, Elata, and El-Mundo for the late-season crop and to Spunta, Elata and El-Mundo for the extra-early crop. The highest fungi counts were noted in the rhizosphere of cv. El-Mundo at the late-season crop and in Spunta for the extra-early trial.

Keywords: Cropping season, Development stage, Potato cultivars, Soil microbial community, Variation

Introduction

The relationship between plants and soil microbial community is very complex leading either to beneficial effects like nitrogen fixation, phosphate solubilization, production of plant growth stimulants, improved water retention, and biosuppression of plant diseases or to negative effects like occurrence of diseases (Ferreira et al., 2008; Berendsen et al., 2012; Singh et al., 2017).

Rhizosphere microbiota are highly dynamic (da Rocha et al., 2009) and they play a key role in plant health and growth and in the preservation of soil fertility (Berendsen et al., 2012). They are also considered as second genome for the plant and

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a key trait in major breeding programs (Marques et al., 2014).

It has been demonstrated that the composition of microbial communities is influenced by the seasonal and the diel changes in temperature (Turpault et al., 2007), the water content (Liddell et al., 2007), pH (Nelson and Mele, 2006), CO_2 concentration, O_2 levels (Jossi et al., 2006) and the biochemical composition of root exudates (Sung et al., 2006).

Different cultivars of the same plant species grown under similar cropping conditions might potentially promote the selection of a distinct microbial community associated to their tissues (Gomes et al., 2003; Ferreira et al., 2008). These shifts in the microbial community may occur due to the direct interaction with plants or as a result of an occurred stress (McDonald et al., 2004; Keswani et al., 2019). According to Sung et al. (2006), plants are capable to increase soil microbial population through their root exudates serving as nutrient sources for associated microorganisms. The chemical composition of root exudates varies between and within plant species (Grayer et al., 2004). The chemical composition of root exudates is the result of different belowground interactions and factors such as the nutritional status, plant age, biotic and abiotic stresses, and environmental conditions; all these factors may affect the microbial community associated to the rhizosphere (Griffiths et al., 1999). Although the effects of plant cultivar on rhizosphere communities has been evidenced on various crops i.e potato, maize, cannabis, and ray-grass (Chiarini et al., 1998; McDonald et al., 2004; Ferreira et al., 2008; Hannula et al., 2010; Winston et al., 2014), these effects are reported to be minimal as compared to the edaphic factors (particularly pH) or the plant development stage (van Overbeek and van Elsas, 2008; Marques et al., 2014; Pfeiffer et al., 2017). The root-associated microbiome variation can be greatly influenced not only by biotic and abiotic stressors, but also by traditional agricultural practices, such as crop rotation (Mardanova et al., 2019).

Potato (*Solanum tuberosum* L.) is an economically important crop worldwide and in Tunisia. Despite its significant role in food security (Devaux et al., 2014), studies about its interactions with microbial communities are scarce (Ferreira et al., 2008). Understanding microbial partnerships with the economically important crop *Solanum tuberosum* L. has the potential to improve plant production and yield, and obviously to maintain soil fertility (Berendsen et al., 2012; Winston et al., 2014). The characterization of soil microbial communities can be part of plant breeding programs and may be useful for studies of environmental risk assessment of selected potato cultivars (Ferreira et al., 2008). Moreover, analysis of the microbial community structure can be used as an indicator of soil quality and bio-fertility (van der Heijden and Wagg, 2013).

In the rhizosphere of potato plants grown under highly different conditions, the root bacterial taxa seem to be tightly linked to cultivars irrespective of the geographical site and the development stage (Pfeiffer et al., 2017). However, Weinert et al. (2011) observed similarities in the relative dominance of the bacterial phyla in potato rhizosphere irrespective of soil type and cultivar. As for the specific effects of the plant developmental stage, İnceğlu et al. (2013) showed that some bacterial genera are universally present at the plant flowering stage and this based on a 3-year monitoring of the microbial community associated to different potato genotypes grown on the same site.

According to İnceğlu et al. (2013), potato cultivars are associated with a core microbiome and that the specific patterns of that microbiota are more linked to the local environmental variations. Therefore, to test this hypothesis under Tunisian conditions, the structure of rhizosphere microbial community associated to four potato cultivars grown for two consecutive cropping seasons was monitored at plant emergence, senescence and 15 days post-harvest.

Materials and Methods

Plant Material

Four potato cultivars (cvs. Spunta, Elata, Cerata, and El-Mundo) were used in this study. The morpho-physiological characteristics of tested potato cultivars are listed in Table 1. Seed tubers were gratefully provided by the Regional Research Centre on Horticulture and Organic Agriculture, Tunisia.

Before use, tubers were previously disinfected by dipping for 5 min into 10% sodium hypochlorite solution, rinsed with tap water and air dried. For the initiation of their germination prior to planting, tubers were incubated for two weeks under 15-20°C, 60-80% relative humidity and natural room light.

Table 1. Characteristics of potato cultivars used in the study[aa] Seed tubers were gratefully provided by the Regional Research Centre on Horticulture and Organic Agriculture, Tunisia

Characteristic	Spunta	Elata	Cerata	EL-Mundo
Tuber				
Shape	Elongated oval	Elongated oval	Round	Elongated
Skin color	Yellow	Yellow	Pink	Yellow
Pulp color	Yellow	Yellow	White	Pale yellow
Length/Widgth	1.73	1.74	0.85	1.79
Dry matter content (%)	18.9	19.5	20.7	17.1
Stem				
Number/plant	2.55	3.05	2.75	4.40

[a]Seed tubers were gratefully provided by the Regional Research Centre on Horticulture and Organic Agriculture, Tunisia

Site Description and Experimental Design

Field trial was conducted at the experimental farm of the Regional Research Centre on Horticulture and Organic Agriculture located in Teboulba region (N35°38'38,256"; E10°56'48,458"). This site is under conventional farming system and has a history of potato and other vegetable crops rotations. The soil has a sandy clay texture (Organic matter 76 g/kg at 0-20 cm depth). The precipitation is daily measured and the monthly mean values are given in Table 2 and particularly from September to March corresponding to the experiment duration.

At their pre-germination, potato tubers were planted on October 03, 2017 and November 09, 2017 corresponding to the planting dates of two consecutive cropping seasons (i.e. late season and extra-early). Seeds were arranged into plots consisting of 25 seeds per row and per plot. Seed rows were 0.75 m apart, with four rows per plot, and within-row spacing of 0.33 m.

The trial was carried out according to a completely randomized design with four replications of 100 seed tubers per cultivar. NPK fertilization ratios used for late-season and extra-early cropping seasons are (13:13:24) and (23:9:15), respectively. For both trials, agricultural practices commonly adopted by farmers in the region were used.

Table 2. Average monthly precipitation for the experimental site[a] during the essay (2017/2018 agricultural campaign)

	Precipitation (mm)
September	0
October	26.8
November	11
December	21.5
January	1
February	36
March	27

[a]The experimental farm of the Regional Research Centre on Horticulture and Organic Agriculture in Teboulba region (N35°38'38,256"; E10°56'48,458")

Soil Sampling

For the two crops, composite soil samples were collected from each cultivar and each individual plot at four time points i.e. before planting (soil initial stage), 30 days after planting (plant emergence), 120 days after planting (plant senescence) and 15 days post-harvest.

At each sampling time, 20 soil cores (7 cm in diameter × 15 cm in depth) were collected from the rhizosphere of each sampled plant and were combined to make one composite soil sample per cultivar and per plot. All soil samples were kept in individual plastic bags and were kept under cold conditions during transportation to the laboratory.

Once brought to the laboratory, they were passed through a 2-mm sieve to remove rocks and large organic debris. They were stored at 10°C and processed within 1 to 4 weeks after sampling (Larkin and Honeycutt, 2006). The bulk soil was divided into subparts.

Soil pH and Electrical Conductivity (EC)

Soil samples were air-dried before use. Soil extracts were prepared by suspending soil in distilled water in 1:10 soil/dH_2O ratio. They were filtered through Whatman paper No. 1 and chemically analyzed for the determination of their pH and electrical conductivity (EC) using a glass electrode (VWR sympHony®) and a digital conductivity meter (HANNA®), respectively.

Determination of Soil Microbial Community

The total counts of culturable soil microorganisms focused in this study (bacteria, actinomycetes and fungi) were determined by serial soil dilution and plating on various specific agar media according to Larkin and Honeycutt (2006) with slight modifications. For each soil subsample, 10 g were suspended into 90 ml of sterile distilled water, vigorously stirred for 30 min, serially diluted and a 100 µl sample was spread onto 10% Tryptic Soy Agar (TSA) for total bacterial counts, selective King's B medium (KB) amended with 75 mg/l of penicillin and 75 mg/L of cyclohexamide for *Pseudomonas* spp. counts, Yeast Malt Agar (ISP medium No. 2) amended with 75 mg/L of nalidixic acid and 100 mg/L of cyclohexamide for actinomycete counts, and Potato Dextrose Agar (PDA) amended with 300 mg/L of streptomycin sulphate for total fungal counts. Four replicates of one plate each were used for each soil subsample.

Bacterial and actinomycete plates were incubated at 28°C for 2 and 14 days, respectively, and fungal plates were maintained at 25°C for 7 days. *Trichoderma* spp., *Aspergillus* spp., *Penicillium* spp., and *Fusarium* spp. Colonies were identified based on their macro- and micro-morphological traits (Barnett and Hunter, 1987) under light microscope and counted separately.

Statistical Analysis

Data were subjected to a one-way analysis of variance (ANOVA) using Statistical Package for the Social Sciences (SPSS) software for Windows version 16.0. Data for the microbial community populations counts noted as Colony-forming Unit (CFU) per g of soil were analyzed after a logarithmic transformation to log CFU per g of soil. Data analyses for the pH and EC measurements and the microbial colonies counts were performed according to a completely randomized facto-

rial model with three factors (sampling period, field plot, and cultivars used). Four measures were processed for each soil subsample. The experiment was conducted over two consecutive cropping seasons. Means were separated using LSD or Duncan's Multiple Range tests at $P \leq 0.05$.

Data analyses for the microbial community counts at the initial stage (before planting) were carried out according to a completely randomized design and means were separated using Duncan's Multiple Range test at $P \leq 0.05$. Correlations between soil characteristics (pH and EC), and soil microbial community structure were carried out using bivariate Pearson's test at $P \leq 0.05$.

Results and discussion

Determination of pH and EC of Soil Samples

For both cropping seasons and at each sampling period, no differences in pH values were recorded between potato cultivars (Table 3). ANOVA analysis of the pH values of the soil samples collected from the rhizosphere of the four potato cultivars varied significantly (at $P \leq 0.05$) upon sampling periods and this for both cropping seasons. In fact, for the late-season trial and for all potato cultivars combined, the pH of rhizospheric soils sampled at plant senescence and 15 days post-harvest was 3.9 to 6.9% higher than that removed at plant emergence (Table 3). However, for the extra-early experiment, a significant decrease of about 9.5-10.1%, as compared to the plant emergence, was noted at senescence and at 15 days post-harvest (Table 3). For both cropping seasons and particularly at plant senescence and 15 days post-harvest, no differences were recorded between the pH values of rhizospheres of potato cultivars and that of the initial soil state (Table 3).

The electrical conductivity of the rhizosphere of the four cultivars tested was 50.6-60.6% and 63.9-67.9% higher at plant senescence and 15 days post-harvest for the late-season crop and at 15 days post-harvest for the extra-early trial, respectively (Table 3). For both cropping seasons, no differences were recorded between cultivars at each sampling period (Table 3). At all sampling periods combined, a significant increase in EC values by 18.9-71.1% and 16.8-73.4% was recorded in the rhizosphere of tested cultivars as compared to the initial soil state and this for the late-season and the extra-early crops, respectively (Table 3).

Some works suggest that rhizosphere communities are mostly influenced by edaphic factors (particularly pH) or plant growth stage (van Overbeek and van Elsas, 2008; Winston et al., 2014). Indeed, pH and EC are important determinants of community structure and diversity of soil microbiome. Bacterial communities appeared to differ strongly between the two fields used in Hannula et al. (2012) study, both for bulk soil and rhizosphere.

Soil Microbial Structure in the Rhizosphere of Tested Potato Cultivars

Among the aims of this study is to evaluate the variation of the microbial community in potato rhizosphere according to the environmental changes. For this reason, the field trial was conducted under two cropping seasons namely late-season and extra-early. The composition of microbial communities can fluctuate in response to seasonal and temperature changes (Turpault et al., 2007) and water content (Liddell et al., 2007) among other factors.

Bacterial Population

The total number of bacterial colonies (individual colonies looking like distinct and separate dots) grown on TSA medium varied significantly (at $P \leq 0.05$) depending on sampling periods, field plots and cultivars tested and their interactions (Figure 1). For the two cropping seasons, soil samples removed from the rhizosphere of the four potato cultivars showed 41.-50.2% and 34.6-54.9% significantly higher populations of the total culturable bacterial community (Figure 1) as compared to the initial stage (pre-planting) (1.39-1.47 log CFU/ g of soil) (Table 4). Bacteria are also found to be more abundant in the rhizosphere of rice plants than in bulk soil (Breidenbach et al., 2016).

For the late-season crop, bacterial colonies recovered from the rhizosphere of all potato cultivars at plant emergence (2.64-3.26 log CFU per g of soil) and 15 days post-harvest (2.66-3.05 log CFU per g of soil) 10.3 to 13.2% significantly higher than at plant senescence (2.46-2.66 log CFU per g of soil) (Figures 1A and 2A) and this for all field plots combined. The plant developmental stage is considered as a main factor affecting bacterial communities in the potato rhizosphere (van Overbeek and van Elsas, 2008; Marques et al., 2014).

The distribution of bacteria significantly varied upon field plots whatever sampling times and cultivars tested where the soil samples removed from the second, the third and the first plots had 3.7-7.1% more abundant bacterial community than the last one. Microorganisms are not distributed uniformly in the environment, rather their abundance and activity change along environmental gradients (Nunan et al., 2002).

The total culturable bacteria were significantly more abundant in the rhizosphere of potato cultivars Spunta, Elata and El-Mundo with about 2.76 to 2.82 log CFU per g of soil as compared to 2.63 log CFU per g of soil counted in Cerata rhizosphere (Figure 1A) and this for all sampling periods and field plots combined.

As shown in Figures 1B and 2B, the total bacterial population estimated at the extra-early crop was significantly 4.2-6.4% higher at plant senescence than at plant emergence and 15 days post-harvest. Combined data for all sampling periods and cultivars tested revealed that the total rhizosphere bacterial communities were 1.05 and 1.12 times more abundant in the third and last plots than in the first and the second ones, respectively. For all plots and sampling times combined, the highest population of culturable bacteria, of about 2.67 and 2.62 log CFU per g of soil, was noted in the rhizosphere of potato cultivars Spunta and El-Mundo which was 1.04-1.06 times more than that of Elata, and Cerata (Figure 1B). In the present investigation, shifts noted in the rhizosphere bacterial communities associated to the rhizosphere of the tested cultivars were related to both cultivars and plant developmental stages. These findings are in agreement with those of Inceoğlu et al. (2013) who also demonstrated that the plant growing stage influences the potato rhizosphere microbiota. Also, Chapapro et al. (2014) noted that plant developmental changes affect the rhizosphere microbial community.

As for the composition and the diversity of the bacterial community, the relative abundance of *Pseudomonas* spp. was found to be 17.4% higher in the rhizosphere of potato cultivars grown at the late-season than at the extra-early crop (Figure 3). *Pseudomonas* spp. distribution within potato rhizosphere varied significantly (at $P \leq 0.05$) depending on field plots and cultivars used, and the interactions between the last ones and the sampling periods, and this for the two cropping seasons. As given in Figures 2A and 4A, no significant variation was noted between *Pseudomonas* spp. population estimated at plant emergence, senescence and 15 days post-harvest and this for all field plots and cultivars combined. *Pseudomonas* spp. were found to be more abundant in the fourth and second field plots (1.1-1.3 times higher) than in the remaining plots and this whatever the sampling times and potato cultivars used. Soil systems are particularly heterogeneous, and this heterogeneity arises as a result of the interaction of a hierarchical series of interrelated variables that fluctuate at many different spatial and temporal scales (Ettema and Wardle, 2002). Different subsets of the community are distributed differently across the plot, and this is thought to be due to the variable response of individual populations to the spatial heterogeneity associated with different soil properties (Franklin and Mills, 2003).

As for the variation between tested potato cultivars, the highest *Pseudomonas* spp. counts, of about 2.13 to 2.31 log CFU per g of soil, were noted in soils sampled from Cerata, Elata and El-Mundo rhizosphere followed by those of Spunta, 1.94 log CFU per g of soil, , and this for all plots and sampling periods combined (Figure 4A).

Rhizosphere of all potato cultivars showed an increase in its *Pseudomonas* spp. population at all sampling period of about 1.6 to 2.39 log CFU per g of soil as compared to 1.09 log CFU per g of soil counted at the pre-planting stage (Table 4 and Figure 4A).

Table 3. Soil pH and electrical conductivity (EC) of soil samples[a] removed from the rhizosphere of four potato cultivars grown for two cropping seasons

pH			
Late-season crop			
Initial stage	7.8		
Sampling period	Emergence	Senescence	15 days post-harvest
Spunta	7.3 a B	7.9 a A	7.8 a A
Elata	7.4 a B	8 a A	7.6 a B
Cerata	7.3 a B	7.9 a A	7.8 a A
El-Mundo	7.5 a B	7.9 a A	7.6 a B
Extra-early crop			
Initial stage	7.1		
Sampling period	Emergence	Senescence	15 days post-harvest
Spunta	7.9 a A	7.1 a B	7 a B
Elata	7.9 a A	7.1 a B	7.1 a B
Cerata	7.9 a A	7.1 a B	7 a B
El-Mundo	8 a A	7.1 a B	7.1 a B

EC (dS/m)			
Late-season crop			
Initial stage	0.09		
Sampling period	Emergence	Senescence	15 days post-harvest
Spunta	0.117 a B	0.297 a A	0.259 a A
Elata	0.119 a B	0.267 a A	0.266 a A
Cerata	0.103 a C	0.250 a A	0.184 a B
El-Mundo	0.115 a B	0.297 a A	0.230 a A
Extra-early crop			
Initial stage	0.121		
Sampling period	Emergence	Senescence	15 days post-harvest
Spunta	0.087 a B	0.135 a B	0.449 a A
Elata	0.241 a B	0.135 a B	0.460 a A
Cerata	0.172 a B	0.156 a B	0.449 a A
El-Mundo	0.155 a B	0.135 a B	0.448 a A

[a] Soil sampled at the initial stage (Pre-planting), the emergence stage (30 days post-planting), the senescence stage (120 days post-planting), and at 15 days post-harvest.Values within each column, followed by the same lower letter are not significantly different according to Duncan Multiple Range test at $P \leq 0.05$. Values within each line, followed by the same up letter are not significantly different according to Duncan Multiple Range test at $P \leq 0.05$.

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Table 4. Soil culturable microbiome estimated at the initial stage (pre-planting)

Culturable microbiome (log CFU/g soil)			
Late-season crop			
Bacteria	*Pseudomonas* spp.	Actinomycetes	Fungi
1.47	1.09	0.68	1.91
Extra-early crop			
Bacteria	*Pseudomonas* spp.	Actinomycetes	Fungi
1.39	0.54	0.68	1.07

Pseudomonas population monitored for the extra-early crop varied significantly (at $P \leq 0.05$) upon sampling times, field plots and cultivars used, and their interactions. In fact, as shown in Figure 4B, the highest abundance of *Pseudomonas* spp. colonies, for all field plots and cultivars combined, was noted at plant emergence, with 2.23 log CFU per g of soil, as compared to plant senescence and 15 days post-harvest with 1.52 log and 0.29 log CFU per g of soil, respectively. Based on Ferreira et al. (2008) study, differences among rhizosphere bacterial communities are reported to be clearest at the earliest plant developmental stages and tend to decrease in later stages like senescence or after harvest. Whatever the sampling times and the cultivar grown, *Pseudomonas* spp. community was found to be more abundant in the first, the second and the third plot (1.3 to 1.5 times higher) than in the last one. For all sampling times and field plots combined, culturable *Pseudomonas* spp. were more abundant in the rhizosphere of cvs. Spunta, Elata and El-Mundo, 1.46-1.33 log CFU per g of soil, as compared to Cerata with 1.24 log CFU per g of soil. Weinert et al. (2011) reported that the composition of bacterial communities in the rhizosphere of potato plants is dynamic and is strongly influenced by the plant cultivar and the geographical site. Different microbial communities are found as defined by cultivar. According to Inceoğlu et al. (2012) soil and cultivar type shaped the potato root-associated bacterial communities that are responsive to some of the substrates in phenotype arrays.

Rhizospheric soils removed around the four potato cultivars sampled at plant senescence and emergence showed a significant increase (of about 5.2 and 7.6 times higher, respectively) in their average *Pseudomonas* community as compared to the initial soil stage (Table 4 and Figure 4B).

Actinomycetes Population

Soil samples removed from the rhizosphere of the four potato cultivars grown as a late-season crop showed an increment in the average actinomycetes populations of about 1.2 to 1.5 times higher than the initial soil (0.68 log CFU per g of soil) (Table 4 and Figure 5A).

The relative abundance of actinomycetes populations from all potato cultivars was more abundant at the late-season crop, of about 0.58-1.17 log CFU per g of soil, than at the extra-early crop where 0.21-0.86 log CFU per g of soil were noted (Figure 3). For both cropping seasons, no differences in actinomycetes populations were recorded between potato cultivars.

The culturable actinomycetes community monitored for the late-season crop varied significantly (at $P \leq 0.05$) depending on sampling periods × cultivars and field plots × cultivars interactions (Figure 5A). The highest average actinomycetes colonies, in rhizospheric soils of all tested potato cultivars grown in all field plots combined, was estimated at 0.84-1.04 log CFU per g of soil at 15 days post-harvest and plant senescence as compared to 0.72 log CFU per g of soil noted at plant emergence (Figures 2A and 5A).

In the extra-early crop, actinomycetes community varied significantly (at $P \leq 0.05$) depending on the interaction between sampling periods, field plots (within-field plots) and cultivars tested (Figure 5B). The actinomycetes population estimated in the rhizospheric soils associated to all tested potato cultivars, for all field plots combined, were 1.2-1.5 times more abundant at 15 days post-harvest and plant senescence than at emergence (0.45 log CFU per g of soil) (Figures 2A and 5B). Our results confirmed those of Broekling et al. (2008) who found that microbial community structures are abundant at the senescence stage and 15 days-post harvest.

Fungal Population

Soil samples removed from the rhizosphere of the four tested potato cultivars grown as late-season and extra-early crops showed a significant increase in their average fungal populations for all sampling periods which was estimated at 1.91-2.23 and 1.31-2.14 log CFU per g of soil, as compared to 1.91 and 1.07 log CFU per g of soil noted at the initial soil stage (pre-planting), respectively (Table 4 and Figure 5A). These results confirmed previous findings reporting that fungal composition and abundance is strongly influenced by the presence of potato roots (i.e. a strong rhizosphere effect) (Hannula et al., 2010). Mardanova et al. (2019) reported that bacterial and fungal microbiomes in the rhizosphere and rhizoplane of potato plants is remarkably diverse and is dependent on the host plant.

For both cropping seasons, the total culturable fungal community varied significantly (at $P \leq 0.05$) depending on sampling periods, field plots, cultivars grown and their interactions (Figure 6). The highest abundance of the fungal population was noted at 15 days post-harvest, with 2.09 log CFU per g of soil, as compared to 2.02 log and 1.92 log CFU per g of soil estimated at plant senescence and emergence, respectively and this for all field plots and cultivars combined (Figures 2A and 6A). Whatever the sampling times and the cultivars grown, the fungal population was more abundant in the first, the second and the third field plots (1.04- 1.06 times higher) than in the

last one. As shown in Figure 5A, for the late-season crop and for all plots combined, the highest fungal population, estimated at 2.09 log CFU per g of soil, was noted in the rhizosphere of cv. El-Mundo compared to 1.97-1.98 log CFU per g of soil noted in cvs. Cerata, Elata and Spunta rhizospheres.

For the extra-early cropping season, the total fungal population was 5.4 and 28.4% significantly higher at 15 days post-harvest than at plant senescence and emergence, respectively (Figures 2B and 6B). Hannula et al. (2012) indicate that at the senescence stage, plants harbor the most diverse, active and abundant fungal communities. The presence of the highest fungal biomass and diversity at senescence is more expected as decomposable plant material (dead roots and leaves) is already available while root exudation still continues thereby broadening the spectrum of substrate availability (Broeckling et al., 2008).

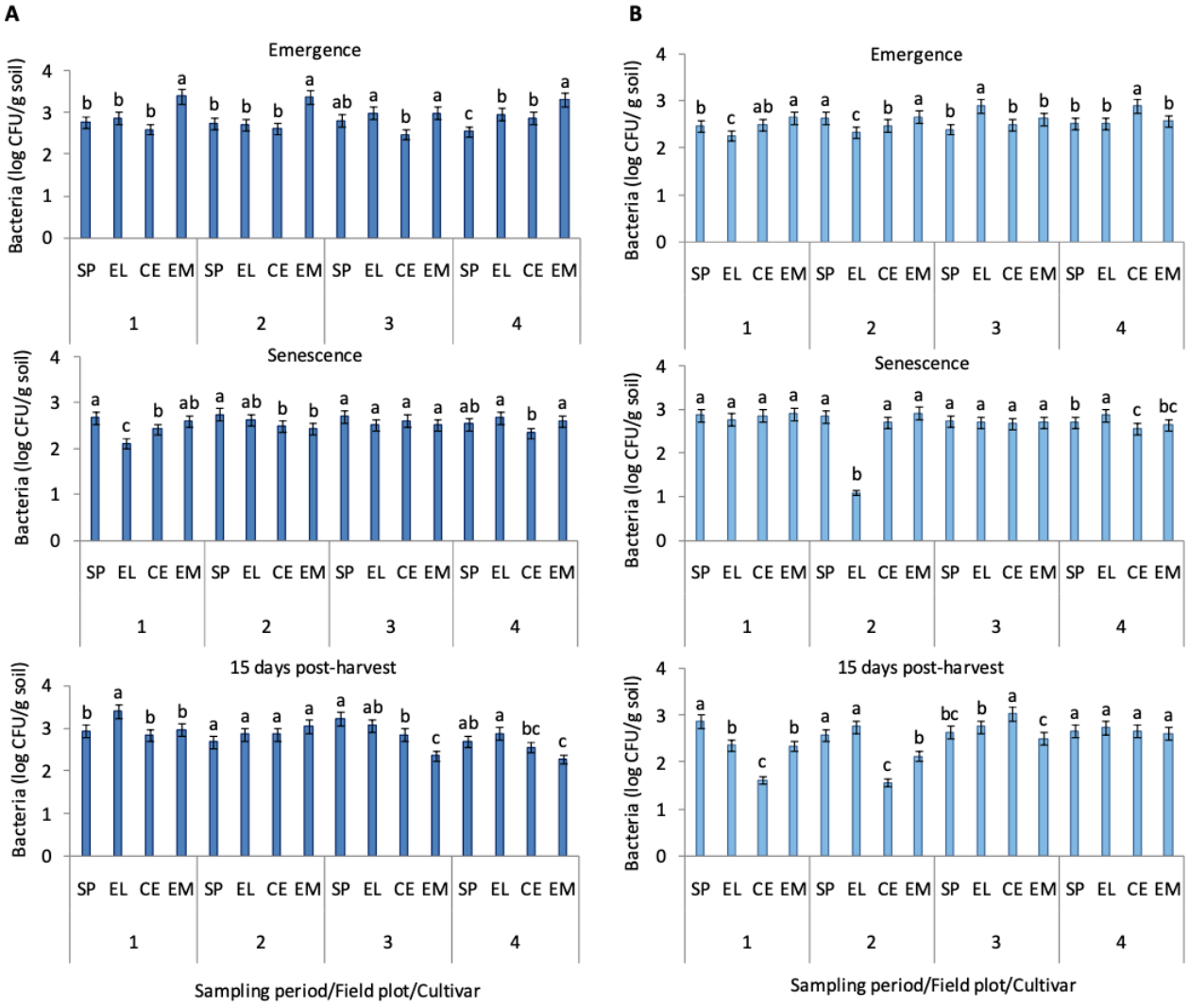

Figure 1. Variation in the total culturable bacterial population in the rhizosphere of four potato cultivars[a] depending on cropping seasons[b], sampling periods[c] and field plots[c]

[a] SP: Spunta; EL: Elata; CE: Cerata; EM: El-Mundo.

[b] (A) Late-season crop; (B) Extra-early crop.

[c] Sampling periods: Emergence (15 days post-planting), Senescence (120 days post-planting), and 15 days post-harvest.

[d] 100 plants per cultivar were grown per field plot.

Results are presented as mean ± SE (n = 8, $P \leq 0.05$).

For each sampling period and each field plot, bars (cultivars) sharing the same letter are not significantly different according to Duncan Multiple Range test at $P \leq 0.05$.

Soil dilution was made from a concentration of 10% (w/v).

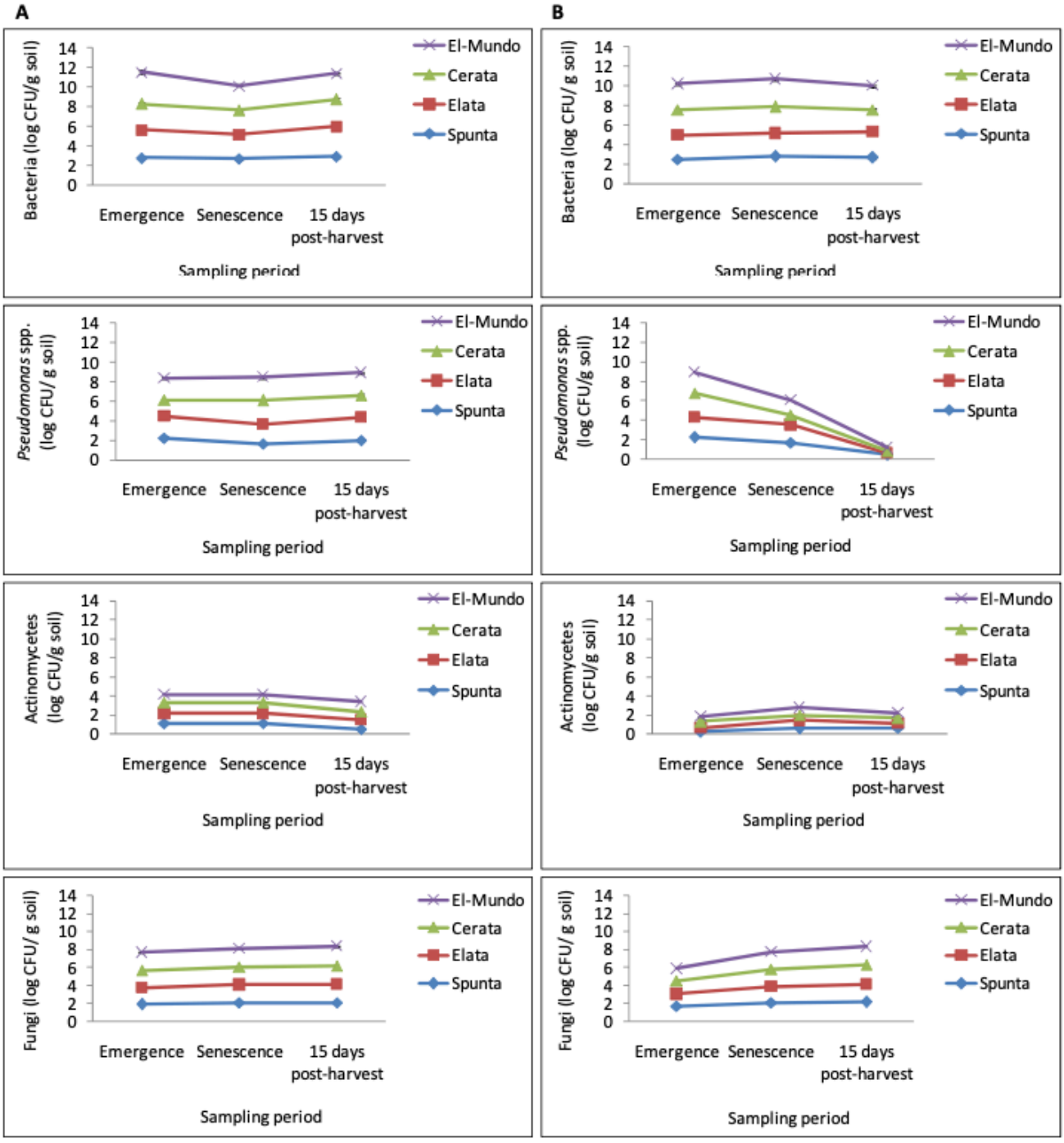

Figure 2. Variation in the total culturable bacterial population in the rhizosphere of four potato cultivars depending on cropping seasons[a] and sampling periods[b]

[a] (A) Late-season crop; (B) Extra-early crop.

[c] Sampling periods: Emergence (15 days post-planting), Senescence (120 days post-planting), and 15 days post-harvest. Results are presented as mean ± SE (n = 8, $P \leq 0.05$). Soil dilution was made from a concentration of 10% (w/v).

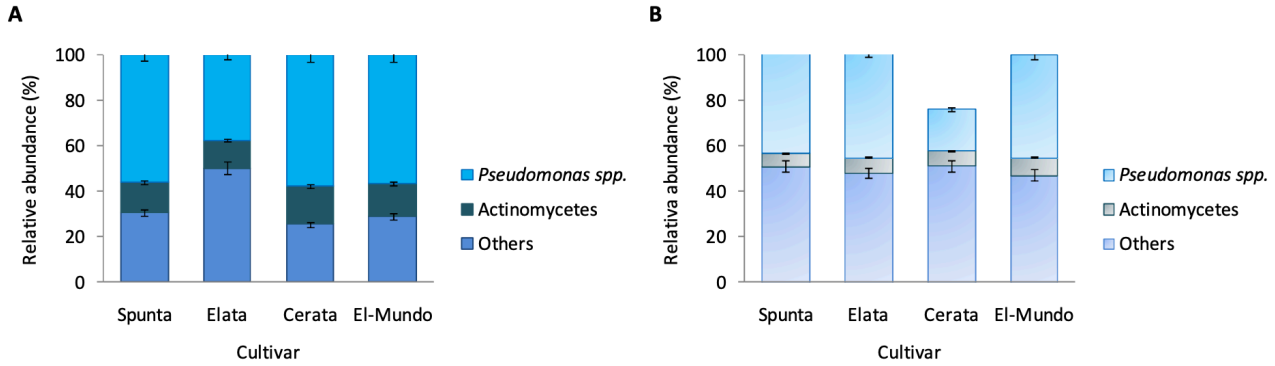

Figure 3. Variation in the bacterial community structure in the rhizosphere of four potato cultivars depending on cropping seasons. Results are presented as mean ± SE (n = 8, $P \leq 0.05$). The relative abundance was estimated per the total bacteria counted in each sampled soil. Soil dilution was made from a concentration of 10% (w/v). (A) Late-season crop (B) Extra-early crop.

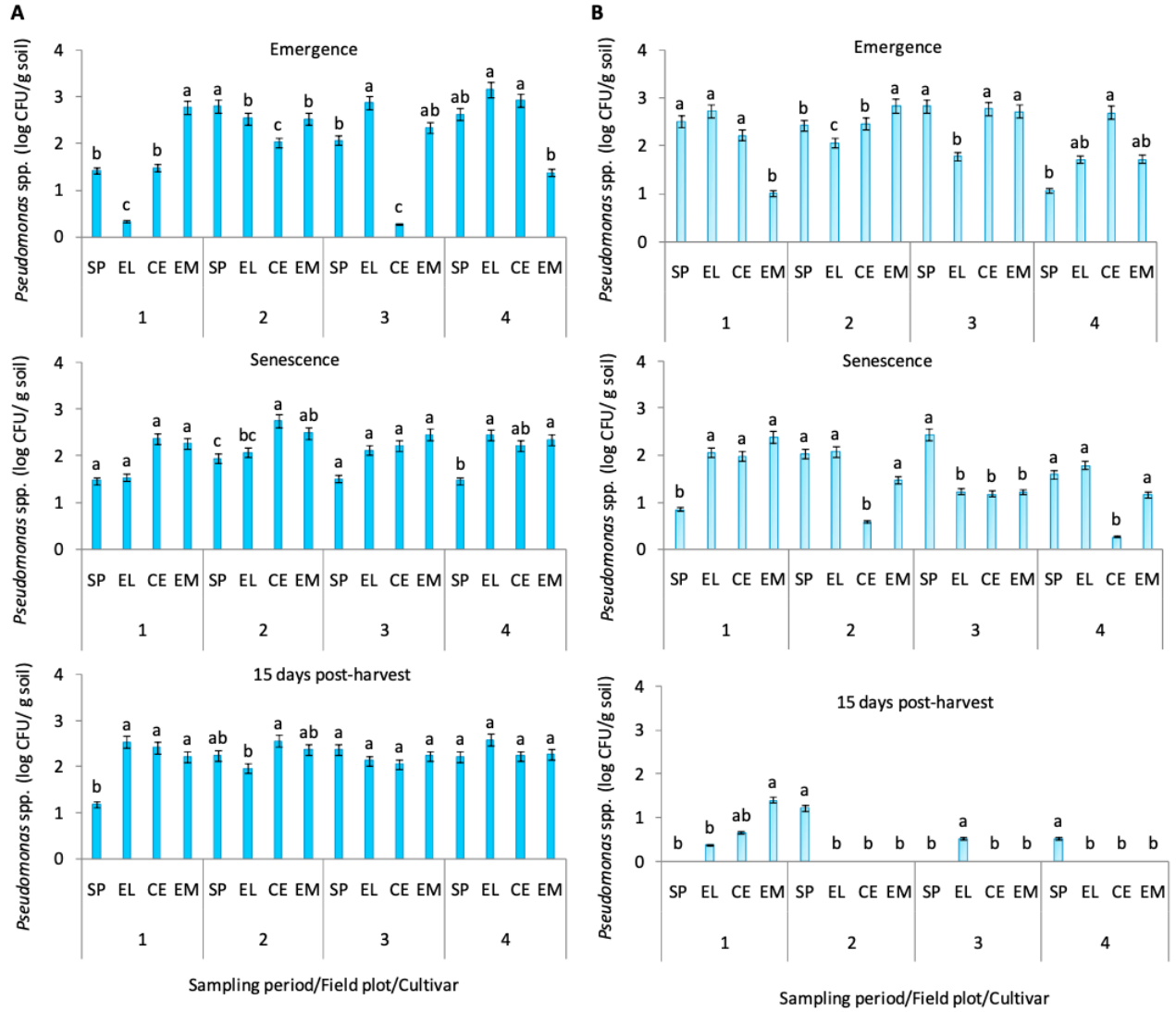

Figure 4. Variation in *Pseudomonas* spp. community in the rhizosphere of four potato cultivars[a] depending on cropping seasons[b], sampling periods[c] and field plots[d]

[a] SP: Spunta; EL Elata; CE: Cerata; EM: El-Mundo. [b] (**A**) Late-season crop; (B) Extra-early crop [c] Sampling periods: Emergence (15 days post-planting), Senescence (120 days post-planting), and 15 days post-harvest. [d] 100 plants per cultivar were grown per field plot. Results are presented as mean ± SE (n = 8, $P \leq 0.05$). For each sampling period and each field plot, bars (cultivars) sharing the same letter are not significantly different according to Duncan Multiple Range test at $P \leq 0.05$. Soil dilution was made from a concentration of 10% (w/v).

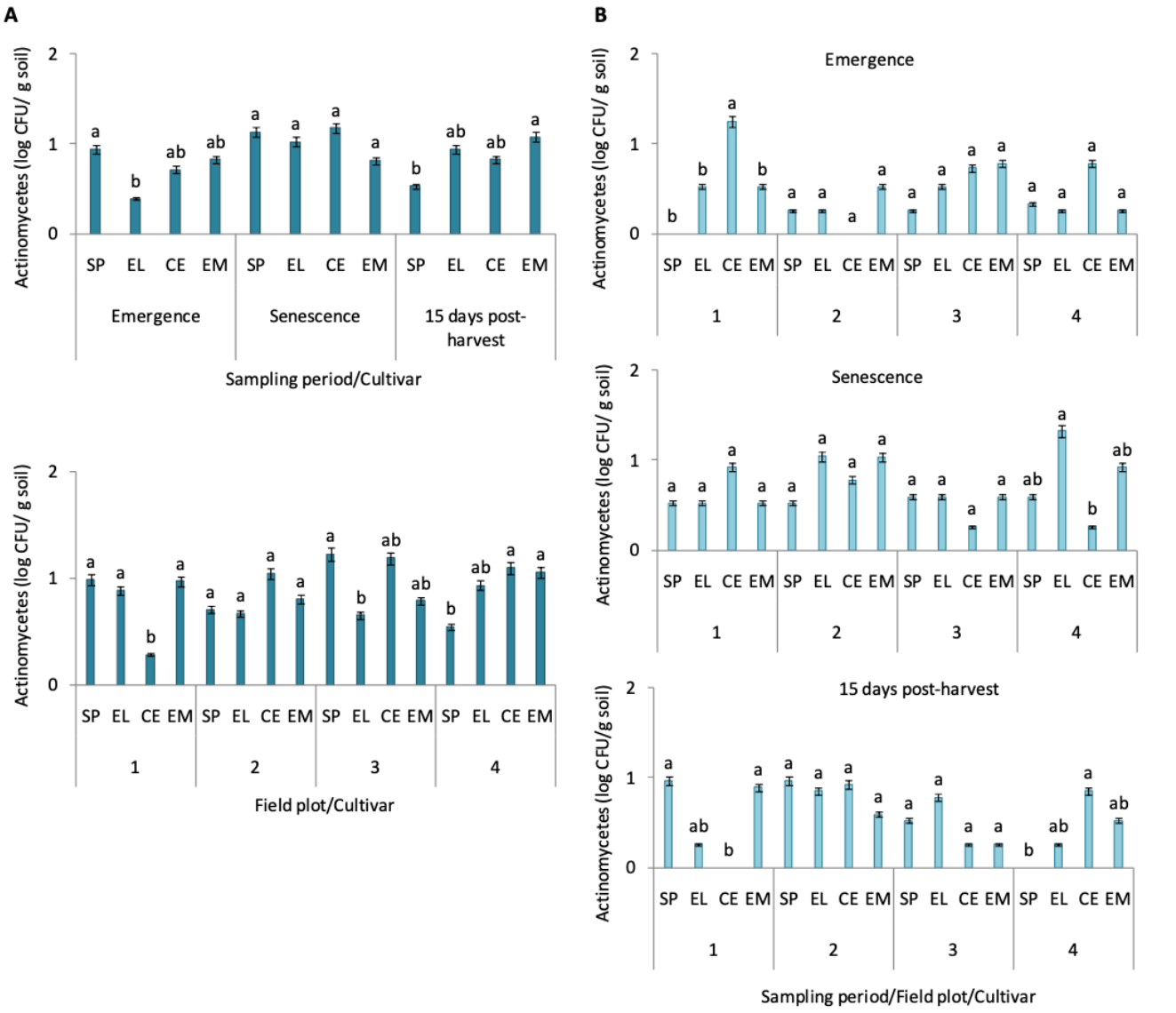

Figure 5. Variation in the Actinomycetes population in the rhizosphere of four potato cultivars[a] depending on cropping seasons[b], sampling periods[c] and field plots[d]

[a] SP: Spunta; EL: Elata; CE Cerata; EM: El-Mundo.

[b] (A) Late-season crop; (B) Extra-early crop

[c] Sampling periods: Emergence (15 days post-planting), Senescence (120 days post-planting), and 15 days post-harvest.

[d] 100 plants per cultivar were grown per field plot.

Results are presented as mean ± SE (n = 8, $P \leq 0.05$).

For each sampling period and each field plot, bars (cultivars) sharing the same letter are not significantly different according to Duncan Multiple Range test at $P \leq 0.05$.

Soil dilution was made from a concentration of 10% (w/v).

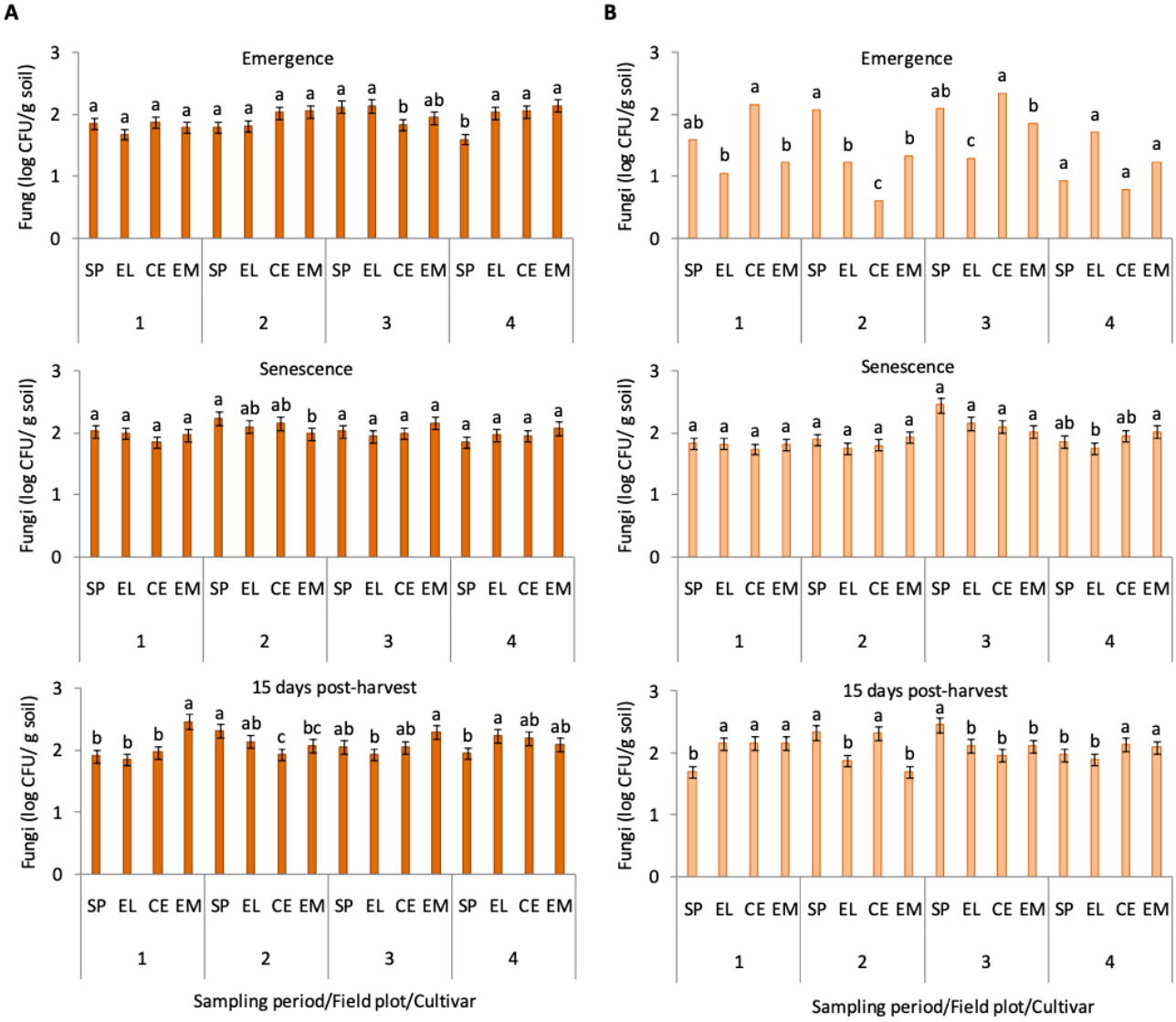

Figure 6. Variation in the total culturable fungal community in the rhizosphere of four potato cultivars[b] depending on cropping seasons[b], sampling periods[c] and field plots[d]

[a] SP: Spunta; EL: Elata; CE: Cerata; EM: El-Mundo.

[b] (A) Late-season crop; (B) Extra-early crop

[c] Sampling periods: Emergence (15 days post-planting), Senescence (120 days post-planting), and 15 days post-harvest.

[d] 100 plants per cultivar were grown per field plot.

Results are presented as mean ± SE (n = 8, $P \leq 0.05$).

For each sampling period and each field plot, bars (cultivars) sharing the same letter are not significantly different according to Duncan Multiple Range test at $P \leq 0.05$.

Soil dilution was made from a concentration of 10% (w/v).

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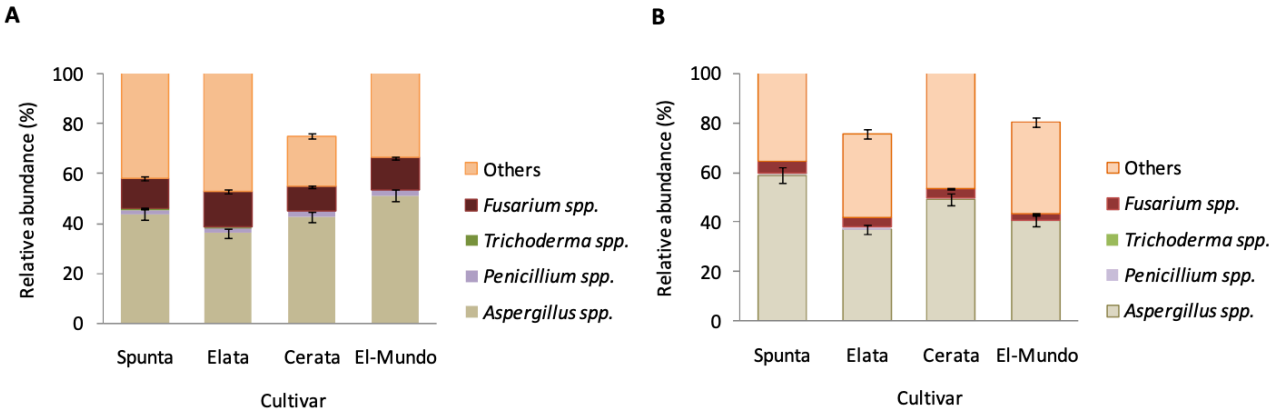

Figure 7. Variation in the fungal community structure in the rhizosphere of four potato cultivars depending on cropping seasons Results are presented as mean ± SE (n = 8, $P \leq 0.05$). The relative abundance was estimated per the total fungi counted in each sampled soil. Soil dilution was made from a concentration of 10% (w/v).
(A) Late-season crop (B): Extra-early crop.

Combined data for all sampling periods and cultivars tested revealed that the total fungal community was 1.2 times more abundant in the third field plot than in the remaining ones.

For all sampling periods and field plots combined (Figure 5B), the rhizospheric soil associated to cv. Spunta showed 1.05 and 1.08-1.11 times more abundant fungal population than those of cvs. Cerata, and El-Mundo and Elata.

It is well known that the rhizosphere microbiome or plant-associated microbial communities are generally influenced by root exudates and thereby change throughout plant development (Chaparro et al., 2014). The chemical compositions of root exudates vary not only among different plant species but also among cultivars of the same plant species (Kerdchoechuen, 2005). Furthermore, the chemical composition of root exudates is a result of the interactions of different factors such as the nutritional status, plant age, stress, diseases, and environmental factors that subsequently influence the microbial community associated to the rhizosphere (Griffiths et al., 1999).

As for composition and the diversity of the fungal community, *Aspergillus* spp. colonies were found to be more abundant in all sampled soils where their populations represented 36.2-51.2% and 37-58.9% of the total culturable fungi isolated from the late-season and the extra-early crops, respectively (Figure 7). For all sampling periods and field plots combined, the highest abundance of *Aspergillus* spp. colonies was 51.2 and 58.9% higher in El-Mundo and Spunta rhizospheres grown as late-season (Figure 7A) and extra-early crop (Figure 7B), respectively. *Fusarium* spp. population in the rhizosphere of all potato cultivars tested represented was estiamted at 9.6-14.2% in the late-season crop (Figure 7A) and at 2.5-5% in the extra-early season (Figure 7B). The variation in the microbial communities depending on cropping seasons can be explained by two possible mechanisms (Wang et al., 2009). The first one is related to temporal changes in abiotic conditions such as soil moisture, precipitation and temperature. The second mechanism may be attributed to the changes in quality and quantity of root exudates and rhizodeposits which are influenced by environmental and edaphic factors and/or root morphology (Marschner et al., 2003). The largest explaining factor for the variation of composition and function of fungal communities in the rhizosphere was the plant phonological growth stage, followed by the year and the soil type (Hannula et al., 2012).

Correlations Between Soil Characteristics (pH and EC), and Soil Microbial Community Structure

Pearson's correlation analysis indicated that, for all sampling periods, field plots and cultivars combined, the pH values were significantly and positively (r = 0.332, P = 0.021) correlated to the *Pseudomonas* spp. population in late-season crop and negatively (r = -0.307, P = 0.034) correlated to *Pseudomonas* spp. community at the extra-early crop . EC values were significantly and positively linked to *Pseudomonas* spp. (r = 0.351, P = 0.015) and fungal populations (r = 0.306, P = 0.034) in the analyzed soil samples of potato cultivars grown at the late-season crop. For the extra-early crop, EC significantly and positively correlated to fungal community (r = 0.321, P = 0.026) and this for all cultivars r, field plots and sampling periods combined. Our findings confirm in part those of Kim et al. (2016) who demonstrated a significant positive correlation between soil chemical parameters such as soil pH, EC, and exchangeable cations and bacterial community. Rousk et al. (2010) reported that both the relative abundance and diversity of bacteria are positively related to pH whereas the relative abundance of fungi is not influenced by pH and the fungal diversity is weakly related with pH. Although the bacterial community composition is clearly influenced by soil pH and EC values, the specific relationships between each bacterial phylum and pH and/or EC can vary (Kim et al., 2016). Besides, *Bacteroidetes*, *Spirochaetes*, and *Tenericutes* are positively correlated with the EC values, but *Acidobacteria* had a negative correlation (Kim et al., 2016). Many studies have shown that soil microbial communities are influenced by various environmental factors, including soil pH (Xu et al., 2014), electrical conductivity (Ma et al., 2016; Min et al., 2016), soil texture (Lauber et al., 2008), soil parental material (Sun et al., 2015), and salinity (Lozupone and Knight, 2007). Pfeiffer et

al. (2017) observed that the taxonomic composition of bacteria repeatedly occurring at particular stages of plant development was almost unaffected by highly diverse environmental conditions.

Conclusions

Four potato cultivars were evaluated for searching the eventual relationships between associated rhizosphere mirobiomes and grown cultivars, plant age and/or cropping seasons. The obtained results clearly demonstrated that the distribution of bacterial and fungal populations varied significantly upon cultivars. For both cropping seasons, fungi were more associated to EL-Mundo and Spunta cultivars, while bacteria were more abundant in cvs. Spunta, Elata and El Mundo rhizospheres. Indeed, *Pseudomonas* spp. were associated to the four tested potato cultivars, but *Aspergillus* spp. were more abundant in the rhizosphere of El-Mundo and Spunta cultivars. In the present study, the highest abundance of the total culturable bacteria was noted at plant emergence and 15 days post-harvest for the late season and at senescence for the extra-early crop. The actinomycetes and fungal populations were more prevalent at plant senescence and 15 days post-harvest and this for both cropping seasons. The relative abundance of *Pseudomonas* spp., actinomycetes and *Fusarium* spp. populations was found to be relatively important in the rhizosphere of all potato cultivars grown for a late-season than for an extra-early crop. Furthermore, the distribution of bacteria, and fungal communities significantly varied upon field plots whatever the sampling time and the cultivar tested and this for both cropping seasons.

Variations in the rhizosphere microbial community composition were noted at different developmental stages for four potato cultivars grown for two cropping seasons. Besides, the microbial community structure significantly correlated with pH and EC of soils sampled from potato rhizopshere. This will help researchers to explore specific microbes that are required for the improvement of potato growth and/or health under different growing conditions and during different developmental stages. In addition, this study can be valorized in order to incorporate associated microbiome in future strategies for plant breeding programs.

Compliance with Ethical Standards

Conflict of interest

The authors declare that for this article they have no actual, potential or perceived the conflict of interests.

Author contribution

The contribution of the authors is equal. All the authors read and approved the final manuscript. All the authors verify that the Text, Figures, and Tables are original and that they have not been published before.

Ethical approval

Not applicable.

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Data availability

Not applicable.

Consent for publication

Not applicable.

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