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The Plant-Associated *Flavobacterium*: A Hidden Helper for Improving Plant Health

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Flavobacterium **is a genus within the phylum Bacteroidota that remains relatively unexplored. Recent analyses of plant microbiota have identified the phylum Bacteroidota as a major bacterial group in the plant rhizosphere. While** *Flavobacterium* **species within the phylum Bacteroidota have been recognized as pathogens in the aquatic habitats, microbiome analysis and the characterization of novel** *Flavobacterium* **species have indicated the great diversity and potential of their presence in various environments. Many** *Flavobacterium* **species have positively contribute to plant health and development, including growth promotion, disease control, and tolerance to abiotic stress. Despite the well-described beneficial interactions of the** *Flavobacterium* **species with plants, the molecular mechanisms and bacterial determinants underlying these interactions remain unclear. To broaden our understanding of the genus** *Flavobacterium***'s role in plant health, we review the recent studies focusing on their ecological niche, functional roles, and determinants in plant-beneficial interactions. Additionally, this review discusses putative mechanisms explaining the interactions between plants and** *Flavobacterium***. We have also introduced the importance of future research on** *Flavobacterium* **spp. and its potential applications in agriculture.**

Keywords : *Flavobacterium*, plant-beneficial interactions, plant microbiome

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The genus *Flavobacterium* was initially proposed by Bergey (Bergey et al., 1923). It belongs to the domain Bacteria, phylum Bacteroidota, class Flavobacteriia, order Flavobacteriales, and family Flavobacteriaceae (NCBI, https://www.ncbi.nlm.nih.gov/datasets/taxonomy/tree/?taxon=237). Members of the *Flavobacterium* genus are characterized as Gram-negative, obligately aerobic, rod-shaped bacteria that do not form spores (Bernardet and Bowman, 2015). Colonies formed by *Flavobacterium* species vary in color from pale to bright yellow due to the production of carotenoid, flexirubin, or a combination of both pigments (Bernardet and Bowman, 2015).

Bacterial species of the genus *Flavobacterium* are found in diverse habitats, including water, soil, and even plant tissues. Initially, *Flavobacterium* was primarily focused as pathogenic bacteria of various fish species in aquatic environments (Bernardet and Bowman, 2015). However, they have not received much attention in the context of plant-associated microbes compared to well-known plant growth-promoting rhizobacteria (PGPR) such as *Pseudomonas* or *Bacillus* (Marín et al., 2021). Recently, there has been a shift in focus, with *Flavobacterium* being identified as a key taxonomic group in plant microbiota (Carrión et al., 2019; Kwak et al., 2018). This recognition has sparked growing interest in investigating interaction between plants and *Flavobacterium* species. In this review, we will provide general information on the beneficial interactions between the plant-associated *Flavobacterium* species and

the host plant. Especially, we will discuss potential mechanisms for plant-beneficial interactions of *Flavobacterium* in plant microbiota.

Ecological Niche

The genome information of 240 species (NCBI, https://www.ncbi.nlm.nih.gov) and 378 isolated strains (BacDive, https://bacdive.dsmz.de/) within the genus *Flavobacterium* has been reported (Fig. 1A). Members of the *Flavobacterium* genus have extensively been investigated in aquatic ecosystems, including freshwater and marine environments (Bernardet and Bowman, 2015) (Fig. 1B). Some of the *Flavobacterium* species, such as *F. psychrophilum* and *F. columnare*, have been identified as pathogens that affect many freshwater fish species, including rainbow trout and coho salmon (Chen et al., 2008; Strepparava et al., 2014) (Fig. 1B). Interestingly, the specific *Flavobacterium* species also showed an algicidal effect in freshwater environments (Fukami et al., 1992) (Fig. 1B). For example, *Flavobacterium* sp. 5N-3 exhibited the high inhibitory activity on the growth of a red-tide forming *Gymnodinium nagasakiense*, especially when the alga was in the logarithmic growth phase (Fukami et al., 1992). Furthermore, members of the genus *Flavobacterium* also play a role as decomposers in aquatic environments (Fig. 1B). It is well known that cultured isolates of *Flavobacterium* spp. can degrade biopolymers like cellulose and chitin, which are parts of the high molecular mass fraction of dissolved organic matter (Kirchman, 2002).
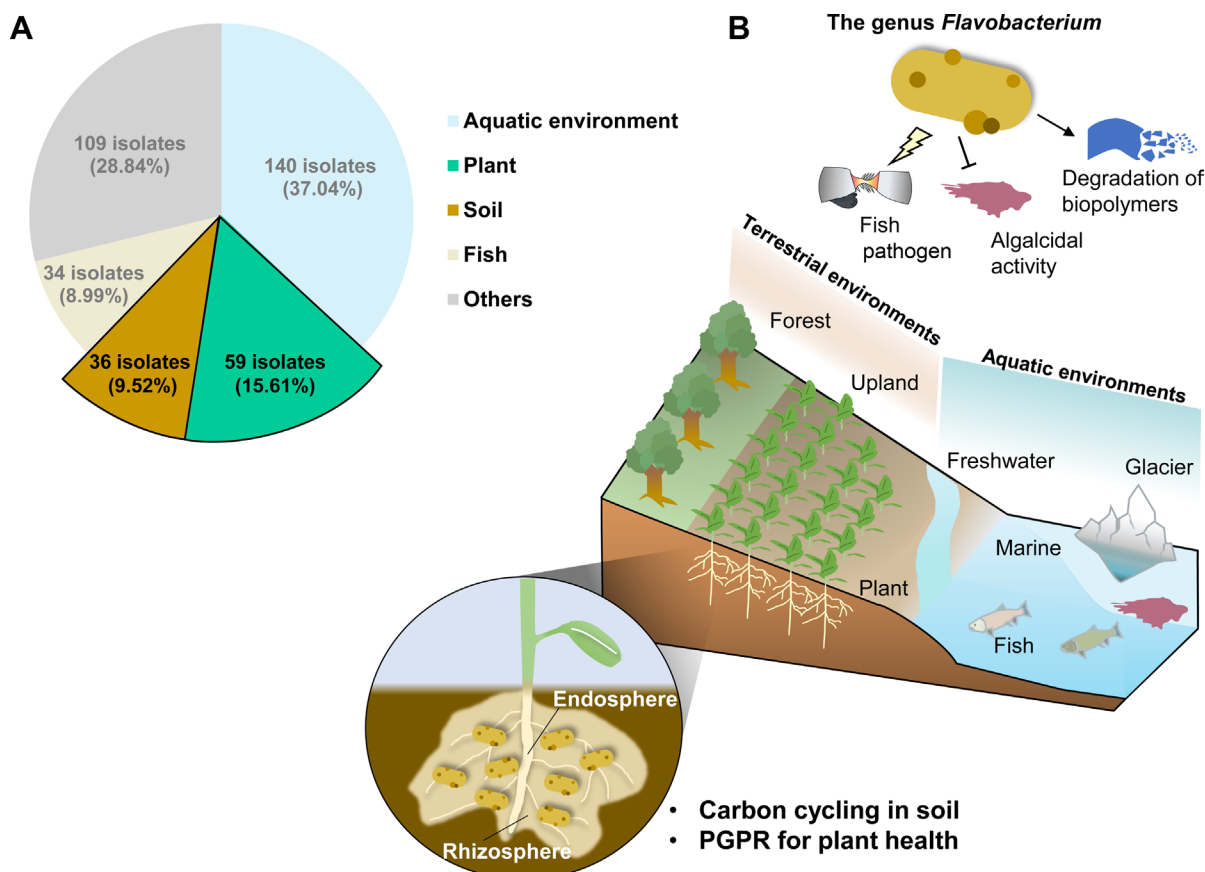
Fig. 1. Composition of the genus *Flavobacterium* in various ecosystems. (A) The number of *Flavobacterium* isolates from different habitats, based on data from BacDive (https://bacdive.dsmz.de/). A total of 387 *Flavobacterium* isolates were obtained from aquatic environments, plants, soil, fish, and other sources. Light blue box, the isolates from aquatic environments; green box, the isolates from plants; light brown box, the isolates from soil; beige box, the isolates from fish; gray box, the isolates from others. (B) Geographic distribution and ecological roles of the genus *Flavobacterium*. Bacteria of the genus *Flavobacterium* are primarily found in aquatic environments where they serve various ecological roles. *Flavobacterium* species act as a pathogen of fish, algicidal organism, and a decomposer of biopolymers. Besides, certain *Flavobacterium* species contribute to carbon cycling and promote plant health in soil environments. PGPR, plant growth-promoting rhizobacteria.

Flavobacterium species are found not only in aquatic ecosystems but also in terrestrial environments, including sludge, frozen soil, polar soil, temperate soil, forest soil, and the rhizosphere soil of plants (Bernardet and Bowman, 2015; Chaudhary et al., 2019; Madhaiyan et al., 2010). *Flavobacterium* species are widely distributed in terrestrial environments, and the isolated portion of *Flavobacterium* species range 15.61% and 9.52% in the plants and soils, respectively (Fig. 1A). Large-scale genomic analysis predicts that the genus *Flavobacterium* in aquatic environments exhibits high activity in peptide and protein utilization, while their counterparts in terrestrial environments are expected to show high activity in carbohydrate metabolism, such as xylose, arabinose, and pectin (Kolton et al., 2013). This suggests their potential contribution to carbon cycling and the promotion of host plant growth in soil (Kolton et al., 2013; Kraut-Cohen et al., 2021) (Fig. 1B).
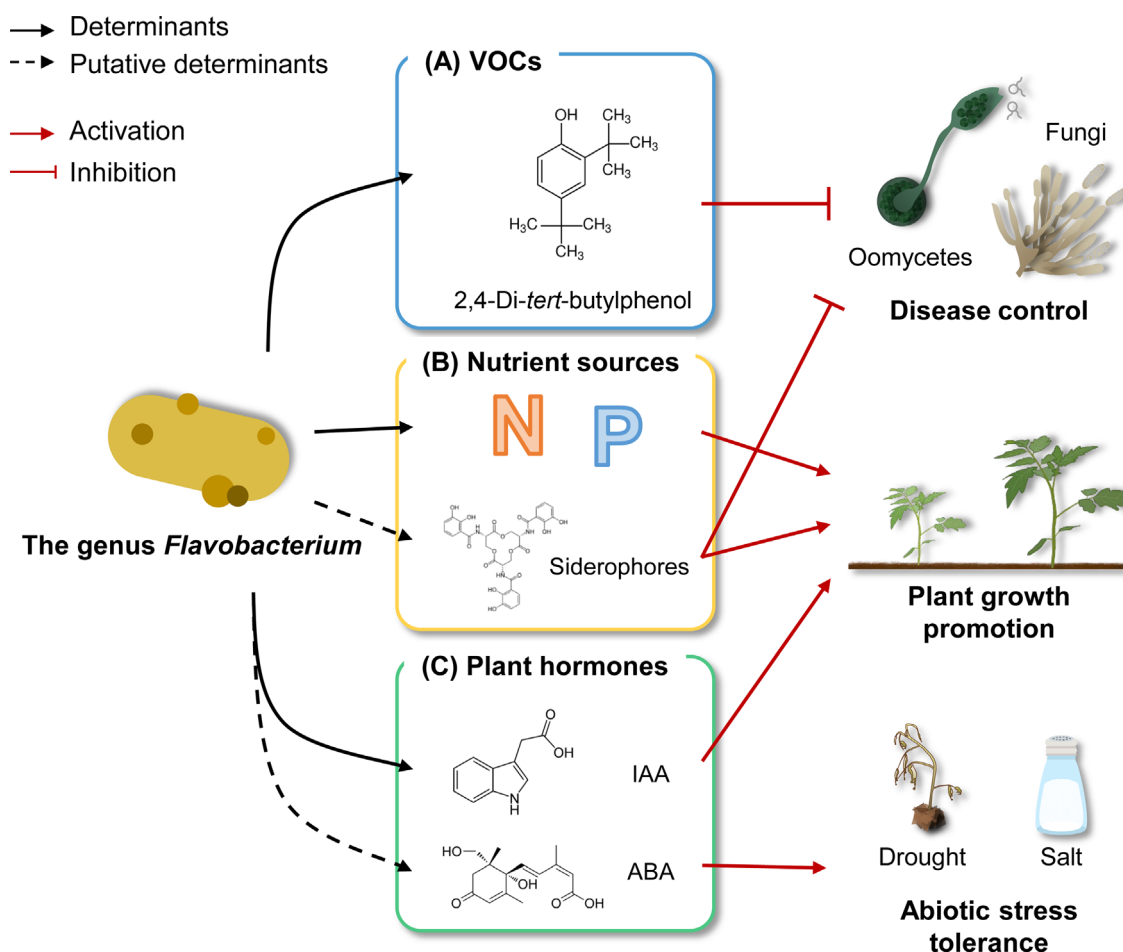
Functional Roles of *Flavobacterium* in Plant Microbiome

Bacterial species in the genus *Flavobacterium* are widely distributed in soil and the plant rhizosphere. Some of *Flavobacterium* species have recently been considered as PGPR (Kolton et al., 2016); however, the role of most *Flavobacterium* species in plant functioning is not well-described. Plant-wide microbiota analysis also suggests that Bacteriodota, including members of the Flavobacteriacea family, are predominant in the microbiota of various plant species (Pérez-Jaramillo et al., 2018), implying that *Flavobacterium* species may have specific plant-beneficial interactions. Extensive microbiome analysis of the plant-rhizosphere suggests that members of the genus *Flavobacterium* have an increased relative abundance in the rhizosphere and have been recognized as a core taxon in the complex rhizosphere microbiome (Carrión et al., 2019; Kwak et al., 2018). Therefore, we will present recent studies on the beneficial effects of plant-associated *Flavobacterium* on host plants and their putative modes of action.

Plant disease control. Certain *Flavobacterium* species protect plants against various diseases caused by bacteria or fungi (Carrión et al., 2019; Choi et al., 2023; Gunasinghe et al., 2004; Hahm et al., 2012; Kwak et al., 2018; Nishioka et al., 2019; Sang and Kim, 2012; Wang et al., 2023) (Fig. 2). A tomato microbiota study reported that the family Flavobacteriaceae is a key taxon in the rhizosphere of a tomato cultivar resistant to bacterial wilt in tomato plants

(Kwak et al., 2018). Particularly, *Flavobacterium* sp. TRM1-10, isolated in the resistant tomato rhizosphere, effectively suppressed bacterial wilt caused by *Ralstonia pseudosolanacearum* in a bacterial wilt susceptible tomato cultivar (Kwak et al., 2018). Members of the genus *Flavobacterium* can also protect host plants from various pathogens, including *Plasmodiophora brassicae* and *Fusarium oxysporum* (Hahm et al., 2012; Nishioka et al., 2019). Treatment with *F. hercynium* EPB-C313 reduced the severity of clubroot disease caused by *P. brassicae* in Kimchi cabbage (Hahm et al., 2012). Individual treatments of *Flavobacterium* sp. GUAF6005, GUAF6009, and GUAC6072 also reduced the severity of fungal wilt caused by *F. oxysporum* f. sp. *cucumerinum* isolate GUS77 in cucumber seedlings (Nishioka et al., 2019). These beneficial *Flavobacterium* species showed antifungal activity against *F. oxysporium*, *Colletotrichum musae*, *Botryodiplodia theobromae*, and *Cladosporium cladosporioides* by inhibiting spore formation and the multiplication of fungal pathogens (Gunasinghe et al., 2004; Hahm et al., 2012; Nishioka et al., 2019) (Fig. 2). Furthermore, *Flavobacterium* species have been considered a keystone in determining disease resistance in host plants, however, their precise mechanisms have yet to be fully understood (Kwak et al., 2018).

Plant growth promotion. *Flavobacterium* species have been studied as biostimulants in diverse monocot and dicot plants (Choi et al., 2023; Kwak et al., 2018; Menon et al., 2020; Samad et al., 2017; Yakubovskaya et al., 2019; Youseif, 2018; Zhang et al., 2021) (Fig. 2). For example, all 32 *Flavobacterium* strains, isolated from tomato rhizosphere soil, including *F. anhuiense*, *F. aquidurense*, *F. beibuense*, *F. daejeonense*, and *F. dauae*, showed plant growth promotion (PGP) activity in tomato plants (Jung et al., 2021; Kwak et al., 2018). Similarly, *Flavobacterium* sp. NGB-31, *F. succinicans* DSM4002, and *Flavobacterium* sp. 72, isolated from wheat root and rice rhizosphere, also exhibited the PGP in maize, rice, and ryegrass plants (Yakubovskaya et al., 2019; Youseif, 2018; Zhang et al., 2021). The effects of PGP on plants caused by the *Flavobacterium* species may be linked to the production of substances that help plants grow, like the phytohormone auxin and nitrogen resources (Yakubovskaya et al., 2019; Youseif, 2018; Zhang et al., 2021) (Fig. 2). However, there have been cases where certain strains showing PGP effects lack genes related to auxin production or nitrogen fixation. Thus, further molecular mechanistic studies are required to understand plant-*Flavobacterium* interactions better.

Fig. 2. An overview of diverse determinants and functional roles within the genus *Flavobacterium* in plant-beneficial interactions. (A) Volatile organic compounds (VOCs). Bacteria in the genus *Flavobacterium* release 2,4-Di-*tert*-butylphenol, which exhibits biological control activity. (B) Nutrient sources. Bacteria in the genus *Flavobacterium* can provide inorganic nitrogen and solubilized phosphorus for plant growth promotion. They may supply ferric ions to the host plant via the secretion of siderophores. (C) Plant hormones. Plant hormones such as indole acetic acid and abscisic acid produced by *Flavobacterium* species contribute to plant growth and abiotic stress tolerance. *Flavobacterium* species secrete determinants (indicated by black arrows) or putative determinants (indicated by black dashed arrows) for plant-beneficial interactions. These various determinants either promote plant health (indicated by red arrows) or inhibit plant pathogens (indicated by red blunt-ended lines). IAA, indole-3-acetic acid; ABA, abscisic acid.

Abiotic stress tolerance. Members of the genus *Flavobacterium* can confer tolerance to abiotic stress, including drought and salt stress, in both monocot and dicot plants (Belimov et al., 2005; Gontia-Mishra et al., 2016; Kim et al., 2020; Walitang et al., 2017; Zhang et al., 2021) (Fig. 2). *Flavobacterium* sp. IG 15, *Flavobacterium* sp. IR29-16, *Flavobacterium* sp. IC27-25, and *Flavobacterium* sp. IC31-28 enhanced the induction of drought and stress tolerance in monocot plants such as wheat and rice (Gontia-Mishra et al., 2016; Walitang et al., 2017). Besides, *F. crocinum* HYN0056 activated the stress tolerance to drought and salt stress in *Arabidopsis thaliana* (Kim et al.,

2020). These stress tolerances induced by *Flavobacterium* species were mainly involved in the activation of the molecular pathway associated with the plant hormone abscisic acid (ABA), which regulates stress tolerance in host plants (Gontia-Mishra et al., 2016; Kim et al., 2020; Yang et al., 2009) (Fig. 2). In addition to ABA signaling, the diverse stress-inducible genes including *WRKY* transcription factor and the antioxidant enzyme-encoding genes were also regulated by *Flavobacterium* species (Gontia-Mishra et al., 2016; Kim et al., 2020; Walitang et al., 2017).

Determinants Produced by *Flavobacterium* for Improving Plant Health

Volatile organic compounds. Bacteria-derived volatile organic compounds (VOCs) play a crucial role in plant-microbe interactions and are known as plant immune elicitors; this is well-documented in 2,3-butanediol-producing *Bacillus* species (Riu et al., 2022; Ryu et al., 2003, 2004; Sharifi et al., 2022). In addition to *Bacillus* species, VOC from *F. johnsoniae* GSE09 can also affect host plants (Sang et al., 2008) (Fig. 2A). *F. johnsoniae* GSE09, isolated from cucumber root tissues, not only promoted the yield and ripening of pepper fruits but also significantly inhibited the development of phytopathogens, including the oomycete *Phytophthora capsici* and the fungus *C. acutatum* (Sang et al., 2008). In particular, 2,4-di-*tert*-butylphenol derived from the strain GSE09 is a VOC that was identified as the antimicrobial agent against *P. capsici* and *C. acutatum* (Sang and Kim, 2012; Sang et al., 2011) (Fig. 2A). Similarly, *Flavobacterium* sp. R96, isolated from the rhizosphere of potatoes, can produce VOCs inhibiting the mycelial growth of *P. infestans*, causing potato late blight disease (Hunziker et al., 2015).

Macro- and micronutrient sources. Several plant-associated bacteria, including *Flavobacterium* species, provide the macro- and micronutrient resources to host plants (Carrión et al., 2019; Choi et al., 2023; Kraut-Cohen et al., 2021; Menon et al., 2020; Tilak et al., 2005; Youseif, 2018; Zhang et al., 2021) (Fig. 2B). For example, *Flavobacterium* sp. R6S-5-6 can provide a nitrogen source to the host plant by activating nitrogen fixation-related genes, including the *nif* gene (*nifU*), *fix* gene (*fixF*), and global nitrogen regulator (*ntcA*) (Choi et al., 2023) (Fig. 2B). Furthermore, solubilized phosphorus produced by *Flavobacterium*-specific alkaline phosphatase PhoX and PafA can contribute to tolerance against abiotic stress, PGP, and help plants overcome phosphorus depletion (Choi et al., 2023; Lidbury et al., 2021; Youseif, 2018; Zhang et al., 2021) (Fig. 2B). In addition to macronutrients, plant-associated *Flavobacterium* species are expected to supply the ferric ions to host plant. A study of the functional genomes of *Flavobacterium* species that are associated with plants found gene clusters that make iron-chelating siderophores, such as the ferric aerobactin, and its receptor *lutA* gene (Máté et al., 2022; Menon et al., 2020) (Fig. 2B). Therefore, siderophores derived from *Flavobacterium* species may provide ferric ions to host plants, thereby contributing to photosynthesis, seedling development, and inhibiting the growth of plant pathogens (Arnon, 1965;

Connorton et al., 2017; Inoue et al., 2009; Murata et al., 2015; Pahari et al., 2017; Singh et al., 2022).

Plant hormone-mimicking compounds. Plant hormones act as global regulators for cellular processes in plants and can be synthesized not only by plants but also by microorganisms (Costacurta and Vanderleyden, 1995; Tsukanova et al., 2017) (Fig. 2C). A number of plant-associated *Flavobacterium* species can produce the auxin, indole acetic acid (IAA), affecting plant growth and abiotic stress tolerance in crop plants (Tsukanova et al., 2017; Walitang et al., 2017; Yakubovskaya et al., 2019; Youseif, 2018) (Fig. 2C). The amount of auxin that plant-associated *Flavobacterium* produces is about 4.88 µg/ml (Lin et al., 2023). *Flavobacterium* species associated with plants might synthesize auxin through the tryptophan-dependent pathway rather than the tryptophan-independent pathway (Tillmann et al., 2021; Tsavkelova et al., 2007; Xu et al., 2023; Wang et al., 2015). For example, *Flavobacterium* sp. 11 showed tryptophan-dependent IAA production regulated by the indole-3-glycerol phosphate synthase gene (*trpC*), which converts 1-(*o*-ecarboxyphenylamino)-1-deoxyribulose-5-phosphate to indole-3-glycerol-phosphate (Kagan et al., 2008; Xu et al., 2023). In addition to auxin, the treatment of *Flavobacterium* sp. HYN0056 or *Flavobacterium* sp. GJW24 activated the expression of ABA-responsive genes in *Arabidopsis thaliana*, but not ABA-biosynthesis genes, implying the production of ABA by *Flavobacterium* species (Kim et al., 2020, 2023) (Fig. 2C). Further mechanistic studies on the biosynthesis of various plant hormones, including ABA, in the genus *Flavobacterium*, should be required to understand the interaction between *Flavobacterium* species and host plants.

Unveiled Mechanisms for Plant-*Flavobacterium* Interactions

Colonization in root microbiome. Both culture-dependent and independent studies have shown the potential for root colonization of bacterial strains in the genus *Flavobacterium* (Acuña et al., 2023; Anzalone et al., 2022; Bodenhausen et al., 2013; Samad et al., 2017; Yuying et al., 2021). Members of the genus *Flavobacterium* are highly abundant in the rhizosphere, ranging from 5.0% to 20.2% and in root endosphere compartments ranging from 0.53% to 20.9% (Acuña et al., 2023; Anzalone et al., 2022; Bodenhausen et al., 2013; Samad et al., 2017). However, the exact mechanism of the root colonization of the *Flavobacterium* species is largely unknown. Among speculative mecha-

nisms, we will mainly discuss the potential role of the type IX secretion system (T9SS) in root colonization of the *Flavobacterium* species. T9SS is a Bacteroidota-specific secretion system, first discovered in *F. johnsoniae* and *Porphyromonas gingivalis* (Braun et al., 2005; Sato et al., 2005; Trivedi et al., 2022). Interestingly, the T9SS-related *gldJ* mutant of *Flavobacterium* sp. F52 showed reduced colonization activity in the root environment (Kolton et al., 2014). The T9SS of *Flavobacterium* species is expected to enhance root colonization through gliding motility and the secretion of hydrolytic enzymes. The loss of T9SS showed a reduction in the gliding motility of the *Flavobacterium* species (Kita et al., 2016; McBride, 2014; McBride and Nakane, 2015). T9SS-mediated gliding motility might correlate with chemotaxis for nutrient searching and surface attachment by biofilm formation of bacterial strains in the genus *Flavobacterium* in root environments (Eckroat et al., 2021; Nakane et al., 2021). T9SS in the genus *Flavobacterium* can also facilitate the secretion of hydrolase enzymes, such as pectinase and cellulase, which are plant cell wall-degrading enzymes (Kolton et al., 2014; Kraut-Cohen et al., 2021; Kwak et al., 2018; Mawdsley and Burns, 1994). These hydrolases can confer *Flavobacterium* species on the utilization of extracellular nutrients and the invasion activity into the plant endosphere. Because of the presence of *Flavobacterium* species in aboveground tissues and seeds, further investigation of the translocation from roots to flowers and inheritance to offspring of the *Flavobacterium* species should be elucidated (Hahm et al., 2012; Sang et al., 2008; Wang et al., 2023; Youseif, 2018).

Outer membrane vesicles. Numerous bacteria including the *Flavobacterium* species can produce small (40-200 nm in diameter) spherical particles derived from the outer membrane called outer membrane vesicles (OMVs) (Jung et al., 2021; McMillan et al., 2021; Møller et al., 2005). Among *Flavobacterium* species such as *F. psychrophilum*, *F. johnsoniae*, and *F. columnare*, OMVs have been intensively investigated in aquatic conditions (Arias et al., 2012; Møller et al., 2005; Sato et al., 2021). The OMVs have been also detected in plant-associated bacteria. The plant-associated bacterial OMVs contain diverse immune triggers, including lipopolysaccharides and elongation factor Tu (EF-Tu), eliciting plant immunity against pathogenic bacteria and oomycetes (Bahar et al., 2016; Chowdhury and Jagannadham, 2013; McMillan et al., 2021; Rybak and Robatzek, 2019; Sidhu et al., 2008). Interestingly, the OMVs from aquatic *Flavobacterium* species contain diverse molecules that can modulate host immunity including small RNA, mRNA, various enzymes, antigenic proteins,

and oligosaccharides (Chapagain et al., 2021, 2023; Møller et al., 2005). In addition, OMVs have been observed in some *Flavobacterium* strains with PGP activity (Jung et al., 2021); however, little is known about the role of these OMVs in interactions with plants. Further study is needed to investigate if OMVs of plant-associated *Flavobacterium* species may play an essential role in beneficial interactions with plants.

Microbiome stimulants. Members of the genus *Flavobacterium* might not only directly interact with the host plant but also indirectly activate microbe-microbe interactions for plant health and growth (Carrión et al., 2019; Wang et al., 2023; Zhu et al., 2021). Compared to individual treatments, the combination of *Flavobacterium* species with other bacterial isolates has shown a synergistic effect on disease control activity and immune responses against the bacterial pathogen *R. solanacearum* and the fungal pathogen *Rhizoctonia* sp. in crop plants (Carrión et al., 2019; Wang et al., 2023). These synergistic interactions, especially, might enhance the biosynthesis of secondary metabolites. For example, *Flavobacterium* species can elevate the formation of biofilm, which stimulates the root colonization of PGPR and plant immunity, produced by other bacterial species or a microbial consortium (Wang et al., 2023; Zhu et al., 2021). The T9SS of the *Flavobacterium* species can contribute to establishing a community either among themselves or with various microorganisms (Li et al., 2021; Shrivastava et al., 2018; Trivedi et al., 2022). This indicates that strains of the genus *Flavobacterium* might play a role as a network hub in microbe-microbe interactions for plant health and the biosynthesis of specific metabolites.

Perspective and Conclusion

In order to dissect the microbial traits of *Flavobacterium* species, genetic tools such as mutagenesis, shuttle vectors, and transformation protocols should be established for these specific microbes. While the gene manipulation tools for Proteobacteria did not work in Bacteroidota, techniques for genetic manipulation of *Flavobacterium* species have been developed (Alvarez et al., 2004; McBride and Kemp, 1996; Shoemaker et al., 1986). Therefore, these techniques would be applicable to plant-associated *Flavobacterium* species.

To improve our understanding of *Flavobacterium*-plant interactions, further research should address key questions surrounding the contribution of the *Flavobacterium* species in the plant microbiome. Here are the key questions. These

questions include (1) How can we isolate certain crucial uncultured *Flavobacterium* species and establish stable, large-scale cultivation methods for agricultural applications?, (2) How do bacteria in the genus *Flavobacterium* engage in competition or cooperation with indigenous microorganisms in its natural plant environment?, (3) How do plants recognize the *Flavobacterium* species, and what mechanisms enable the *Flavobacterium* species to colonize within or around plant tissues? To address these questions, we will need to use both traditional molecular biological methods and multi-omics analyses like metagenomics, metatranscriptomics, proteomics, and metabolomics. Until recently, members of the genus *Flavobacterium* received little attention as a plant beneficial bacterium in the plant microbiota. However, advances in metagenomic analysis now highlight their significance in improving host plant health. Despite this, compared to well-established PGPR like the genera *Pseudomonas* or *Bacillus*, the roles of *Flavobacterium* species remain enigmatic in the plant microbiome and need to be explored.

Conflicts of Interest

No potential conflict of interest relevant to this article was reported.

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