Reverchon *et al.*
CABI Agriculture and Bioscience (2023) 4:23
https://doi.org/10.1186/s43170-023-00167-1

CABI Agriculture and Bioscience

DATA NOTE

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Shifts in the rhizosphere microbiome and exudation profile of avocado (*Persea americana* Mill.) during infection by *Phytophthora cinnamomi* and in presence of a biocontrol bacterial strain

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Abstract

Background Rhizosphere microbiomes are fundamental for plant health, development, and productivity, but can be altered by the incidence of soil-borne pathogens. The dysbiosis (disturbance of the microbiome structure of healthy plants) caused by these pathogens, combined with the recruitment of beneficial microorganisms by the diseased plant, may cause shifts in the rhizosphere microbiome during the infection process. These shifts are likely to be associated with changes in the rhizosphere metabolic profile, as the biochemical dialog, or crosstalk, between host plants and their microbiome is mostly mediated by root exudates. Our objective was to elucidate the shifts in the avocado rhizosphere microbiome and associated changes in the rhizosphere metabolome induced by the infection of the oomycete *Phytophthora cinnamomi*. We also evaluated the effect of inoculating a bacterial biological control agent (BCA) of *P. cinnamomi* on the avocado rhizosphere microbiome, in the presence and absence of the pathogen, and on morphological and physiological plant variables, to confirm the potential of the BCA to alleviate the stress induced by the disease.

Dataset presentation Here, we present a novel dataset collected from a time-course experiment with four treatments: (1) control trees; (2) trees infected with *P. cinnamomi*; (3) trees inoculated with the BCA; (4) trees infected with *P. cinnamomi* and inoculated with the BCA. During the infection process, we measured plant morphological and physiological variables and collected rhizosphere soil samples for bacterial and fungal amplicon sequencing, bacterial RNA-seq and metabolomic analyses.

Conclusions Collectively, our data elucidate the shifts in the avocado rhizosphere microbiome after infection by *P. cinnamomi* and when inoculated with a BCA, and help understand how a pathogen or a beneficial bacterium can alter plant-microbiome crosstalk. Understanding the effect of *P. cinnamomi* or a BCA on the avocado tree physiology and on the avocado rhizosphere microbiome and metabolome will direct our search for disease biomarkers

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or potential pathogen antagonists, help identify metabolites related to the recruitment of microorganisms, and assist us in developing integrated disease management strategies.

Keywords Bacterial and fungal communities, Biological control, Pathobiome, Phytophthora root rot, Rhizosphere metabolome

Background

The rhizosphere microbiome plays an important role for plant health and productivity (Bulgarelli et al. 2013; Trivedi et al. 2020). Rhizosphere microorganisms are involved in different processes such as nutrient acquisition, production of phytohormone-like molecules, induction of host resistance to biotic and abiotic stressors and competition with possible pathogens, which may benefit their host directly or indirectly (Méndez-Bravo et al. 2018; Lazcano et al. 2021; Syed-Ab-Rahman et al. 2022). Microbial community structure in the rhizosphere depends on several factors, such as plant genotype and phenological stage, soil type and other environmental conditions (Philippot et al. 2013). Increasing evidence also shows that plants can recruit beneficial microorganisms to suppress pathogens (Liu et al. 2021; Thoms et al. 2021), thus modifying their rhizosphere microbiome upon infection. However, the molecular and biochemical pathways through which plants alter their associated microbiome when infected remain largely unknown, especially in non-model plants (Santoyo 2022), thus calling for future efforts to elucidate the underlying mechanisms of plant-microbiome interactions.

Changes in the rhizosphere microbiome induced by soil-borne pathogens have been demonstrated in different pathosystems. For example, the bacterial pathogen *Ralstonia solanacearum* modified bacterial community structure in the tomato rhizosphere and caused a decrease in the diversity of non-pathogenic bacteria (Wei et al. 2018). More recently, the plant pathogenic fungus *Fusarium graminearum* was shown to modify the rhizosphere microbiome in wheat, altering community structure and composition (Liu et al. 2023). Key bacterial taxa such as *Stenotrophomonas* sp. were detected in the rhizosphere of infected plants and associated with disease resistance, thus suggesting a "cry-for-help" strategy. The recruitment of a health-promoting microbiome by plants is most likely mediated through their root exudates, which are altered following pathogen infection (Rolfe et al. 2019; Liu et al. 2021). Linking the metabolic profile of root exudates with shifts in the rhizosphere microbiome of infected plants would thus improve our understanding of plant-microbe interactions and our ability to harness microbiomes for sustainable crop production (Pang et al. 2021).

Integrated management of diseases caused by soil-borne pathogens includes the use of microbial biological control agents (BCA) (Niu et al. 2020). Soil inoculation of BCA with demonstrated activity against soil-borne pathogens is expected to reduce the incidence of the pathogen population and limit its infective capacity. However, the effects of BCA application on soil and rhizosphere native microbiomes are not well understood. Previous reports showed that BCA inoculation modifies the structure of the rhizosphere microbiome (Li et al. 2021), enriching soil microbial communities in beneficial taxa with antagonistic properties against the targeted pathogen (Tienda et al. 2020; Zhu et al. 2023) or decreasing the interactions between the pathogen and other potential members of the pathobiome (Ahmed et al. 2022). These findings highlight the need to better understand how BCA inoculation may affect the rhizosphere microbiome of infected plants in order to elucidate underlying biocontrol mechanisms and possibly identify other beneficial microorganisms.

Our study focuses on avocado (*Persea americana* Mill.), a tree crop of great economic importance, in particular for Mexico, the world´s first producer and exporter (FAOSTAT 2021). Avocado production has been dramatically affected by the pathogen *Phytophthora cinnamomi*, causal agent of the disease known as Phytophthora root rot (Fernández-Pavia et al. 2013; Solís-García et al. 2021). Our objective was to determine the compositional and functional shifts in the avocado rhizosphere microbiome and the associated changes in the metabolic profile of root exudates during the infection by the oomycete *P. cinnamomi*. Moreover, we included a treatment with a bacterial BCA, with previously demonstrated antagonistic activity against *P. cinnamomi in vitro* (Méndez-Bravo et al. 2018; Cortazar-Murillo et al. 2023), to confirm the potential of the BCA to alleviate the stress induced by the disease *in planta* and to elucidate the effect of the BCA on the avocado rhizosphere microbiome, in the absence and in the presence of *P. cinnamomi*. Overall, our dataset offers an integral approach towards a better understanding of the effects of beneficial and pathogenic belowground interactions of avocado, a perennial tree crop, on its rhizosphere microbiome.

Dataset presentation

The experiment was established in a greenhouse at the *Escuela Nacional de Estudios Superiores* (ENES-Morelia) of the *Universidad Nacional Autónoma de México* (UNAM), Mexico, in March 2021. Ninety asymptomatic avocado trees of the « Mendez » variety, of approximately 2 years old, were purchased in a local nursery and acclimatized for three months in the greenhouse. The experiment consisted of four treatments: (1) control trees (C), not infected with *P. cinnamomi*, n = 30; (2) trees infected with *P. cinnamomi* (Pc), n = 30; (3) trees not infected with *P. cinnamomi* and inoculated with the BCA (B), n = 15; (4) trees infected with *P. cinnamomi* and inoculated with the BCA (BPc), n = 15.

Phytophthora cinnamomi strain TGR1-5, obtained from a Michoacán avocado orchard, was provided by Dr. Sylvia Fernández-Pavia (*Universidad Michoacana San Nicolás de Hidalgo*, Mexico). The BCA used in this study was the bacterial strain *Bacillus* sp. A8a (Méndez-Bravo et al. 2018). The thirty trees from treatments B and BPc were randomly selected and inoculated with 250 ml of a BCA suspension (1.5×10^8 CFU ml^{-1}). Two weeks later, trees from the Pc and BPc treatments were immersed in a bath containing a suspension of *P. cinnamomi* zoospores (4.9×10^2 zoospores ml^{-1}) for two hours. Trees from the C and B treatments were immersed in a water bath without zoospores of *P. cinnamomi* for the same duration. After the root immersion procedure, trees were transplanted in polyethylene bags containing a mixture of peat moss, perlite, vermiculite and original soil (3:1:1:1). One day after transplanting, trees from the B and BPc treatments were inoculated again with 250 ml of BCA suspension at the same concentration, to reinforce the presence of the beneficial bacterium at the root level after immersion.

Samples and measurements were taken at different times during the infection process: t_0 (1 day after infection (dai) with *P. cinnamomi*), t_1 (4 dai), t_2 (7 dai), t_3 (13 dai) and t_4 (25 dai). At t_4, trees from the Pc treatment presented a 100% incidence of wilt symptoms. At each sampling time, six trees from the C and Pc treatments, and three trees from the B and BPc treatments, were randomly selected to be measured and sampled. Plant morphological variables such as total number of leaves, number of wilted leaves, stem diameter and tree height, were measured for each tree at each sampling time (**Data file 1**). In addition, physiological variables such as stomatal conductance, photosynthetic rate and transpiration rate were measured as an average from two leaves of three selected trees, from 8 am to 11 am, and leaf water potential was recorded at 5 am and 12 pm, on each sampling day (**Data file 1**). Substrate humidity, pH (1:5 H_2O) and electrical conductivity were also recorded at each sampling time (**Data file 2**). Moreover, soil total carbon (C) and total nitrogen (N) contents, and N-NH_4^+, N-NO_3^- and available phosphorus (P) concentrations were measured for soil samples collected at the initial (t_0) and final (t_4) times of the experiment (**Data file 2**). Total C and N contents were measured with a Perkin-Elmer 2400 CHN analyzer. The N-$NH_4^+$and N-NO_3^- concentrations were determined with KCl extractions (Anderson and Ingram 1993). Soil available P was measured following the Bray and Kurtz method (Bray and Kurtz 1945). Approximately 20 mg of rhizosphere soil samples (i.e., strongly adhered to the roots) were taken from the selected trees at each sampling time. Half of the collected samples were immersed in LifeGuard® Soil Preservation Solution (Qiagen) and stored at −80 °C for subsequent RNA extraction; the other half was kept at −20 °C for DNA extraction. Approximately 50 g of soil loosely attached to the roots were collected and frozen in liquid nitrogen, and stored at −80 °C for subsequent metabolomics analyses.

Genomic DNA extraction was performed with the ADN PowerSoil® and DNeasy PowerMax® Soil kits (Qiagen), following the manufacturer´s instructions. The libraries for the V3 and V4 regions of gene 16S rRNA (bacterial communities) were constructed following the protocol "16S Metagenomic Sequencing Library Preparation" of Illumina® (Set A Illumina), using primers reported in **Data file 3** (bacteria). The same protocol was followed to construct libraries for the ITS2 region (fungal communities), using the mix of seven primers suggested by Tedersoo et al. (2014), as described in **Data file 4**. Purification steps were performed with ProNex® Size-Selective (Promega), following the manufacturer´s instructions. Two pools, one for 16S region and one for the ITS2 region, were sent to CD Genomics (Shirley, NY, USA) for sequencing on a Illumina® MiSeq platform (2 × 300 bp, paired-end). Bacterial and fungal sequences (**Data files 3 and 4**) were deposited in the Sequence Read Archive of NCBI under accession number PRJNA963057.

For bacterial RNA-seq analyses, rhizosphere soil samples were collected from C and Pc trees only. The RNA extractions were carried out with the RNeasy® PowerSoil® Total RNA Kit (Qiagen), following the manufacturer´s instructions. Subsequently, due to limited success in extracting RNA from all samples and low obtained RNA quantities, RNA extracts from different trees were pooled to obtain one RNA sample per experimental condition (C and Pc). RNA extracts were sent to CD Genomics (Shirley, NY, USA) for DNA depletion, ribosomal RNA remotion, library preparation and sequencing on a Illumina® platform (2 × 150 bp, paired-end). Transcript sequences (**Data file 5**) were also

submitted to the Sequence Read Archive of the NCBI with the accession number PRJNA963057.

Rhizosphere soil samples for metabolomics analyses were processed and analyzed following the methodology described by Monribot-Villanueva et al. (2022). Briefly, soil samples were lyophilized for four to five days. Methanolic extracts were obtained using an accelerated solvent extraction system (ASE 350, Dionex, Thermo Scientific) and solvent was eliminated in the extracts with a rotatory evaporator (Büchi, RII). Dried crude extracts were analyzed by ultra high-performance liquid chromatography (UPLC, Acquity Class I, Waters™, U.S.A.), coupled to a high-resolution quadrupole time-of-flight mass spectrometer (QTOF, HDMI Synapt G2-Si model, Waters™). Mass spectrometry analysis was performed with an electrospray ionization (ESI) source in positive and negative mode. Mass/charge ratios (*m/z*) and retention times data were acquired and processed with MassLynk (version 4.1) and MarkerLynk (version 4.1) software of Waters TM Corp. **Data file 6** and **Data file 7** correspond to positive and negative ESI databases, respectively.

A summary of the available data files is presented in Table 1.

Discussion and conclusions

Our dataset elucidates the shifts in the avocado rhizosphere microbiome after infection by *P. cinnamomi*. Previous reports have demonstrated that *P. cinnamomi* modified the structure and species composition of microbial communities in the avocado rhizosphere (Yang et al. 2001; Shu et al. 2019; Solís-García et al. 2021), affecting dominant taxa and their metabolic pathways. However, these reports did not investigate the functional implications of such changes, overlooking the possible shifts in microbial gene expression or plant-microbiome signaling pathways; combining metatranscriptomic (bacterial RNA-seq) data with plant physiological measurements and rhizosphere metabolomic information will help us understand how a pathogen can alter plant-microbiome crosstalk and unravel the critical role of plant-derived and microbial metabolites in disease mitigation by the plant microbiome (Berg et al. 2021; Pereira et al. 2023). Furthermore, the dataset compiled from this time-course experiment will provide insights into changes in host-associated microbial communities through disease progression, which have been previously demonstrated in other pathosystems, such as wheat infected by the fungal pathogen *Zymoseptoria tritici* (Seybold et al. 2020). Understanding the mode of action of *P. cinnamomi*, its effect on tree physiology and its impact on the avocado rhizosphere microbiome and metabolome could assist us in designing new tools for early disease detection and mitigation, for example through the identification of disease biomarkers or of potential microbial BCA.

As *P. cinnamomi* has been shown to be associated with a cohort of other opportunistic pathogens that collectively contribute to root rot (Vitale et al. 2012; Carranza-Rojas et al. 2015; Solís-García et al. 2021), our dataset will allow to identify the pathobiome, i.e., the set of microorganisms positively interacting with *P. cinnamomi*, and to gain a better understanding of microbial interactions in the rhizosphere through disease progression (Qiu et al. 2022). This information will be useful for future targeted isolation approaches aimed at investigating root

Table 1 Overview of data files

Label	Name of data file	File type (extension)	Data link on FigShare
Data file 1	Plant physiological data	MS Excel file (.xlsx)	https://figshare.com/articles/dataset/Plant_physiological_data/22720291
Data file 2	Substrate data	MS Excel file (.xlsx)	https://figshare.com/articles/dataset/Substrate_data/22721164
Data file 3	16S amplicon sequences (Sequence Read Archive submission template)	MS Excel file (.xlsx)	https://figshare.com/articles/dataset/16S_amplicon_sequences_Sequence_Read_Archive_submission_template_/22721176
Data file 4	ITS amplicon sequences (Sequence Read Archive submission template)	MS Excel file (.xlsx)	https://figshare.com/articles/dataset/ITS_amplicon_sequences_Sequence_Read_Archive_submission_template_/22722610
Data file 5	RNA sequences (Sequence Read Archive submission template)	MS Excel file (.xlsx)	https://figshare.com/articles/dataset/RNA_sequences_Sequence_Read_Archive_submission_template_/22722958
Data file 6	UHPLC-HRMS metabolomic data (positive mode)	MS Excel file (.xlsx)	https://figshare.com/articles/dataset/UHPLC-HRMS_metabolomic_data_positive_mode_/22721182
Data file 7	UHPLC-HRMS metabolomic data (negative mode)	MS Excel file (.xlsx)	https://figshare.com/articles/dataset/UHPLC-HRMS_metabolomic_data_negative_mode_/22721206

rot-associated pathogens and developing integrated disease management strategies.

Finally, the addition of a BCA treatment in our dataset provides further information regarding the modulation of the plant rhizosphere microbiome by microbial inoculants (Berg et al. 2021) and confirmed the beneficial effect of strain *Bacillus* sp. A8a *in planta*. Understanding how BCA inoculation influences microbial community composition and exudate production in the avocado rhizosphere through time will allow us to develop novel strategies based on microbiome-engineering to enhance plant immune responses and counteract pathogen-induced dysbiosis. This is particularly important in export crops such as avocado, where current limitations to agrochemical applications call for more sustainable practices and integrated pest and disease management to maintain crop productivity (Stout et al. 2004; Guevara-Avendaño et al. 2022; Wangithi et al. 2022).

Acknowledgements
This study was funded by project SEP-CONACYT (Programa Presupuestario F003) number A1-S-30794. We thank Silvana Martén-Rodríguez for facilitating the greenhouse at ENES-Morelia, UNAM; Sylvia Fernández-Pavia, Alejandra Mondragon-Flores and Marlene Díaz-Celaya for facilitating the *P. cinnamomi* strain and guiding us through the protocol for obtention of zoospores; Yareli Pérez Batista and Alejandro Méndez-Bravo for their assistance in the greenhouse experiment and RNA extractions; Eduardo Thome for his help with the extraction and quantification of genomic DNA at the *Laboratorio de Genómica* (ENES-Morelia, UNAM) and Sandra Rocha and Karla Tapia at the *Laboratorio de Análisis Químicos de Suelos, Aguas y Plantas* (Instituto de Ecología, A.C.) for their assistance with soil analyses.

Author contributions
FR, WD, JAGA, AMB, JLM and EAR designed the study. FR, EGA, IASG, FPG and AMB performed the experiment and collected the samples. MGM, EGA performed the DNA extractions and analyzed the amplicon sequencing data, supervised by FR, WD, VPC and EAR. AMB performed the RNA extractions. EGA, OMC, JAGA and JLMV performed the metabolomic analyses. FR, EGA, JAGA, AMB and JLMV wrote the paper. All authors read and approved the final version of the manuscript.

Funding
This study was funded by project SEP-CONACYT (Programa Presupuestario F003) number A1-S-30794.

Availability of data and materials
The data described in this Data note can be freely and openly accessed on FigShare. Please refer to Table 1 for details and links to the data.

Declarations

Ethics approval and consent to participate
Not applicable

Consent for publication
Not applicable.

Competing interests
The authors declare that they have no competing interests

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Received: 5 May 2023 Accepted: 28 June 2023
Published online: 07 July 2023

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