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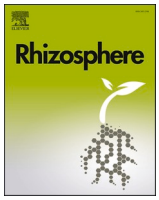

Wheat as model to study avocado root rot and interactions with rhizobacteria

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ABSTRACT

Avocado white root rot (AWRR), caused by *Rosellinia necatrix*, presents significant research challenges due to the practical difficulties and limited availability of using avocado plants as experimental model. To address these limitations, a novel wheat-based model has been developed. This model facilitates the study of rhizospheric interactions between *R. necatrix* and beneficial bacteria isolated from avocado roots. Wheat seeds were challenged in pots with *R. necatrix*, which effectively colonizes and infects wheat roots, inducing observable aerial symptoms that enable quantitative assessment of disease severity. Additionally, beneficial bacteria, originally isolated from avocado roots, demonstrate comparable colonization efficiency on wheat roots. The use of fluorescent-tagged microbial strains allowed visualization of the interactions taking place at the wheat root. This wheat model proved effective for evaluating biocontrol agents, yielding consistent results with previous observations in avocado plants. These findings indicate that wheat can be considered an additional tool for investigating AWRR-related rhizospheric dynamics.

The avocado plant (*Persea americana Mill.*) is severely affected by the soil-borne fungal pathogen *Rosellinia necatrix*, which causes white root rot, a devastating disease in woody plants worldwide (Pliego et al., 2012). Controlling avocado white root rot (AWRR) is considered complex, prompting several studies focused on microbial species with the potential to biocontrol *R. necatrix*, mainly *Pseudomonas* spp. and *Bacillus* spp. (Pliego et al., 2011). However, the use of avocado plants as a model to study AWRR showed considerable challenges. As large, woody perennials, avocado plants possess extensive and intricate root systems that are inherently difficult to manipulate in controlled experimental settings, complicating the direct observation and sampling of microbial communities, essential for understanding rhizospheric interactions. Additionally, avocado plants growth slowly and have long reproductive cycle, which often leads to experiments extending over months (Tienda et al., 2020). This makes them impractical for high-throughput screening or detailed temporal studies. The size of avocado plants also demands significant laboratory space, specialized equipment for handling, and substantial resources for maintenance, further limiting their utility as a versatile research model.

To overcome these difficulties, an alternate model for studying rhizospheric interactions would be desirable. Thus, wheat (*Triticum aestivum*) emerges a potential plant model due to its favourable characteristics, allowing for shorter experimental durations and higher throughput in assessing plant-microbe dynamics. Wheat has been used as a plant model to study microbial interactions at the rhizosphere (Arafat et al., 2025; Muzlera et al., 2024) and biocontrol bacteria against different soilborne pathogens (Kang et al., 2024).

Extensive knowledge of wheat physiology and pathogen susceptibility provides a strong framework for investigating plant-microbe associations. Wheat's fibrous root system is ideal for controlled rhizosphere studies. Its manageable size simplifies observation, sampling, and manipulation, aiding detailed research on microbial colonization of roots (Sultana et al., 2023). Interestingly, *R. necatrix* inoculum is prepared on sterile wheat seeds (Freeman et al., 1986). This aims us to explore wheat as alternate model for interactions with *R. necatrix*.

In this work, we infected pots containing wheat seedlings with *R. necatrix*, and described the typical root and aerial symptoms after 28 days under greenhouse conditions. Microscopic observations of fungal interactions at the roots revealed similar behaviours to that in avocado roots. Similarly, we described bacterial interactions on the wheat

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rhizosphere, demonstrating efficient root colonization. Finally, a biocontrol test on this wheat/*R. necatrix* pathosystem showed results consistent with previous observations of beneficial biocontrol bacteria in the avocado/*R. necatrix* model.

Fluorescently labelled derivatives of wild-type *Pseudomonas chlororaphis* (Pc) and *P. alcaligenes* (Pa) strains previously isolated from avocado roots were utilized (Table 1). Strains were routinely cultured in tryptone-peptone-glycerol (TPG; Calderón et al., 2014) at 25 °C for 36 h. When required, media were supplemented with gentamicin (Gm, 25 μg/ml), rifampicin (Rif, 10 μg/ml), or tetracycline (Tc, 20 μg/ml). Bacterial stocks were maintained at −80 °C in TPG with 15 % glycerol.

The virulent fluorescent-tagged fungal strain *Rosellinia necatrix* CH53-GFP (Pliego et al., 2009) was used (Table 1). This fungus was cultured on potato dextrose agar (PDA) at 25 °C for 5–7 days, with hygromycin (50 μg/ml) supplementation when required. *R. necatrix* was stored at 4 °C as previously described (Gutiérrez-Barranquero et al., 2012).

Pathogenicity of *R. necatrix* CH53-GFP was assessed on commercial wheat (*Triticum aestivum* cv. Nogal). Surface-disinfected and pre-germinated wheat seeds were transplanted into 10 cm-pots containing pasteurized commercial potting soil, composed by 15 % plant-nutrient loaded zeolite and 85 % coconut fiber substrate, infected with the pathogen as described previously (Freeman et al., 1986). Non inoculated plants (20 pots) were used as control. Four independent experiments of twenty plants per replicate (80 pots in total), were maintained in a greenhouse for 28 days under controlled conditions (25 °C, 70 % relative humidity, 16-h photoperiod), and watered twice per week. Disease severity was evaluated using a 0–3 aerial symptom scale (0 = healthy, 3 = dead plant; Fig. 1) that allowed calculation of a Disease Index (DI; Cazorla et al., 2006). Additionally, visualization of fluorescent *R. necatrix*-GFP on infected roots was performed under confocal microscopy as previously described (Pliego et al., 2009).

For bacterial colonization assays and visualization on wheat roots, wheat seedlings were inoculated with a suspension of fluorescently labelled bacterial (approximately 10^9 CFU/mL) for 20 min. Single and combined (3P) inoculations of three *Pseudomonas* species were performed, as previously assayed on avocado plants (Tienda et al., 2024). After the inoculations, seedlings were transplanted into 10 cm-pots containing potting soil. Additional 10 pots were used per treatment, and three independent experiments were performed. Control seedlings received sterile TPG media. At 10-, 20-, and 40-days post-inoculation (DPI), root samples were collected for confocal laser scanning microscopy (CLSM) and bacterial quantification. Root sections for CLSM were directly mounted and examined (Tienda et al., 2024). For bacterial counts, root samples from the same plants were homogenized in 2 mL sterile saline solution using a stomacher® (Colworth Stomacher-400, Seward Ltd.). Serial 10-fold dilutions were prepared in 0.85 % sterile saline solution, and 100 μL of each dilution was plated on TPG agar supplemented with appropriate antibiotics. Plates were incubated at 25 °C for 36 h, and antibiotic-resistant fluorescent colonies with characteristic morphology were counted. Three independent experiments, each with three replicates, were conducted. The competitive index (CI) for combined 3P inoculations was calculated as the ratio of each strain's count to the total inoculated cell population.

Finally, biocontrol assays were performed using the wheat-*R. necatrix* system after inoculation of the strains individually or as a microbial consortium (3P), and sowing the inoculates wheat seedlings into potting soil infected with *R. necatrix* (as described above). Four independent sets of twenty wheat plants were tested per treatment. A set on wheat seedlings were placed on uninfected potting soil as controls. The plants were grown for 21–28 days in a greenhouse at 25 °C with 70 % relative humidity and 16 h of daylight, and irrigated twice per week. After 28 days of incubation, a substantial number of the plants (>60 %) in the untreated control were diseased and the disease index (DI) was calculated reporting the aerial symptom evaluation over the 28-day period, and the area under the disease progress curve (AUDPC) was calculated at the end of the assay. The use of fluorescent-tagged *R. necatrix* and *Pseudomonas* spp. allowed CLSM visualization of their interaction on wheat roots, as described above.

The pathosystem wheat/*Rosellinia necatrix* assayed in this work, showed typical, progressive and reproducible symptoms of browning and softening of roots, yellowing and wilting of leaves, dieback, and finally dead of the plant (Fig. 1), symptoms that are common of root rot in other plants (Pliego et al., 2009). Because of the difficulty of observing the symptoms on the wheat roots and because of the development of *R. necatrix* on the root surfaces, we calculated the disease index percentage of foliar symptoms (Fig. 1A), as previously did in other plant models challenged by *R. necatrix* (Cazorla et al., 2006). Thus, the pathogenic strain *R. necatrix* CH53-GFP colonize most of the root system, covering predominantly the main roots and the plant crown. An extensive mycelial network was observed on the wheat root and seed surface, either as a diffuse mycelium or in the form of hyphal strands (Fig. 1B and C). CLSM visualization showed the characteristics pea-shaped structures of the *R. necatrix* mycelia, mycelial aggregations and developing of fungal hyphae into the spaces between the epidermic cells (Fig. 1D), as similarly observed in *R. necatrix* infected avocado roots (Pliego et al., 2009).

The three fluorescent-tagged bacterial strains used in this work have been previously probed to constitute a compatible bacterial consortium (Tienda et al., 2024). CLSM assays allowed visualization of

Table 1
Microbial strains and plasmid used in this study.

Strain	Relevant characteristic [a]	Reference
Bacterial strains		
Pseudomonas chlororaphis		
PCL1601 (01)	Wild type strain, isolated from avocado rhizosphere, producer of antifungal phenazines. Biocontrol against phytopathogenic fungi; PCA+	Vida et al. (2017)
01-dsRed	Wild type PCL1601 strain transformed with pJA-dsRed plasmid. Red fluorescence; Tc^r	Tienda et al. (2024)
PCL1606-Rif^r (06)	Spontaneous mutant rifampicin resistant of wild type strain PCL1606 (PCL1606 was isolated from avocado rhizosphere, producer of antifungal 2- hexyl, 5-propyl resorcinol. Biocontrol against phytopathogenic fungi); HPR+, Rif^r	González-Sánchez et al. (2010); Cazorla et al. (2006)
06-Rif^r-eCFP	Derivative PCL1606-Rifr transformed with the plasmid pMP4641. Cyan fluorescence; Rif^r, Tc^r	Tienda et al. (2024)
Pseudomonas alcaligenes		
AVO110 (110)	Wild type, isolated from avocado rhizosphere, non-antifungal producer. Efficient root colonizer. Biocontrol against phytopathogenic fungi.	Pliego et al. (2007)
110-GFP	Wild type strain AVO110 transformed with the plasmid pBHA-8-GFP. Green fluorescence; Gm^r	Tienda et al. (2024)
Fungal strains		
Rosellinia necatrix		
CH53	Wild type strain, isolated from avocado root, cause avocado white root rot.	Pérez-Jiménez (1997)
CH53-GFP	Wild type strain CH53 tagged with GFP, Green fluorescence, Hyg^r	Pliego et al. (2009)

Gm^r: gentamicin resistant (25 μg/ml); Hyg^r: hygromycin resistant (50 μg/ml); Rif^r: Rifampicin resistant (10 μg/ml); Tc^r: tetracycline resistant (20 μg/ml).

[a] PCA+: Phenazine-1-carboxylic acid production; HPR+: 2-hexyl, 5-propyl resorcinol production.

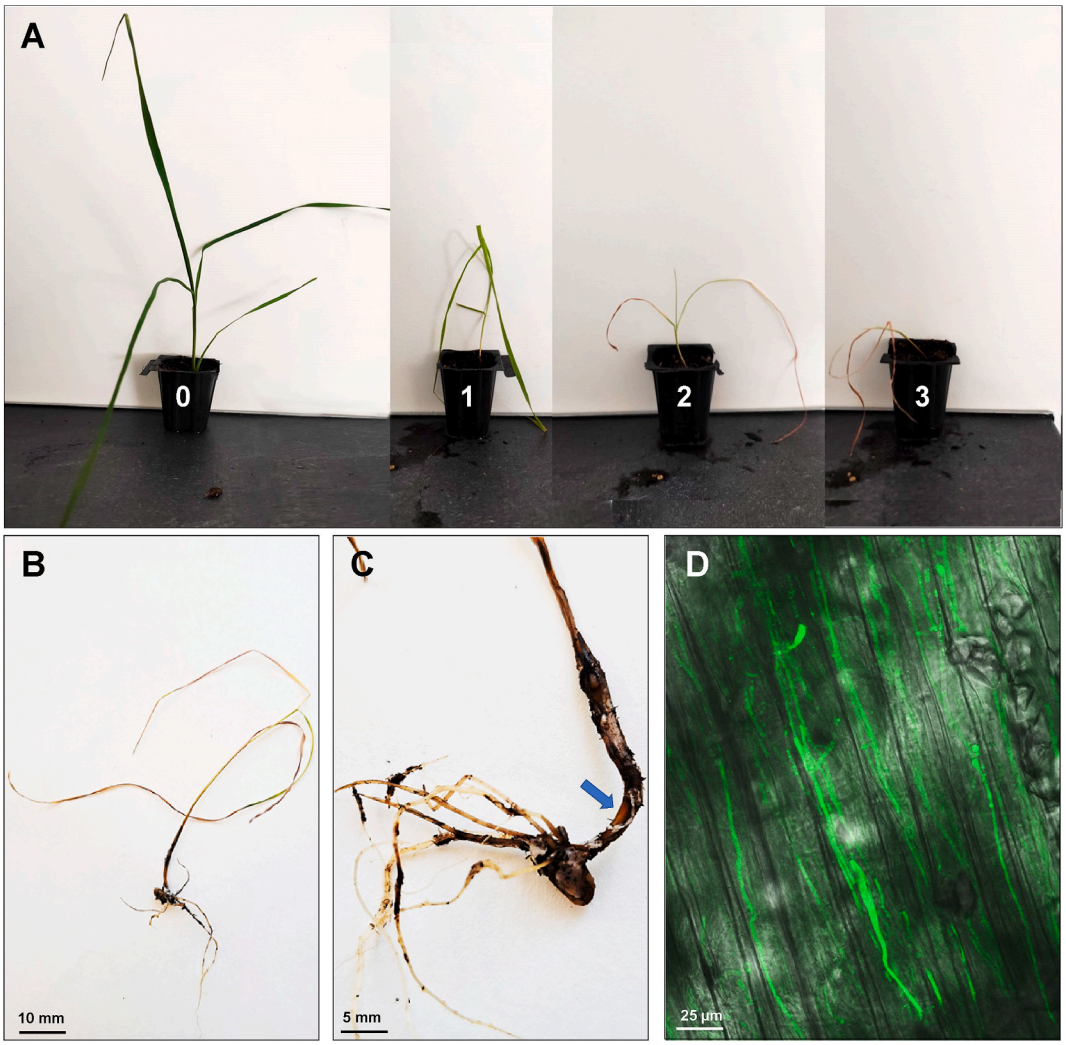

Fig. 1. Wheat-*Rosellinia necatrix* pathosystem. A) Wheat seeds (cv. Nogal) were pregerminated for 5 days, sowed and the soil infected with *R. necatrix*. Progressive aerial parts showed symptoms of disease compared with a healthy uninoculated plant (disease index 0), characterized by a progressive wilting of the plant (disease index 1), dryness of leaf tips (disease index 2), and finally dead of the plant (disease index 3) after 28 days post inoculation with *R. necatrix*. B) Wheat plantlet challenged with *R. necatrix*-GFP showing a disease index of 2, displaying aerial browning and wilt of leaves, and root browning and softening symptoms. The seed was also colonized by the fungal pathogen. C) Detail of a wheat plantlet at disease index 2, showing crown and root symptoms of *R. necatrix* infection. Typical mycelial strands of *R. necatrix* can be observed on the affected tissues (arrow). D) Use of GFP-tagged *R. necatrix* strain for plant infections, allowed visualization of the fungal colonization (in green) of wheat root, showing the characteristics pea-shaped structures of the mycelia, mycelial aggregations, and hyphae following the spaces between the epidermic cells of the root.

fluorescent-tagged bacteria on wheat roots, confirming a similar colonization pattern to that described previously on avocado roots (Tienda et al., 2024). Pc PCL1601-dsRed colonizes as microcolonies between the epidermal cells of the wheat roots (Fig. 2A) and PcPCL1606-Rif^{r}-eCFP showed a scattered distribution along the surfaces of wheat roots (Fig. 2B). Finally, *P. alcaligenes* AVO110-GFP was observed distributed as small microcolonies along the wheat root (Fig. 2C). Interestingly, when the three strains (3P) were inoculated together, all fluorescent-tagged strains exhibited a homogeneously distribution into mixed microcolonies developing into the junctions between the epidermal cells of the wheat roots (Fig. 2D). Bacterial counts after single (Fig. 2E) or combined (3P) inoculations (Fig. 2F), allowed detection of the three inoculated strains throughout the experiment. Individual bacterial populations stabilized at approximately 10^{5-7} cfu/g root at the end of the assay (40 days after the inoculation). Interestingly, when combination of 3P was inoculated on wheat roots, very stable values were observed during the experiment, with all the strains having values around 10^{6} cfu/g root, similar to the data previously observed for avocado roots (Tienda et al., 2020, 2024). These results confirm the efficient colonization of the beneficial bacteria tested in this plant model. Additionally, the competitive indices obtained on wheat roots inoculated 3P consortium, showed stable and similar CI values for the three bacterial strains, with no clear negative effects among the inoculated bacterial strains (Figure Supplementary 1), as similarly observed previously for these strains in avocado (Tienda et al., 2024).

Biocontrol assays using wheat/*R. necatrix* were conducted. Biocontrol results were similar to that previously performed on avocado, with a clear reduction in the percentage of diseased plants when single and combined bacterial inoculations were performed (Figure Supplementary 2). However, no differences were observed between the different bacterial treatments (Fig. 3A). CLSM visualization of the interactions taking place on the wheat roots during biocontrol, showed evidence of interactions among both the fungus and each of the strains, with the last ones forming dispersed mixed microcolonies on the wheat root surface (Fig. 3B).

Rosellinia necatrix is a fungal pathogen affecting a broad range of plants. Since it affects mainly woody host and even different varieties (Dafny-Yelin et al., 2024), the use of specific plant models for its study is

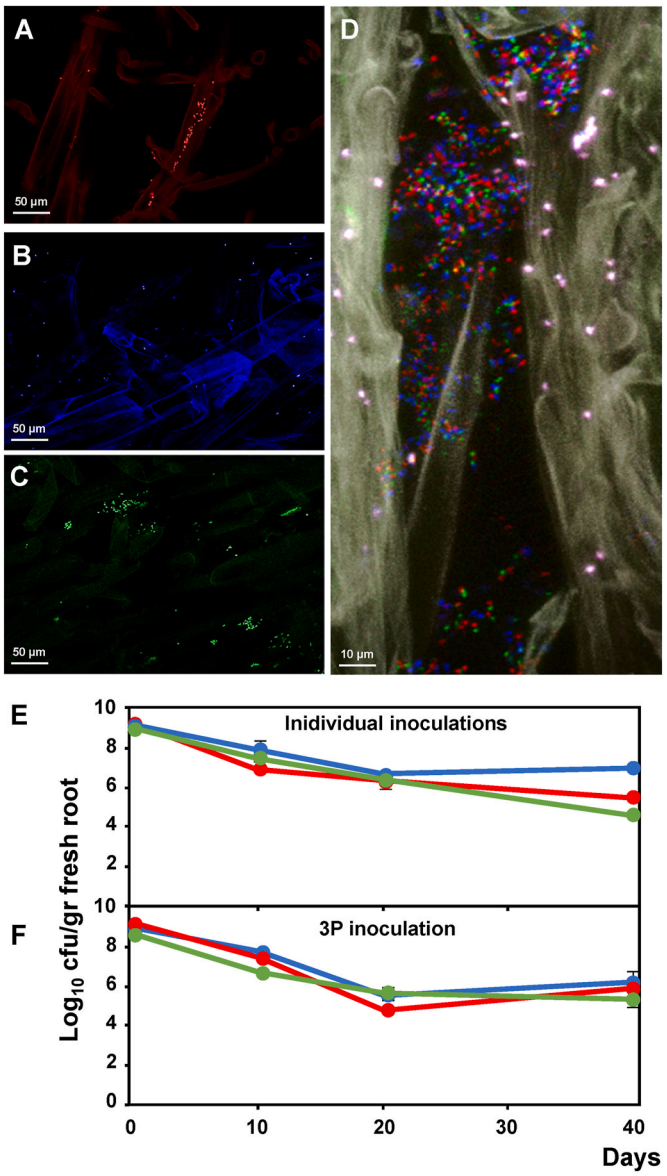

Fig. 2. Rhizobacterial colonization of wheat roots. Beneficial rhizobacteria previously isolated from avocado roots and tagged with different fluorescent proteins, where inoculated individually or combined (3P) on pregermined wheat seeds. After 21 days, observation of roots samples under confocal microscopy, showed presence and colonization pattern of A) *Pseudomonas chlororaphis* PCL1601 (red), B) *P. chlororaphis* PCL1606 (cyan) and C) *P. alcaligenes* AVO110 (green). Combined inoculations (D), showed formation of mixed microcolonies on the spaces interepidermic root cells. Bacterial counts along time of single inoculations (E) showed stable colonization of the wheat roots of the inoculated bacteria. Combined inoculations (3P) resulted in similar results (F), with stabilized populations of the inoculated bacteria on the wheat roots. Three independent experiments with three replicates were carried out. Bars indicated standard error.

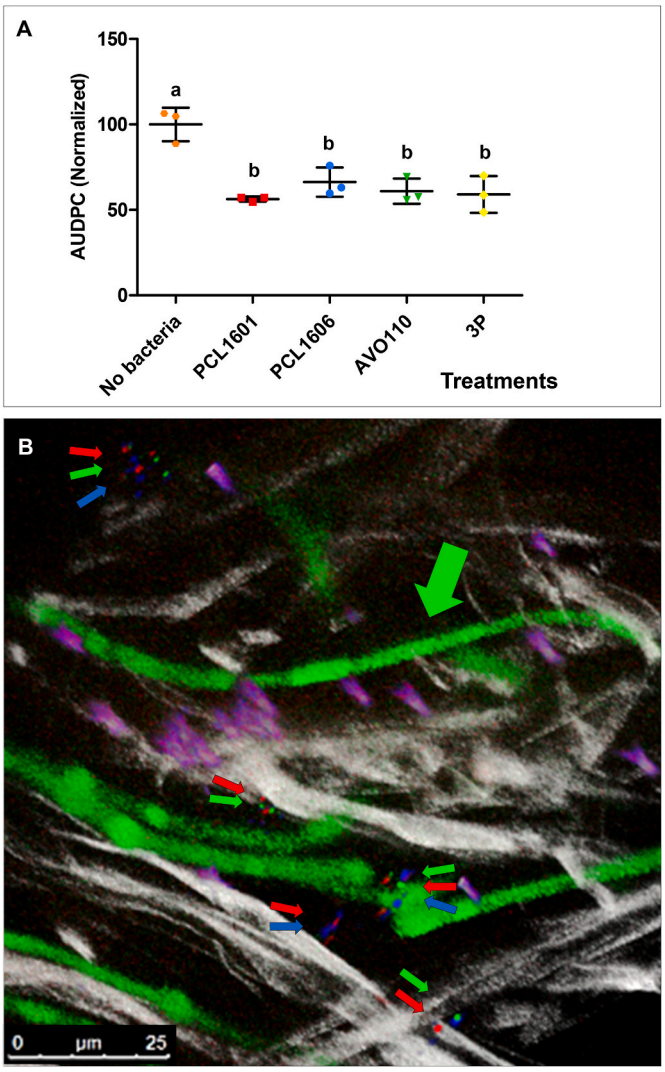

Fig. 3. Use of Wheat-*Rosellinia necatrix* pathosystem for biocontrol experiments. A) Wheat was pregerminated, bacterized with single and mixed bacterial cultures, sowed and the soil infected with *R. necatrix*. Area under the disease progress curve (AUDPC) was calculated after 28 days post *R. necatrix* inoculation. Statistical data analysis was tested using one-way analysis of variance (ANOVA) followed by Fisher's least significant difference test with Bonferroni's correction ($P = 0.05$). All data analyses were performed using IBM SPSS statistics 25 software (SPSS, Inc., Chicago, IL, United States). B) Use of fluorescent-tagged strains of *R. necatrix* (green big arrow) and biocontrol bacteria (small arrows), allowed visualization of the colonization and interactions on the wheat root during biocontrol.

being difficult because their inherent characteristics of a woody plant. On the other hand, the use of wheat as a model to test biocontrol against above- and below-ground pathogens have been confirmed previously (Weller et al., 1995). Remarkably, the strains used in this work have showed biocontrol in different plant models, such as avocado and tomato, and now in wheat, demonstrating a superior adaptability to the different plant roots. However, expanding wheat as a model of study also could have limitations. Using a wheat model in a controlled greenhouse environment may not accurately predict results in real-world field conditions, especially for woody plants. This could be attributed to several key differences, including alteration in root architecture, the instability of the external environment, the heterogeneity of soil properties, and the concomitant microbial adaptation (Nunan, 2017). In any case, the results on the wheat model here, were in agreement with those previously obtained in avocado under greenhouse conditions (Tienda et al., 2024).

In conclusion, the wheat/*Rosellinia necatrix* model developed in this study is an effective tool for evaluating biocontrol agents. It produced results consistent with previous observations in avocado plants. These findings suggest wheat as a complementary model system for investigating AWRR-related rhizospheric dynamics. Its potential to high-throughput experimentation offers an advantage over avocado plants, thereby expanding research capabilities.

CRediT authorship contribution statement

Sandra Tienda: Writing – review & editing, Writing – original draft, Software, Methodology, Investigation, Formal analysis, Data curation. **Carmen Vida:** Methodology, Investigation, Formal analysis, Data curation. **Antonio de Vicente:** Supervision, Resources, Methodology, Funding acquisition. **Francisco M. Cazorla:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Investigation, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix B. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.rhisph.2025.101138.

Data availability

No data was used for the research described in the article.

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