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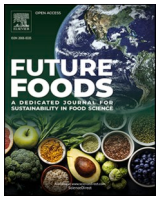

Exploring the microbiota of tomato and strawberry plants as sources of bio-protective cultures for fruits and vegetables preservation

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ABSTRACT

This review explores the agri-food residues of tomato and strawberry as sources of bacteria with bio-protective potential against different pathogenic and spoilage microorganisms for enhancing product shelf life and improving food safety. A comprehensive review of research highlights that *Pseudomonas* (e.g., *P. fluorescens*) and *Bacillus* (e.g., *B. subtilis*) are relevant genera in the microbiota of both tomato and strawberry plants, as opposed to lactic acid bacteria which are a minority in both plants. Interestingly, those dominant microbial groups have been reported to exhibit potential bio-protective capabilities. This work also discusses different innovative and sustainable methods, such as the use of protective coating or microencapsulation, and the importance of related factors (produce surface properties, bacterial adhesion, etc.) for applying bio-protective cultures in tomato and strawberry, emphasizing the pros and cons. As a conclusion, we suggest that bio-protective cultures are applied at an earlier stage, at crop, exploiting the antimicrobial abilities in the pre- and post-harvest continuum. This bio-protective approach contributes to a more bio-based strategy to sustainably preserve fruits and vegetables from farm to fork.

1. Introduction

The production of fruit and vegetables is a fundamental sector for many European Union (EU) Member States, especially those of the Mediterranean region, with Spain being the leading producer in the EU (EUROSTAT, 2023). Among the richly diversified produce of the EU, tomato is the second most produced fresh vegetable in this region, both in terms of output value and volume of harvested production (i.e., 6,169,000 tonnes in 2022) (Fruit Logistica, 2023). On the other hand, strawberries are one of the main fresh fruits produced in European countries such as Spain, Poland, Belgium, Germany or Italy (FAOSTAT, 2023).

Strawberry and tomato are both susceptible to contamination and proliferation of pathogenic bacteria such as *Salmonella enterica, Escherichia coli* O157:H7 or *Listeria monocytogenes*, which have been the causative agents of several foodborne outbreaks (Kwinda et al., 2015; Oliveira et al., 2019; Viñas et al., 2020). Furthermore, different fungi belonging to the genera *Botrytis* and *Rizhopus* have been found to be responsible for the spoilage of strawberry and tomato, respectively, both at pre- and post-harvest stages (Moss, 2008).

Disinfection with chlorine is the most common method to improve the microbial safety of fruits and vegetables (Meireles et al., 2016). However, the current consumption trends are focused on chemical-free and sustainable food products (Nath et al., 2015). In line with this, post-harvest bio-protection, also called bio-preservation, applied to fruits and vegetables has been recently studied (Comitini et al., 2023; Settanni and Corsetti, 2008; Ma et al., 2017). This biological method is based on the use of controlled viable microorganisms or their metabolites with antimicrobial activity to extend food shelf life with a minimal impact in the sensory properties (Gyawali and Ibrahim, 2014; Singh, 2018). In this context, the use of the agricultural waste and fresh produce as a source of bio-protective microorganisms with antimicrobial activity is an emerging perspective for more sustainable food systems (Jackson et al., 2015). Plant microbiota community composition varies among the different plant anatomical parts (Trivedi et al., 2020), so different fractions of agri-food residues could be used to obtain specific bio-protective microorganisms (Jackson et al., 2015).

In recent years, there has been a notable advancement in the study of the roles and relationships between plant microbiota and the host

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macroorganism (plant), which is defined as a holobiont (Vandenkoornhuyse et al., 2015). Plant microbiota can enhance the immune system of the host through the production of antimicrobial compounds and the activation of plant defense mechanisms (Berendsen et al., 2012). These symbiotic interactions between microorganisms and their hosts have been broadly studied in other ecosystems, e.g., humans (Afzaal et al., 2022; Wu et al., 2022). The microorganisms that are natural or endogenous in the plant microbiota and can holistically protect their host from diseases are so-called soterobionts (Cernava and Berg, 2022). The application of these soterobionts as bio-protective cultures after harvest would be a promising strategy to prevent post-harvest fruit and vegetable diseases. However, to date, there are not soterobionts identified as specific to post-harvest diseases (Wassermann et al., 2022).

The bio-protective potential of the microbiota present in agri-food residues is still little explored. This review investigated endogenous microorganisms present in strawberry and tomato plants and discussed their bio-protective properties against different pathogenic microorganisms for product shelf life and/or human health. Furthermore, this work provided a critical analysis of the different methods used for the application of bio-protective cultures in fruits and vegetables, emphasizing the pros and cons and potential alternatives. In addition, the authors underlined the application of bio-protective cultures at an earlier stage, at crop, for exploiting their antimicrobial abilities in the pre- and post-harvest continuum.

2. Materials and methods

2.1. Research strategy

A comprehensive review was performed based on the EFSA guidelines (EFSA, 2010). The literature search was conducted using Web of Science database for studies in English published between 2010 and (31 Jan) 2023 written in English. The search was performed separately for strawberry and tomato. In order to include or exclude studies, two protocols were developed for each crop and divided into two search levels based on questions and eligibility criteria. The selected studies were included in the reference manager Mendeley Desktop software package (Mendeley Ltd, London, UK).

The first search level consisted of an advanced automatic search using field labels, Boolean operators, and other types of operators such as brackets and query sets. For this purpose, a combination of key terms related to the objectives to be achieved were used. Studies were excluded if the content of the title or abstract was not related to the search objectives. The second search level was based on reading the articles selected in the previous level to check their adequacy according to inclusion or exclusion criteria, which are presented in Table 1. These criteria were elaborated to answer a question related to the objectives of the review: *Does the article describe the bacteria present in the microbiota of the different anatomical parts of the strawberry and tomato plant*?

During the full reading of the selected articles, the reference list was checked for the existence of key or relevant studies that were not detected in the process described above. These papers were attached in a separate folder in the Mendeley software. Duplicate articles were removed using the "Check for Duplicates" option in Mendeley. The selected studies were tabulated using Microsoft Excel 2016 (Redmond, USA). Tables and graphs were elaborated to facilitate the classification of the extracted data.

3. Results

3.1. Endogenous microbiota in strawberry and tomato plants

A total of 193 and 217 records were obtained related to the microbiota of strawberry and tomato plants, respectively. Following the 1st and 2nd levels of the search process and applying the eligibility and exclusion criteria as represented in Fig. 1, 28 % and 29.5 % of the articles were selected for strawberry and tomato, respectively. Fig. 2 illustrates the number of articles describing the bacterial families present in the different anatomical parts of the strawberry (Fig. 2A) and tomato plants (Fig. 2B). In general, the predominant bacterial families reported for both plants in the reviewed literature correspond to *Pseudomonadaceae* (45 % of articles) and *Bacillaceae* (36 % of articles). Additionally, other families such as *Enterobacteriaceae, Xanthomonadaceae* and *Sphingomonadaceae* are also reported in both plants.

Within *Pseudomonadaceae, Pseudomonas* is the most frequently isolated genus. In particular, species such as *P. fluorescens, P. aeruginosa, P. rhizospherae* and *P. orientalis* are described to be part of the strawberry and tomato plant microbiota (Basurto-Cadena et al., 2012; Hammami et al., 2013; Hautsalo et al., 2016; Krimm et al. (2005). In strawberry, this genus is mainly located in the fruit and aerial parts (Table 2), while in tomato plant, *Pseudomonas* spp. are also present in the rhizosphere and root (Table 3).

In relation to *Bacillaceae, Bacillus* spp., *B. cereus* and *B. subtilis* are the most abundant species in both plants reported in the literature (Tables 2 and 3). Other species such as *B. pumulis, B. megaterium, B. weihenstephanensis, B. mycoides* and *B. licheniformis* are reported in strawberry fruit and the aerial parts of both plants (Abanda-Nkpwatt et al., 2006; Basurto-Cadena et al., 2012; Krimm et al. (2005); Logan and De Vos, 2015).

Only a few studies have tried to identify *Enterobacteriaceae* isolates at genus or species level, although *Enterobacter* can be highlighted as the most mentioned genus in both plants. The *Sphingomonadaceae* and *Xanthomonadaceae* families are often present in both plants. *Sphigomonas, Novosphingobium, Sphingobium* and *Sphingobbacterium* are genera of

Table 1
Inclusion and exclusion criteria used in the second search level.

Key element	Eligibility criteria	Exclusion criteria
Population	– Fresh strawberries and tomatoes – Fresh fruits and vegetables	– Food from non-vegetable origin – Processed vegetables and fruits (juices, yoghurt…)
Outcome	– Bacteria with antimicrobial activity – Bacteria with antifungal activity	– Food preservation by chemical and/or physical treatments – Bio-protection by extracts, essential oils…
Study design	– Studies *in vitro* and/or i*n vivo*, of bacteria with antimicrobial capacity against other pathogens and spoilers – Bio-protection reviews – Bio-protective bacteria isolated from fresh vegetables or vegetable plants – Post-harvest application of bio-protective bacteria	– Preharvest application of bio-protective bacteria – Bio-protective bacteria isolated from animal origin products – Application of bio-protective microorganisms in non-vegetable foods
Type of publication	– Peer-reviewed scientific articles – Research articles (primary) – Review articles (secondary)	– Opinion articles – Editorial – Conference abstract books – Non-governmental reports
Language restriction	English	Any other language
Time period	2010 to 2023	Previous dates in each case

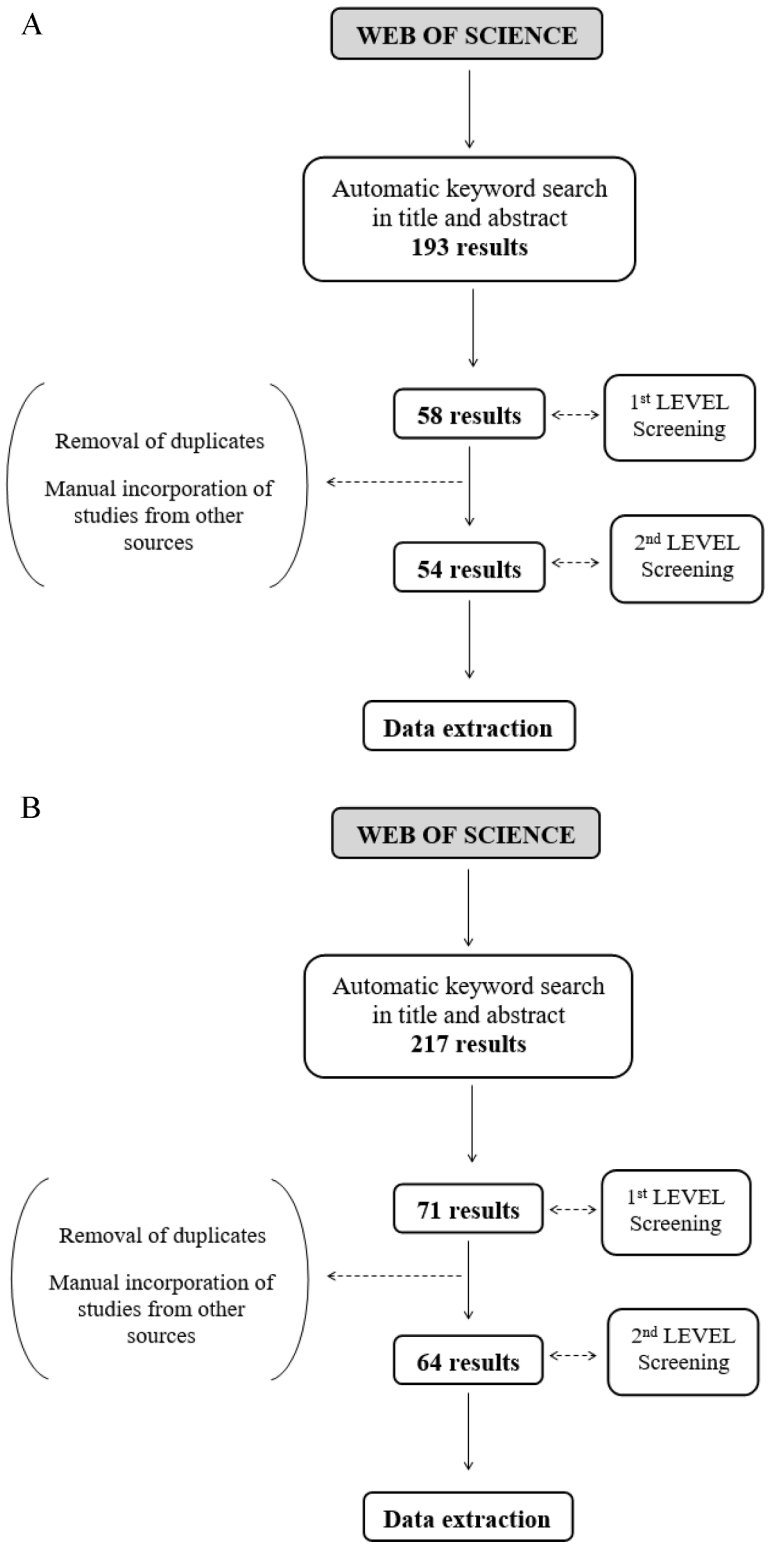

Fig. 1. Flow chart of the search process for (A) strawberry and (B) tomato plants microbiota by applying two search levels, including the number of results obtained at each level.

Sphingomonadaceae that are found mainly in the roots and rhizosphere of both plants as well as in the tomato fruit and aerial parts. The most relevant genus from *Xanthomonadaceae* is *Xanthomonas*, found in the aerial part of the strawberry plant and in the roots of the tomato plant, where the presence of *X. campestris* has been described (Marquez-Santacruz et al., 2010).

Regarding lactic acid bacteria (LAB), they are not abundant in the microbiota of either strawberry or tomato plant. However, some authors have described the presence of the genera *Enterococcus* (McGowan et al., 2006), *Latilactobacillus* and *Leuconostoc* in strawberry fruits (de Pereira et al., 2012; Kim et al., 2021) (Table 2).

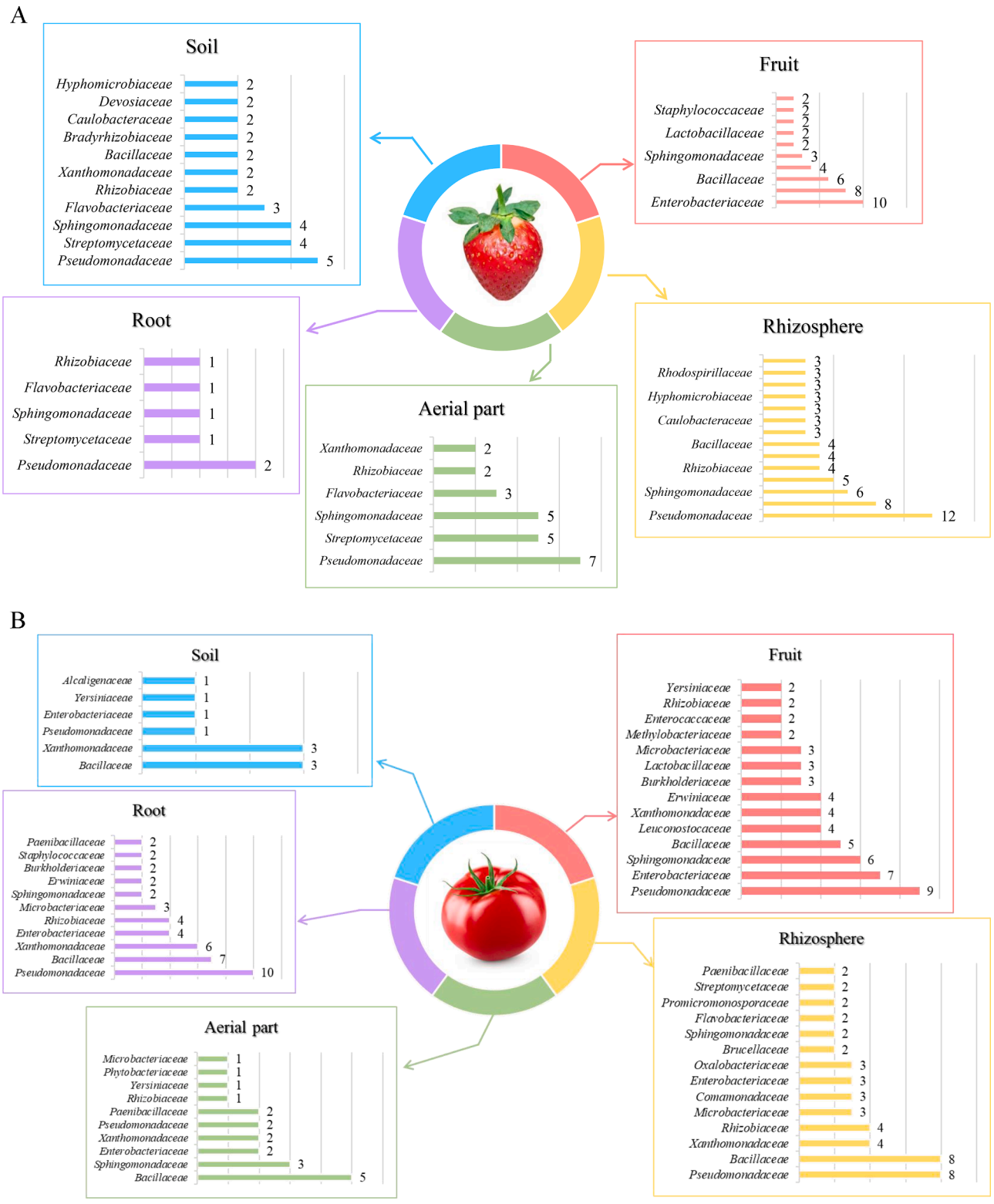

Fig. 2. Number of articles describing the bacterial families present in the different anatomical parts of strawberry (A) and tomato (B) plants.

4. Discussion

4.1. Bio-protective potential of bacteria present in strawberry and tomato plants

The most common sources of bio-protective cultures are natural starters from fermented foods such as dairy or meat products (Lozo et al., 2021). However, as noted by Swain et al. (2014), it is also possible to obtain microorganisms with antimicrobial properties from non-dairy sources, including cereals, fruits, and vegetables, to be used as bio-protective cultures. In this regard, bacteria naturally present in plant tissues are adapted to that environment and are better at developing natural competitive abilities against microorganisms that cause post-harvest diseases (Lopes et al., 2018; Trotel-Aziz et al., 2008).

Table 2
Families, genera, and species of the most reported bacteria present in the different anatomical parts of strawberry plant.

Family	Genus/Specie	Anatomical part	Refs.
Bacillaceae	*Bacillus* spp.	Fruit	de Pereira et al. (2012)
		Rhizosphere	Chen et al. (2020b)
		Rhizosphere	LI et al. (2018)
		Rhizosphere	Manici et al. (2018)
		Rhizosphere	Abbamondi et al. (2016)
		Rhizosphere	Su et al. (2022)
		Soil	Li et al. (2018)
		Soil	Zhang et al. (2019)
		Aerial part	Sylla et al. (2013)
		Aerial part	Wei et al. (2016)
		Aerial part	Abanda-Nkpwatt et al. (2006)
		Aerial part	Olimi et al. (2022)
		Soil	Cai et al. (2017)
	B. subtilis	Fruit	de Pereira et al. (2012)
		Rhizosphere	Basurto-Cadena et al. (2012)
		Root	Kukkurainen et al. (2005)
		Aerial part	Basurto-Cadena et al. (2012)
	B. pumulis	Fruit	Baugher and Jaykus (2016)
		Rhizosphere	Berg et al. (2006)
	B. megaterium	Fruit	Jensen et al. (2013)
	B. cereus Delaporte	Fruit	Krimm et al. (2005)
		Aerial part	Krimm et al. (2005)
	B. cereus	Fruit	Li et al. (2019)
		Rhizosphere	Berg et al. (2006)
		Rhizosphere	Basurto-Cadena et al. (2012)
		Rhizosphere	Laili et al. (2017)
		Soil	Berg et al. (2006)
		Root	Kukkurainen et al. (2005)
		Aerial part	Basurto-Cadena et al. (2012)
		Aerial part	Abanda-Nkpwatt et al. (2006)
	B. mycoides	Fruit	Krimm et al. (2005)
		Aerial part	Krimm et al. (2005)
		Aerial part	Abanda-Nkpwatt et al. (2006)
	B. weihenstephonensis	Fruit	Krimm et al. (2005)
		Aerial part	Krimm et al. (2005)
	B. licheniformis	Rhizosphere	Basurto-Cadena et al. (2012)
		Aerial part	Basurto-Cadena et al. (2012)
Enterobacteriaceae		Aerial part	Olimi et al. (2022)
	Citrobacter spp.	Rhizosphere	Berg et al. (2006)
		Soil	Berg et al. (2006)
	Echerichia spp.	Fruit	Zhang et al. (2020)
		Fruit	Kurtböke et al. (2016)
		Soil	Zhang et al. (2020)
	E. fergusonii	Soil	Zhang et al. (2020)
	Enterobacter spp.	Fruit	Zhang et al. (2020)
		Fruit	Baugher and Jaykus (2016)
		Fruit	Olimi et al. (2022)
		Fruit	Kukkurainen et al. (2005)
		Soil	Zhang et al. (2020)
	E. ludwigii	Fruit	de Pereira et al. (2012)
	E. agglomerans	Fruit	Jensen et al. (2013)
	Klebsiella spp.	Fruit	Zhang et al. (2020)
		Soil	Zhang et al. (2020)
	Shigella spp.	Fruit	Zhang et al. (2020)
	Pantoea spp.	Fruit	Kurtböke et al. (2016)
		Fruit	Kim et al. (2021)
		Fruit	Fang et al. (2019)
		Fruit	Kukkurainen et al. (2005)
		Fruit	Campaniello et al. (2008)
		Fruit	Olimi et al. (2022)
		Rhizosphere	Berg et al. (2006)
		Soil	Berg et al. (2006)
		Root	Kukkurainen et al. (2005)
		Aerial part	Kukkurainen et al. (2005)
		Aerial part	Olimi et al. (2022)
	P. ananatis	Fruit	Zhang et al. (2020)
		Fruit	Smith et al. (2013)
	P. puctata	Fruit	de Pereira et al. (2012)
	P. aglomerans	Fruit	Baugher and Jaykus (2016)
	Rahnella inusitata	Fruit	Zhang et al. (2020)
	Rahnella aquatius	Fruit	Jensen et al. (2013)
	Kluyvera intermedia	Fruit	Zhang et al. (2020)
	Klebsiella spp.	Fruit	Kurtböke et al. (2016)
	K. oxytoca	Fruit	Baugher and Jaykus (2016)
		Fruit	Campaniello et al. (2008)
		Fruit	Kukkurainen et al. (2005)
	Shigella spp.	Fruit	Kurtböke et al. (2016)
	Citrobacter spp.	Fruit	Kurtböke et al. (2016)
	Cronobacter spp.	Fruit	Kurtböke et al. (2016)
	Raoutella spp.	Fruit	Kurtböke et al. (2016)
	Enterococcus spp.	Fruit	McGowan et al. (2006)
	Leclercia adecarboxylata	Rhizosphere	Laili et al. (2017)
Pseudomonadaceae	*Pseudomonas* spp.	Fruit	de Pereira et al. (2012)
		Fruit	Kim et al. (2021)
		Fruit	Olimi et al. (2022)
		Rhizosphere	Visscher (2019)
		Rhizosphere	Yang et al. (2020)
		Rhizosphere	Dai et al. (2020)
		Rhizosphere	De Tender et al. (2016)
		Rhizosphere	Manici et al. (2018)
		Rhizosphere	Berg et al. (2006)
		Rhizosphere	Abbamondi et al. (2016)
		Rhizosphere	Decoste et al. (2010)
		Rhizosphere	Su et al. (2022)
		Soil	Mazzola et al. (2018)

(*continued on next page*)

Table 2 (*continued*)

Family	Genus/Specie	Anatomical part	Refs.
		Soil	Berg et al. (2006)
		Soil	Lazcano et al. (2021)
		Soil	Zhang et al. (2019)
		Aerial part	Krimm et al. (2005)
		Aerial part	Sylla et al. (2013)
		Aerial part	Antoniou et al. (2017)
		Aerial part	Olimi et al. (2022)
	P. moraviensis	Fruit	Baugher and Jaykus (2016)
	P. putida	Fruit	Jensen et al. (2013)
	P. syringae phaseolica	Fruit	Jensen et al. (2013)
	P. lurida	Fruit	Krimm et al. (2005)
		Aerial part	Krimm et al. (2005)
		Aerial part	Abanda-Nkpwatt et al. (2006)
	P. rhizospherae	Fruit	Krimm et al. (2005)
		Aerial part	Krimm et al. (2005)
		Aerial part	Abanda-Nkpwatt et al. (2006)
	P. orientalis	Fruit	Krimm et al. (2005)
		Aerial part	Krimm et al. (2005)
		Aerial part	Abanda-Nkpwatt et al. (2006)
	P. fulva	Fruit	Krimm et al. (2005)
		Aerial part	Krimm et al. (2005)
	P. parafulva	Fruit	Krimm et al. (2005)
		Aerial part	Krimm et al. (2005)
		Aerial part	Abanda-Nkpwatt et al. (2006)
	P. fluorescens	Fruit	Hautsalo et al. (2016)
		Fruit	Parikka et al. (2017)
		Root	Wada et al. (2009)
		Root	Kukkurainen et al. (2005)
		Aerial part	Kukkurainen et al. (2005)
	P. aeruginosa	Rhizosphere	Basurto-Cadena et al. (2012)
		Aerial part	Basurto-Cadena et al. (2012)
	P. umsongensis	Rhizosphere	Laili et al. (2017)
	Chryseomonas luteola	Root	Kukkurainen et al. (2005)
Streptomycetaceae	*Streptomyces* spp.	Rhizosphere	Visscher (2019)
		Rhizosphere	Yang et al. (2020)
		Rhizosphere	De Tender et al. (2016)
		Rhizosphere	Mazzola et al. (2018)
		Rhizosphere	Berg et al. (2006)
		Rhizosphere	Yamamura et al. (2014)
		Rhizosphere	Lazcano et al. (2021)
		Rhizosphere	Kim et al. (2019)
		Rhizosphere	Su et al. (2022)
		Soil	Mazzola et al. (2018)

Table 2 (*continued*)

Family	Genus/Specie	Anatomical part	Refs.
		Soil	Berg et al. (2006)
		Soil	Lazcano et al. (2021)
		Soil	Zhang et al. (2019)
		Root	Yamamura et al. (2014)
	S. thermocarboxydus	Aerial part	Marian et al. (2020)
	S. griseus	Rhizosphere	Cho et al. (2017)
	S. hygroscopicus	Rhizosphere	Shen et al. (2016)
Xanthomonadaceae	*Xanthomonas* spp.	Aerial part	Wei et al. (2016)
	Pseudolabrys spp.	Rhizosphere	Yang et al. (2020)
		Rhizosphere	De Tender et al. (2016)
	Lysobacter spp.	Rhizosphere	Singh et al. (2015)
	Stenotrophomonas spp.	Rhizosphere	Berg et al. (2006)
		Soil	Berg et al. (2006)
	S. maltophilia	Aerial part	Krimm et al. (2005)
		Aerial part	Abanda-Nkpwatt et al. (2006)
		Aerial part	Alijani et al. (2020)
Sphingomonadaceae		Rhizosphere	Olimi et al. (2022)
	Sphingomonas spp.	Fruit	Olimi et al. (2022)
		Rhizosphere	Chen et al. (2020b)
		Soil	Li et al. (2018)
		Soil	Zhang et al. (2019)
		Soil	Cai et al. (2017)
		Soil	Min et al. (2016)
		Aerial part	Sylla et al. (2013)
		Aerial part	Olimi et al. (2022)
	S. paucimobilis	Root	Kukkurainen et al. (2005)
	Novosphingobium spp.	Rhizosphere	Visscher (2019)
		Rhizosphere	Yang et al. (2020)
		Soil	Cai et al. (2017)
	Sphingopyxis spp.	Rhizosphere	Li et al. (2018)
		Rhizosphere	Chen et al. (2020b)
Flavobacteriaceae		Soil	Olimi et al. (2022)
		Rhizosphere	Olimi et al. (2022)
	Flavobacterium spp.	Rhizosphere	Basurto-Cadena et al. (2012)
		Rhizosphere	Berg et al. (2006)
		Aerial part	Basurto-Cadena et al. (2012)
	F. tyrosinilyticum	Rhizosphere	Du and Yi (2016)
Lactobacillaceae	*Lactiplantibacillus plantarum*	Fruit	de Pereira et al. (2012)
		Fruit	Chen et al. (2020a)
Leuconostocaceae	*Leuconostoc* spp.	Fruit	Kim et al. (2021)
		Fruit	Campaniello et al. (2008)

4.1.1. *Pseudomonas spp.*

Bacteria belonging to the genus *Pseudomonas* spp. are Gram-negative, straight, or slightly curved rods and motile by one or several polar flagella. This genus constitutes part of the microbiota of some fruits and vegetables such as apples, peaches, nectarines, pineapple, tomatoes, and strawberries (Alegre et al., 2013; Decoste et al., 2010; Olanya et al., 2015). Some strains of *P. aeruginosa* are responsible for infections in humans through their attachment to tissues and expression of virulence factors such as the secretion of toxins (exotoxins) and exoenzymes (Wu et al., 2014). Nevertheless, *Pseudomonas* spp. can inhibit other microorganisms by several mechanisms. One mechanism is based on the production of siderophores, such as pseudobactin 358 synthetized by *P. putida* WBS358. Pseudobactin 358 acts by removing iron required by other organisms that lack systems for using ferric siderophores (Palleroni, 2015). Other mechanisms of action comprise competition for nutrients and space and the formation of biofilms that

Table 3
Families, genera, and species of the most reported bacteria present in the different anatomical parts of tomato plant.

Family	Genus/Specie	Anatomical part	Refs.
Pseudomonadaceae		Fruit	Allard et al. (2016)
		Fruit	Allard et al. (2016)
		Rhizosphere	Allard et al. (2016)
		Aerial part	Allard et al. (2016)
	Pseudomonas spp.	Fruit	Habiba et al. (2016)
		Fruit	Telias et al. (2011)
		Fruit	Habiba et al. (2017)
		Fruit	Ottesen et al. (2013)
		Fruit	Lamelas et al. (2020)
		Fruit	Shi et al. (2022)
		Fruit	Gorrasi et al. (2022)
		Rhizosphere	Antoniou et al. (2017)
		Rhizosphere	Cordovez et al. (2021)
		Rhizosphere	Leoni et al. (2020)
		Root	Abbamondi et al. (2016)
		Root	Ma et al. (2017)
		Aerial part	Ottesen et al. (2013)
		Aerial part	López et al. (2020)
	P. anguilliseptica	Rhizosphere	Antoniou et al. (2017)
	P. hibiscicola	Rhizosphere	Antoniou et al. (2017)
	P. putida	Rhizosphere	Antoniou et al. (2017)
		Rhizosphere	Hammami et al. (2013)
		Rhizosphere	Pastor et al. (2012)
		Rhizosphere	Narendra Babu et al. (2015)
	P. stutzeri	Rhizosphere	Antoniou et al. (2017)
		Root	Marquez-Santacruz et al. (2010)
	P. aeruginosa	Rhizosphere	Narendra Babu et al. (2015)
		Rhizosphere	Hammami et al. (2013)
		Rhizosphere	Pastor et al. (2012)
		Rhizosphere	Narendra Babu et al. (2015)
		Root	Iasur Kruh et al. (2020)
		Soil	Karunasinghe et al. (2020)
	P. putida	Rhizosphere	Narendra Babu et al. (2015)
	P. fluorescens	Rhizosphere	Hammami et al. (2013)
		Rhizosphere	Pastor et al. (2012)
		Rhizosphere	Pérez-Rodriguez et al. (2020)
		Root	Pérez-Rodriguez et al. (2020)
	P. thivervalensis	Rhizosphere	Pérez-Rodriguez et al. (2020)
	P. brassicacearum	Rhizosphere	Pérez-Rodriguez et al. (2020)
	P. guariconensis	Root	Tian et al. (2017)
	P. mohnii	Root	Tian et al. (2017)
	P. plecoglossicida	Root	Tian et al. (2017)
		Root	Upreti and Thomas (2015)
	P. thivervalensis	Root	Pérez-Rodriguez et al. (2020)
	P. brassicacearum	Root	Pérez-Rodriguez et al. (2020)
	P. oleovorans	Root	Upreti and Thomas (2015)
	P. wadenswilerensis	Root	López et al. (2021)
	P. kilonensis	Root	López et al. (2021)
	P. syringae	Root	Marquez-Santacruz et al. (2010)
		Root	Marquez-Santacruz et al. (2010)
	P. corrugata	Rhizosphere	Pérez-Rodriguez et al. (2020)
		Root	Pérez-Rodriguez et al. (2020)
	P. kribbensis	Root	López et al. (2021)
	P. kribbensis	Aerial part	López et al. (2021)
	P. chengduensis	Aerial part	López et al. (2021)
	P. kilonensis	Aerial part	López et al. (2021)
	Chryseomonas spp.	Root	Ottesen et al. (2013)
		Aerial part	Ottesen et al. (2013)
	Azotobacter chroococcum	Rhizosphere	Narendra Babu et al. (2015)
Enterobacteriaceae		Fruit	Allard et al. (2016)
		Fruit	Allard et al. (2020)
		Fruit	Ottesen et al. (2015)
		Aerial part	Allard et al. (2020)
	Enterobacter spp.	Fruit	Telias et al. (2011)
	E. hirae	Fruit	Arellano-Ayala et al. (2020)
	E. munditii	Fruit	Arellano-Ayala et al. (2020)
	E.s faecium	Fruit	Arellano-Ayala et al. (2020)
	E. asburiae	Fruit	Chaouachi et al. (2021)
		Root	Chaouachi et al. (2021)
		Aerial part	Chaouachi et al. (2021)
	E. cloacae	Fruit	Chaouachi et al. (2021)
		Rhizosphere	Antoniou et al. (2017)
		Rhizosphere	Pérez-Rodriguez et al. (2020)
		Root	Chaouachi et al. (2021)
		Root	Pérez-Rodriguez et al. (2020)
		Root	Upreti and Thomas (2015)
		Aerial part	Chaouachi et al. (2021)
	E. hormaechei	Rhizosphere	Pérez-Rodriguez et al. (2020)
		Root	Pérez-Rodriguez et al. (2020)
	E. luwdigii	Root	Tian et al. (2017)
	E. mori	Root	Tian et al. (2017)
	Klebsiella variicola	Rhizosphere	Sunera et al. (2020)
	Citrobacter freundii	Root	Upreti and Thomas (2015)
	Cronobacter spp.	Fruit	Zhang et al. (2021)
	Cedecea spp.	Fruit	Gorrasi et al. (2022)
Rhizobiaceae		Fruit	Allard et al. 2020)
		Aerial part	Allard et al. (2020)
	Agrobacterium spp.	Fruit	Allard et al. (2016)
		Root	Abbamondi et al. (2016)
	A. tumefaciens	Rhizosphere	Antoniou et al. (2017)
	Rhizobium spp.	Fruit	Ottesen et al. (2013)
		Rhizosphere	Cordovez et al. (2021)
		Root	Ottesen et al. (2013)
		Root	Tian et al. (2017)
		Root	Abbamondi et al. (2016)
		Aerial part	Ottesen et al. (2013)

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Table 3 (*continued*)

Family	Genus/Specie	Anatomical part	Refs.
	R. radiobacter	Root	Upreti and Thomas (2015)
	R. massiliae	Root	Tian et al. (2017)
	Ensifer spp.	Rhizosphere	Abbamondi et al. (2016)
	Sinorhizobium adhaerens	Rhizosphere	Antoniou et al. (2017)
Bacillaceae		Rhizosphere	Allard et al. (2016)
	Bacillus spp.	Fruit	Telias et al. (2011)
		Fruit	Barretti et al. (2012)
		Fruit	Zhang et al. (2021)
		Rhizosphere	Abbamondi et al. (2016)
		Root	Sahu et al. (2019)
		Aerial part	Barretti et al. (2012)
		Soil	Organic amendment type…
	B. amyloliquefaciens	Fruit	Chaouachi et al. (2021)
		Root	Chaouachi et al. (2021)
		Root	Bhattacharya et al. (2019)
		Root	Tian et al. (2017)
		Aerial part	Chaouachi et al. (2021)
		Aerial part	Lanna-Filho et al. (2013)
	B. pumilus	Aerial part	Filho et al. (2010)
		Aerial part	Lanna-Filho et al. (2013)
	B. vallismortis	Fruit	Chaouachi et al. (2021)
		Root	Chaouachi et al. (2021)
		Aerial part	Chaouachi et al. (2021)
	B. pseudomycoides	Fruit	Chaouachi et al. (2021)
		Root	Chaouachi et al. (2021)
		Aerial part	Chaouachi et al. (2021)
	B. velezenisis	Fruit	Chaouachi et al. (2021)
		Rhizosphere	Yan et al. (2022)
		Root	Chaouachi et al. (2021)
		Aerial part	Chaouachi et al. (2021)
	B. subtilis	Fruit	Chaouachi et al. (2021)
		Fruit	Chaouachi et al. (2021)
		Rhizosphere	Narendra Babu et al. (2015)
		Rhizosphere	Zhou et al. (2021)
		Rhizosphere	Antoniou et al. (2017)
		Root	Marquez-Santacruz et al. (2010)
		Root	Bhattacharya et al. (2019)
		Root	Iqbal et al. (2018)
		Root	Tian et al. (2017)
		Root	Chaouachi et al. (2021)
		Soil	Sharma et al. (2015)
		Aerial part	Chaouachi et al. (2021)
	B. thurigiensis	Fruit	Chaouachi et al. (2021)
		Root	Chaouachi et al. (2021)
		Aerial part	Chaouachi et al. (2021)
	B. toyonensis	Fruit	Chaouachi et al. (2021)
		Root	Chaouachi et al. (2021)
		Aerial part	Chaouachi et al. (2021)
	B. proteolyticus	Fruit	Chaouachi et al. (2021)
		Root	Chaouachi et al. (2021)
		Aerial part	Chaouachi et al. (2021)
	B. nakamurai	Fruit	Chaouachi et al. (2021)
		Root	Chaouachi et al. (2021)
		Aerial part	Chaouachi et al. (2021)
	B. chandigarhensis	Rhizosphere	Antoniou et al. (2017)
	B. circulans	Rhizosphere	Antoniou et al. (2017)
	B. endophyticus	Rhizosphere	Antoniou et al. (2017)
	B. firmus	Rhizosphere	Antoniou et al. (2017)
	B. foraminis	Rhizosphere	Antoniou et al. (2017)
	B. humi	Rhizosphere	Antoniou et al. (2017)
	B. licheniformis	Rhizosphere	Antoniou et al. (2017)
		Root	Bhattacharya et al. (2019)
		Root	Marquez-Santacruz et al. (2010)
	B. megaterium	Rhizosphere	Antoniou et al. (2017)
	B. niacin	Rhizosphere	Antoniou et al. (2017)
	B. novalis	Rhizosphere	Antoniou et al. (2017)
	B.cereus	Rhizosphere	Narendra Babu et al. (2015)
		Rhizosphere	Sunera et al. (2020)
		Root	Tian et al. (2017)
		Soil	Karthika et al. (2020)
	B. cabrialesii	Rhizosphere	Zhou et al. (2021)
	B. endophyticus	Rhizosphere	Zhou et al. (2021)
	B. velezensis	Rhizosphere	Zhou et al. (2021)
	B. anthracis	Root	Tian et al. (2017)
	B. aryabhattai	Root	Tian et al. (2017)
	B. bingmayongensis	Root	Tian et al. (2017)
	B. methylotrophicus	Root	Tian et al. (2017)
	B. pumilus	Root	Tian et al. (2017)
	B. safensis	Aerial part	Draft genome…
	B. tequilensis	Root	Bhattacharya et al. (2019)
	Terribacillus sacchorophilus	Fruit	López et al. (2021)
	Lysinibacillus spp.	Root	Sahu et al. (2019)
Xanthomonadaceae		Fruit	Allard et al. (2020)
		Fruit	Ottesen et al. (2015)
		Fruit	Zhang et al. (2021)
		Aerial part	Ottesen et al. (2015)
		Aerial part	Allard et al. (2020)
	Xanthomonas spp.	Fruit	Ottesen et al. (2013)
		Root	Ottesen et al. (2013)
		Soil	Su et al. (2022)
	X. campestris	Root	Marquez-Santacruz et al. (2010)
	Pseudoxanthomonas	Rhizosphere	Leoni et al. (2020)

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Table 3 (*continued*)

Family	Genus/Specie	Anatomical part	Refs.
	Luteimonas mephitis	Rhizosphere	Antoniou et al. (2017)
	Lysobacter spp.	Rhizosphere	Antoniou et al. (2017)
		Soil	Su et al. (2022)
	Stenotrophomonas spp.	Root	Marquez-Santacruz et al. (2010)
		Root	Sahu et al. (2019)
		Soil	Su et al. (2022)
	S. maltophilia	Rhizosphere	Antoniou et al. (2017)
		Rhizosphere	Pérez-Rodriguez et al. (2020)
		Root	Pérez-Rodriguez et al. (2020)
		Root	López et al. (2021)
	S. rhizophila	Root	Tian et al. (2017)
	Rhodanobacter koreensis	Rhizosphere	Won et al. (2015)
Sphingomonadaceae		Fruit	Allard et al. (2020)
		Fruit	Ottesen et al. (2015)
		Rhizosphere	Oyserman et al. (2022)
		Aerial part	Allard et al. (2020)
		Aerial part	Ottesen et al. (2015)
	Sphingomonas spp.	Fruit	Telias et al. (2011)
		Fruit	Ottesen et al. (2013)
		Fruit	Escobar Rodríguez et al. (2021)
		Fruit	Zhang et al. (2021)
		Rhizosphere	Hu et al. (2020)
		Rhizosphere	Leoni et al. (2020)
		Aerial part	Ottesen et al. (2013)
		Aerial part	Andreadelli et al. (2021)
	Sphingobium spp.	Root	Ottesen et al. (2013)
	Kaistobacter spp.	Rhizosphere	Hu et al. (2020)
	Aeromicrobium spp.	Rhizosphere	Hu et al. (2020)
	Sphingobacterium spp.	Fruit	Zhang et al. (2021)
	S. multivorum	Root	Upreti and Thomas (2015)
Flavobacteriaceae	*Chryseobacterium* spp.	Root	Ottesen et al. (2013)
		Rhizosphere	Abbamondi et al. (2016)
		Rhizosphere	Antoniou et al. (2017)
	Flavobacterium spp.	Fruit	Zhang et al. (2021)
		Rhizosphere	Antoniou et al. (2017)
	Chryseobacterium wanjuense	Rhizosphere	Antoniou et al. (2017)
Burkholderiaceae		Fruit	Zhang et al. (2021)
	Burkholderia spp.	Fruit	Escobar Rodríguez et al. (2021)
Microbacteriaceae		Aerial part	Allard et al. (2020)
		Aerial part	Ottesen et al. (2015)
	Microbacterium spp.	Root	Marquez-Santacruz et al. (2010)
	M. foliorum	Rhizosphere	Antoniou et al. (2017)
		Root	Marquez-Santacruz et al. (2010)
	M. paraoxydans	Rhizosphere	Antoniou et al. (2017)
		Root	López et al. (2020)
	M. esteraromaticum	Rhizosphere	Antoniou et al. (2017)
	Clavibacter spp.	Fruit	Gorrasi et al. (2022)
Leuconostocaceae	*Leuconostoc* spp.	Fruit	Telias et al. (2011)
	L. citreum	Fruit	Fessard and Remize (2019)
		Root	Trias et al. (2008)
	L. pseudomesentoeroides	Fruit	Fessard and Remize (2019)
	Weissella spp.	Fruit	Telias et al. (2011)
	W. confusa	Fruit	Arellano-Ayala et al. (2020)
	W. paramesenteroides	Fruit	Arellano-Ayala et al. (2020)
	W. cibaria	Fruit	Arellano-Ayala et al. (2020)
		Fruit	Fessard and Remize (2019)
		Root	Trias et al. (2008)
Lactobacillaceae	*L. plantarum*	Fruit	Fessard and Remize (2019)
		Root	Trias et al.(2008)
	L. brevis	Fruit	Arellano-Ayala et al. (2020)

inhibit spore germination and mycelial growth. In addition, the synthesis of toxic metabolites such as 2,4-diacetylphloroglucinol (Phl), phenazine-1-carboxylic acid and pyrrolnitrin is shown to be effective against fungi such as *Fusarium* spp. (Wallace et al., 2018).

The application of fluorescent *Pseudomonas* has been studied due to its catabolic versatility and ability to colonize roots and produce antifungal metabolites (Hammami et al., 2013). *In vitro*, isolates of *P. fluorescens* suppressed conidial germination and mycelial growth of *Penicillium expansum* under cold storage by producing inhibitory metabolites such as volatile organic compounds (VOCs), antibiotics and lytic enzymes (Wallace et al., 2017). Oliveira et al. (2015) found that *Pseudomonas* sp. strain M309 was able to reduce more than 3.5 log CFU/g *S. enterica* and 3.7 log CFU/g *E. coli* O157:H7 on lettuce disks at 10 °C after 9 days of storage. They also found that *P. graminis* CPA-7 in combination with nisin significantly reduced *L. monocytogenes* counts on the same lettuce samples. The latter strain (*P. graminis* CPA-7) was also evaluated by Iglesias et al. (2018) in fresh-cut pear against *Salmonella* spp. and *L. monocytogenes* at 5, 10 and 20 °C for 10 days of storage. The pathogen reduction was observed at 10 °C, achieving a reduction of 2 and 4 log units of *Salmonella* spp. and 4-log units of *L. monocytogenes* respectively.

4.1.2. *Bacillus spp.*

They are Gram-positive and their shape can be rod, straight or slightly curved; they occur singly, in pairs, in chains and sometimes as long filaments. Some species are motile by means of peritrichous flagella. This genus produces endospores which are very resistant to many adverse conditions (Logan and De Vos, 2015).

The bio-protective potential of *Bacillus* spp. has been extensively studied. In particular, *B. cereus* (*sensu stricto*) has the ability to synthesize enterotoxins and emetic toxins causing diarrheal syndromes when these toxic substances are produced in the small intestine and emetic syndromes when the toxins are ingested together with the food (Logan and De Vos, 2015). However, some other species, such as *B. subtilis*, produce numerous antimicrobial compounds. It is estimated that around 5 % of its genome is dedicated to the production of antimicrobial compounds including ribosomal peptides, polyketides, no-ribosomal peptides, and volatiles compounds (El-Mougy et al., 2008). Carbohydrase and protease enzymes produced by non-pathogenic *B. subtilis* strains are Generally Recognized As Safe (GRAS) by the United States Food and Drug Administration (USFDA) since 1960 (Nath et al., 2015). In addition, it has been described the ability of *B. subtilis* to produce polysaccharides with prebiotic potential from byproducts, such as levan produced from orange peel waste (Tahir et al., 2023).

Nannan et al. (2021) assessed the ability of different strains of *Bacillus* spp. to produce bacilysin, a broad-spectrum active dipeptide. Strains of *B. amyloliquefaciens, B. velezensis, B. pumilus* and *B. subtilis*

presented the bacilysin gene cluster and its antimicrobial activity against Gram-negative foodborne pathogens (*E. coli, S. enterica, L. ivanovii, B. cereus*) was confirmed *in vitro*. Ayed et al. (2015) showed that *B. amyloliquefaciens* An6 can synthetize antimicrobial compounds. This strain produces a peptide (bacteriocin An6) with bacteriocin-like properties resistant to high temperatures, a wide range of pH and proteolytic action of alcalase, trypsin, chymotrypsin and pepsin. Its antimicrobial activity was evaluated against *S. aureus, S.* Typhimurium and *B. cereus*; cell lysis of the tested pathogens was observed (Ayed et al., 2015). The antifungal activity of *B. amyloliquefaciens* has also been demonstrated. For instance, *B. amyloliquefaciens* NCPSJ7 produces an active peptide (AFP3) after fermentation with the ability to inhibit the growth of *Fusarium oxysporum* f. sp. *niveum*. The peptide AFP3 is active at different temperatures, pH and low concentrations. The mechanism of action is based on the alteration of the integrity of the hyphal membranes, which causes their lysis (Wang et al., 2017). Bacteriocins produced by strains of *B. licheniformis* are stable at different temperatures and pH and their mechanism of action against pathogens is mainly based on the alteration of the cell walls (Shobharani et al., 2015; Vadakedath and Halami, 2019).

The presence of *Bacillus* spp. in fruits and vegetables has been described. *B. amyloliquefaciens* PPCB00 was isolated from the surface of oranges (Osman et al., 2011) and *Bacillus* sp. strain YD1 from carrots (Liao, 2009). The latter strain reduced the growth of *L. monocytogenes, Yersinia enterocolitica, S. enterica* and *E. coli* O157:H7, from 1.4 to 4.1 log units on bell pepper disks (Liao, 2009).

As mentioned above, *Bacillus* spp. are present in strawberries as an endophytic bacterium, but species such as *B. subtilis* are also part of the microbiota of the rhizosphere (de Pereira et al., 2012). de Moura et al. (2021) tested the antifungal activity of *Bacillus* spp. against *B. cinerea in vitro*. The isolated strains inhibited 80 % of the mycelial growth by the production of diffusible compounds and 90 % by the production of volatile antifungal compounds. Strains of *B. amyloliquefaciens* and *B. pumilus* have been isolated from tomato stems and leaves (Filho et al., 2010; Lanna-Filho et al., 2013). *Bacillus* spp. are also found in the aerial parts of the tomato plant and roots. Different species of this genus isolated from these anatomical parts were tested against *B. cinerea*. These strains showed *in vitro* the ability to produce antifungal VOCs. *In vivo, Bacillus* strains protected tomato against fungal spoilage when applied as vegetative cells on tomatoes soaked in a bacterial suspension of 10^8 CFU/mL for 30 min (Chaouachi et al., 2021).

4.1.3. Lactic acid bacteria

The best known and representative bacterial group in bio-protection are LAB (Bolívar et al., 2021). These bacteria are Gram-positive, non-spore forming, non-motile and have a rod or coccus shape (Reis et al., 2012). Their antagonistic activity is based on the production of antimicrobial compounds such bacteriocins, which are active against pathogenic and spoilage microorganisms, especially Gram-positive bacteria (Agriopoulou et al., 2020; OHA, 2011). Nisin is the only bacteriocin authorized as a food preservative (E234) since 1983. It is synthetized by *Lactococcus lactis* and has antimicrobial activity mainly against *Enterococcus* spp., *Staphylococcus* spp., *B. cereus, Latilactobacillus* spp., *Leuconostoc* spp., *L. monocytogenes, C. botulinum, C. sporogenes, Micrococcus* spp. and *Pediococcus* spp. (Batiha et al., 2021).

Diverse studies have isolated LAB species from plants or from specific anatomic parts exhibiting remarkable antagonistic characteristics against certain microbial species. Species of the genera *Latilactobacillus, Lactococcus, Leuconostoc* and *Weissella* have been isolated from sliced apples and lettuce and have shown to be active against *L. monocytogenes* and *S.* Enteritidis under refrigerated conditions (Siroli et al., 2015). Interestingly, *Lactiplantibacillus plantarum* strain CM-3, isolated from strawberries, showed inhibitory capacity against *B. cinerea. In vitro, L. plantarum* CM-3 reduced mycelial growth by 55.27 to 79.80 % and the spore germination was inhibited in the presence of living cell suspensions. *In vivo* studies demonstrated that the decay incidence and lesion diameter of strawberries inoculated with *L. plantarum* CM-3 cells were significantly reduced when compared to non-inoculated fruits (Chen et al., 2020a).

The presence of LAB has also been investigated in other vegetables. Rahman et al. (2019) isolated, from five different fresh vegetables (tomato, ginger, cucumber, okra, and sweet potato), different LAB species and reported that bacteriocins produced by *L. plantarum* inhibited the growth of *E. coli* and bacteriocins produced by *Lactobacillus delbrueckii* inhibited the growth of *S. aureus, E. coli* and *Salmonella* Typhi.

Spoilage and mycotoxin-producing fungi can be negatively affected by the presence of LAB (Sadiq et al., 2019). Species of the genera *Leuconostoc* spp., *Latilactobacillus* spp., *Lactococcus* spp., *Weissella* spp. and *Enterococcus* spp., are able to inhibit the proliferation of fungi such as *B. cinerea, Aspergillus* spp., *Fusarium* spp. *Penicillium* spp. *and Rhizopus* spp. (Ghosh et al. 2015; Maurya et al. 2015; Ogunbanwo et al., 2014; Yang et al. 2012). As mentioned above, *Levilactobacillus brevis* and *L. plantarum* are naturally present in tomato microbiota. The antifungal activity of LAB depends on diverse factors such as the synergy within the matrix, the specific LAB and fungus strains, the production of metabolites, and environmental conditions, particularly temperature and humidity (Ahlberg et al., 2017).

4.2. Challenges in applying bio-protective microorganisms

The first step in developing a bio-protective strategy, which usually consists of screening and selecting suitable microorganisms with antagonistic activity (Emerenini, 2014), is always a particularly time-consuming task. Nonetheless, as a matter of probabilities, when a high number of isolates are examined, final outcomes from this process usually lead the researcher to find, under *in vitro* conditions, certain specimens exhibiting antimicrobial properties. The major challenge lies in scaling up the results from *in vitro* into food, as several unknown factors, intrinsic to the compositional complexity of food or even the variable conditions inherent to food production and distribution chains can be incompatible with the antimicrobial properties or can cancel out their effect. Therefore, a needed step, in a bio-protective strategy, is to verify, in real food conditions, the bio-protection performance. In the following sections, direct and alternative methods for applying bio-protective cultures in produce, along with the related factors, conditions, and limitations, are critically discussed, providing new perspectives in the field.

4.2.1. Direct application methods

Researchers generally test bio-protective capacity by co-inoculating the product surface with the target microorganisms (pathogen or spoilage) and the bio-protective cultures. In some cases, penetration or internalization of target microorganisms can be promoted by performing specific wounds or insertions on the product surface thereby simulating common primary infection (Janisiewicz et al., 1999). However, although these methods are relevant to demonstrate protection effects, the treatment with bio-protective agents in real environments should consider several technological and biological aspects. The application of cell suspensions on produce surface by aspersion or immersion has been tested in the laboratory and these can be, in principle, used post-harvest to incorporate bio-protective cultures into vegetables and fruits (Chen et al., 2020a; de Moura et al., 2021; Kilani-Feki et al., 2016). However, this type of application method for bio-protective cultures can have reduced effectiveness under real conditions. The main limiting factor is related to the difficulty of bio-protective microorganisms that are applied on the outer surface to access the inner regions of the fruit or vegetable where the target microorganism(s) (spoilage or pathogenic) is/are present, as a result of a primary infection of the plants at crop stage. In contrast, it is expected that for secondary infections, bio-protective cultures can exert better action, as there can be more direct contact between microbial populations (Petrasch et al., 2019). This is especially relevant for foodborne pathogens, as contamination is

more likely to occur on food surfaces in both pre- and post-harvest stages (Erickson, 2012). Nonetheless, concentrations should be sufficiently high to be effective on the surface. Note that microorganisms are not expected to grow on the produce surface as conditions are more compatible with inactivation than growth due to the fact that environmental stressing factors (e.g., absence of nutrients, low relative humidity, desiccation, etc.) can impair cell viability and functionality (Usall et al., 2016). Therefore, the initial concentration is critical to ensure a more effective action in post-harvest application. Bacterial adhesion to produce surface should therefore be considered in the effectiveness of the application method. The adhesion of bacteria to solid surfaces such as foods depends on the physicochemical properties of the bacterial cells (surface free energy (SFE), ζ potential, production of extracellular polymeric substances, presence of pili and flagella) and food surface properties (roughness, microtopography, hydrophobicity). If the bacterial suspensions are applied by spray or immersion, adhesion is also mediated by multiple factors including surface tension, pH, ionic strength, temperature, and hydrodynamics of the suspension liquid medium (Zhang et al., 2015). Technical considerations such as droplet size, the use of suitable instruments for aspersion or spraying and the availability of specific facilities for application should be considered (Usall et al., 2009).

4.2.2. Alternative application methods

A possible solution for applying bacterial suspensions and enhancing bacterial adhesion is the use of edible coatings, as reported by diverse authors (Kwak et al., 2021; Nadim et al., 2015; Pacaphol et al., 2019). Coatings are applied to the food surface, thus modifying its properties in addition to conferring protection against water loss and physical damage (Guimarães et al., 2018). Formulating bacteria in or on coatings may provide cells with protection against hydric stress and increase adhesion, as cells would be embedded in the polymeric matrix or attached to the polymeric surface due to cell-polymer interactions (Khodaei and Hamidi-Esfahani, 2019; Romano et al., 2014). In addition, the immobilization of cells within the polymeric matrix ensures that cells cannot be eliminated easily during washing or other mechanical force (Gouin, 2004). Nevertheless, this technology brings some challenges since bio-protective microorganisms should remain viable and functional on food. For this reason, the selection of coating materials and compounds should be based on their benefits in preserving the required cell functions. The use of protein-based matrices can increase bacterial survival via scavenging free radicals and providing nutrient sources such as peptides and amino acids. Furthermore, different studies support the view that the incorporation of fructooligosaccharides (FOS) enhances the survival of microorganisms loaded in the edible coating/films. FOS behave as a plasticizer that protect bacterial cells under low-moisture and refrigeration conditions (de Oliveira et al., 2021). The use of inulin and oligofructose in edible coatings has been demonstrated to improve the viability of *L. rhamnosus* in berries (i.e., blueberry and strawberry) increasing bacterial survival in nearly 1 log with respect to the coating without those compounds (Bambace et al., 2019). This protective effect can also be achieved using natural ingredients such as coconut water, which could increase *Lactobacillus acidophilus* L3 survival up to 4 log CFU/g in minimally processed carrots (Shigematsu et al., 2019). In addition, some strains of *L. rhamnosus* and *L. acidophilus* have been described as potential probiotics (Akram et al., 2024).

In recent years, cellulose, cellulose nanofibers and its derivatives obtained from agri-food residues have been extensively studied for their application in edible films and coatings together with several other compounds used for this purpose (Kwak et al., 2021; Nadim et al., 2015; Pacaphol et al., 2019). Among its characteristics, cellulose is biodegradable, recyclable, renewable and biocompatible (Dai et al., 2020). The derivatives most used are methylcellulose (MC), hydroxypropyl methylcellulose (HPMC) and carboxymethyl cellulose (CMC). CMC shows good film-forming properties in combination with a water-soluble polymer and thermal gelatinization (Mohamed et al., 2020). Nadim et al. (2015) studied the effect of CMC coatings on strawberries stored at 4 °C for 11 days. The obtained results showed that the coating improved the quality of strawberries by reducing the weight loss and fruit decay and maintaining the firmness. In addition, CMC coating significantly affected the surface colour parameters by reducing colour lightness and redness.

In the case of cellulose nanofibers (CNF), they present high surface area, high stiffness, and high strength due to their nano size. CNF are also used in the formation of edible films and coating to preserve foods including perishable vegetables such as spinach. Spinach leaves coated with 0.3 and 0.5 % w/v of nanocellulose and storage at 25 °C showed good stability in appearance, chlorophyll, colour, moisture content, and a reduction of 54–70 % on the respiration rate after 3 days (Pacaphol et al., 2019). In addition, cellulose-based edible coatings and films can act as carriers of bio-protective cultures in biopackaging systems, as recently illustrated for yeasts in the work by Comitini et al. (2023).

Romano et al. (2014) incorporated strains of *L. delbrueckii* subsp. *delbrueckii* and *L. plantarum* in MC films. They found that the addition of 3 % w/v fructo-oligosaccharides into the film improved the viability of *L. delbrueckii*, although this was not observed for *L. plantarum*. However, Karimi et al. (2020) demonstrated that the incorporation of CNF in films enhanced the viability of *L. plantarum*. They also observed that films containing 5 g/100 g of CNF and *L. plantarum* showed inhibition zones against *P. aeruginosa, S. aureus* and *E. coli*.

Khodaei et al. (2019) incorporated *L. plantarum* cells to MC-based coating applied in strawberries stored at 4 °C. The population of the LAB kept constant during storage and these strawberries exhibited better sensorial characteristics and physicochemical properties by reducing the weight loss and the rate of deterioration of ascorbic acid, total phenolics compounds and anthocyanins. In addition, regarding food decay, the number of yeast and moulds were reduced in the surface of coated strawberries. In other study, Tavera-Quiroz et al. (2015) also incorporated a strain of *L. plantarum* to methylcellulose edible coating containing FOS and applied this coating to apple snacks. After 90 days of storage, sensory attributes were in optimal or acceptable range, and the load of added microorganisms was high ($2.0 \times 10^8 \pm 0.7 \times 10^8$ CFU/g). Nevertheless, it is not only the material used that influences the survival of the bacteria, the physiological state of the strain in combination with food matrix properties and storage and processing conditions (e.g., temperature, presence of oxygen, etc.) is also important (de Oliveira et al., 2021).

An additional strategy to extend the viability of bio-protective cultures is microencapsulation. Microencapsulated bacterial cells, entrapped in the polymeric matrix, can improve and extend cell viability by providing cells with a physical and chemical barrier against environmental stress. It does so by improving the effectiveness of cell suspension, maintaining high concentrations of living microorganisms with a prolonged effect on the product's shelf life. For instance, the application of fluid-bed spray-drying formulations with (10 % $MgSO_4$) and without protectants has been proven to maintain the initial microbial load unchanged during 12 months of storage at 22, 4 and -20 °C (Gotor-Vila et al., 2017a). The release of the bio-protective microorganism from the capsule depends mainly on the encapsulation material (starch, cellulose, chitosan, whey protein isolate, prebiotics, etc.) and the technique used, which should be tailored and optimized in each case (spray drying, extrusion, layer-by-layer assembly, etc.) (Xie et al., 2023). However, the application of microencapsulation of bio-protective cultures and their food application is still limited. In this regard, Ribeiro et al. (2021) were pioneers in assessing the application of microencapsulated LAB cultures for food bio-preservation, i.e., for controlling *L. monocytogenes* and *S. aureus* in fresh cheese. Although microencapsulation has been applied for plant bio-control bacteria, protecting cells against soil conditions, and modulating their release, its use for bio-protective cultures in fresh produce has not yet been described in the literature (Riseh et al., 2021).

4.2.3. New perspectives of bio-protective interventions

The use of bio-protective microorganisms in plants at the pre-harvest stage, pursuing a joint effect at harvest and later along the food chain, though less explored, could overcome the limitations mentioned above related to post-harvest application (Hernández et al., 2022; Ippolito and Nigro, 2000). This concept is graphically represented in Fig. 3. When the bio-protective culture is applied in the field, colonization occurs first on the external surface and/or soil of the vegetable or fruit plant through different mechanisms such as biofilm formation or synergistic interactions (Romano et al., 2020). Then, if conditions are favorable, microorganisms can internalize plants through different entry areas (e.g., rhizosphere, lenticels, stomas, wounds, ruptures, nodules) and by vertical transmission through seeds (Kumar et al., 2020). Internal colonization could protect them against phytopathogens during field growth and later throughout the post-harvest stage, exerting an inhibitory effect on spoilage and pathogenic microorganisms, that can originate from both primary and secondary infections (Kandel et al., 2017). Bacterial viability and vitality can be preserved in the external environment via microencapsulation until all bacteria are internalized (Orozco-Mosqueda et al., 2018).

In this context, few studies have focused on the protection effect during post-harvest when bio-protective microorganisms are applied in the field (Sellitto et al., 2021). Positive results were obtained by Vivekananthan et al. (2006) when applying bio-control formulations on mango in the field to overcome pre- and post-harvest infection of mango caused by *Colletotrichum gloeisporioides*. The most effective formulation (*P. fluorescens* FP7 with chitin) significantly reduced disease infection and growth of *C. gloeisporioides* during post-harvest. In addition, *B. amyloliquefaciens* formulations reduced the incidence of *Monilina* spp. during pre- and post-harvest stages in stone fruit (Gotor-Vila et al., 2017b).

On the other hand, Raman et al. (2022) have recently reviewed the potential of LAB as bio-control agents in sustainable agriculture, highlighting that they can also promote plant growth due to the production of auxin indole-3-acetic acid (IAA) and the solubilization of minerals. Laury-Shaw et al. (2019) studied the effect of an aqueous solution made of different LAB species (i.e., *L. acidophilus, Lactobacillus crispatus, Pediococcus acidilactici* and *L. lactis*) against *E. coli* O157:H7 on spinach plant. They showed that the application of LAB on the soil and/or leaf surface during the first 4 weeks of the growing cycle resulted in a 3-log reduction of *E. coli* O157:H7 at harvest. The findings of the aforementioned studies can serve as a proof-of-concept for applying bio-protective cultures at the earliest stages of the food chain (in the field) based on an integrated strategy, demonstrating their potential for real industrial implementations.

Despite the potential of bio-protective cultures for extending the shelf life of fruits and vegetables, further research is needed. The current limitations in the application methods and the challenges arising from the specific properties of produce together with the changing conditions of the food supply chain require a systematic approach, covering the phenomenon at different levels. In this regard, phenomena and interactions between cell dimension, matrix properties, and food environmental conditions should be considered.

5. Conclusions

This review explores strawberry and tomato plants as sources of bio-protective microorganisms. Our comprehensive analysis of scientific literature reveals that the microbiota of both produces host different microbial groups relevant to food bio-protection such as *Bacillus* spp., *Pseudomonas* spp. and, to a lesser extent, lactic acid bacteria. Leveraging the biological fraction of agricultural residues is promising since these

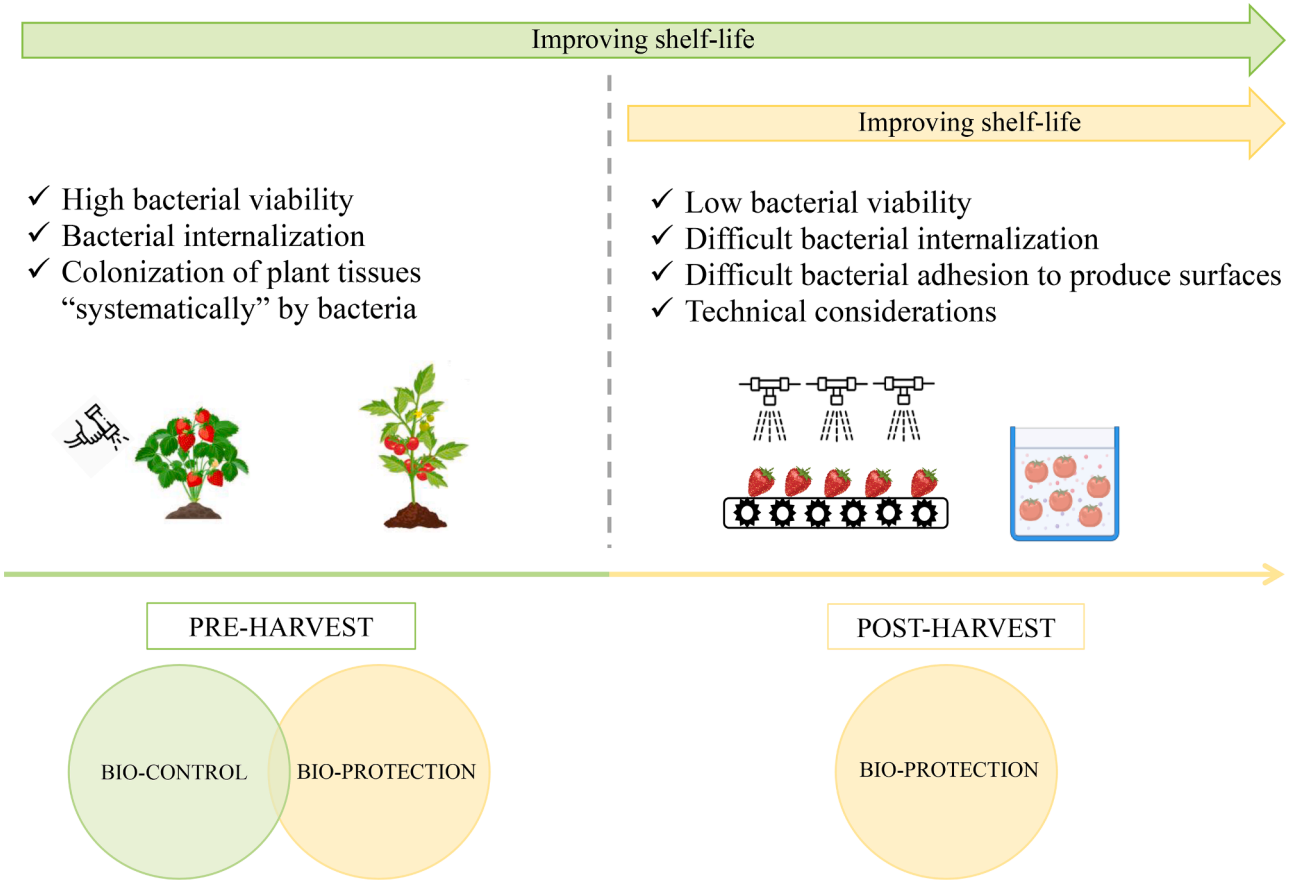

Fig. 3. Graphical representation of the new perspectives of bio-protective interventions.

microorganisms are likely better adapted to the conditions of fruit and vegetables, enabling them to outcompete against phytopathogens and spoilage microorganisms within the same ecosystem. The application of bio-protective microorganisms directly onto produce surfaces (through methods like spraying or immersion) and their integration into edible coatings made from sustainable polymeric materials (such as cellulose or nanofibers) have been explored as strategies to facilitate the use of bio-protective cultures in fruits and vegetables. However, the effective application and performance of bio-protective cultures in actual food contexts pose significant challenges. Limitations arising from post-harvest applications, including difficulty for bio-protectors to access the inner region of fruit and reduced cell viability and functionality due to environmental stressors and unfavorable conditions in the food matrix, underscore the need for an alternative approach. We propose that microorganisms could be introduced at an earlier stage, during pre-harvest, utilizing microencapsulated or lyophilized cultures that have both bio-control and bio-protective properties. This strategy aims to reduce plant disease and mitigate the effects of related spoilage and pathogenic microorganisms, thus enhancing produce shelf life. Although some data support this approach, comprehensive research evaluating the combined bio-control and bio-protective effects in produce, from an integrated approach from farm to fork, remains lacking. The application of these bio-based strategies in produce that are closely associated with food waste generation, such as strawberries and tomatoes, represents a sustainable and bioeconomy solution to improve product shelf life and minimize food waste.

Ethical statement - Studies in humans and animals

Not applicable. This study is a review of already published literature not involving humans or animals.

CRediT authorship contribution statement

Laura Rabasco-Vílchez: Conceptualization, Writing – original draft, Writing – review & editing. **Araceli Bolívar:** Conceptualization, Supervision, Writing – review & editing. **Ramón Morcillo-Martín:** Writing – review & editing. **Fernando Pérez-Rodríguez:** Conceptualization, Supervision, Writing – review & editing, 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.

Data availability

Data will be made available on request.

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