



Advances in biology through agronomy, aquaculture, coastal and environmental sciences

— Volume II —

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**Advances in biology through
agronomy, aquaculture, coastal and
environmental sciences**
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Advances in Biology through Agronomy, Aquaculture, Coastal and Environmental Sciences, Volume II, is an e-book that continues the work of the first version (<https://editorapantanal.com.br/ebooks/2023/advances-in-biology-through-agronomy-aquaculture-coastal-and-environmental-sciences/ebook.pdf>), published in 2023 by Leandris Argente!-Martínez and Ofelda Peñuelas-Rubio.

Our e-book compiles 25 manuscripts that present scientific results and reviews based on biological aspects. All of them contribute to explaining the responses of living organisms to agricultural, aquaculture, and coastal ecosystems, as well as those facing fragility or threat of climate change. This e-book was edited by Leandris Argente!-Martínez, Ofelda Peñuelas-Rubio, and Joe Luis Arias-Mosc!so, members of the Consolidated Academic Group ITVAYA-CA-3.

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Influence of benzoxazinoid metabolites in maize roots interacting with diverse microbes

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ABSTRACT

The rhizosphere has been considered one of the fundamental interacting zones in ecological, chemical, and biological studies. Many plants root-soil microbe interactions occur in the rhizosphere, allowing communication between neighboring plant roots. The chemical reactions occurring in the soil depend greatly on the plant species and on the organisms that coexist around their roots. One of these fundamental processes is detoxification, mainly of potentially toxic secondary metabolites, such as benzoxazinoids (BX). These compounds are released in root exudates as defense against phytopathogens, allowing the selection of beneficial bacteria and the uptake of soil nutrients. Although BX are produced at basal levels, their production tends to increase in response to biotic stimuli. Since *Fusarium verticillioides* (*Fv*) is one of the main fungal pathogens affecting maize, in this chapter, we discuss BX detoxification as a possible evasion mechanism that *Fv* can display against plant defense systems. *Fv* can survive 2-benzoxazolinone (BOA), a metabolite present in root exudates, by transforming it into less toxic compounds, such as 2-aminophenol (AP), which facilitates the successful infection of root cells. Within the rhizosphere, plant growth-promoting rhizobacteria (PGPR) play a crucial role in plant roots and soil-microorganism interactions. They contribute to plant growth, fungi control and may even colonize plant tissues as endophytes. Our group studies the complex interactions among maize roots, *Fv* (a fungal pathogen), and PGPR. The role of PGPR in BX detoxification remains unclear; however, it has been hypothesized that they can participate in plant-bacteria communication during the selection and establishment of endophytic colonization. Transcriptomic data suggest that BX metabolism may be altered in interactions among plant roots, PGPR and *Fv*. Therefore, studying the metabolic strategies

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involved in the production and detoxification of BX in root exudates could provide valuable insights into how PGPR and phytopathogenic fungi coexist or compete in the rhizosphere.

Key words: benzoxazinoids, PGPR, *Fusarium*, bacteria, root exudates, metabolites

BENZOXAZINOIDS: KEY METABOLITES FOR PLANT GROWTH

Secondary metabolites are important for plant growth and defense. The molecules produced by plant secondary metabolism have allowed the development of many pharmaceuticals for human health treatment, and compounds used in agricultural management (Ono; Murata, 2023). The chemical structures of metabolites are highly diverse across plant species, leading to a wide range of biological functions, including antimicrobial and antioxidant activities. However, many of the biological functions of plant secondary metabolites are still undescribed (Twaij; Hasan, 2022).

Secondary metabolites can be classified according to their biological function and/or chemical structure. The major classes include terpenes, phenolics, nitrogen-containing compounds, and sulfur-containing compounds (Saxena et al., 2013). Terpenes are the principal constituents of essential oils and have important functions in plant cell walls and growth. They are hydrocarbons composed of isoprene units (C_5H_8) and can be modified by cyclization reactions (Khanam et al., 2025). Phenolic compounds include many derivative molecules such as flavonoids and non-flavonoids. They are classified according to the number of aromatic rings and their connection patterns. They also play crucial roles in plant responses to environmental and biotic stresses, as well as in the organoleptic properties of plant products (Xu; Wang, 2025). Nitrogen-containing compounds can be associated with peptides, amino acids, and nucleic acids. However, the most important N-containing secondary metabolites are alkaloids which exhibit antimicrobial and antioxidant properties and have great potential for industrial production in the pharmaceutical and biotechnological sectors (Zandavar; Babazad, 2023).

N-containing compounds include the benzoxazinoids (BXs) which are indole-derived and are found primarily in maize, wheat, and rye. BXs contain a 1,4-benzoxazin-3-one skeleton, also known as benzoxazinones, while benzoxazolinones are their degradation products. BXs are classified according to the nitrogen substituents: N-H, N-OH, and N-OCH₃ (de Bruijn et al., 2016; Li et al., 2025a) and are related primarily to plant defense against insects and phytopathogenic fungi. The BXs biosynthetic pathway has been extensively studied in various plant species, particularly in maize. This pathway begins primarily in the chloroplast (Figure 1), where the BX1 lyase enzyme catalyzes the conversion of indole-3-glycerol phosphate into indole, thereby initiating BX synthesis (Frey et al., 2000). Indole can enter the endoplasmic reticulum, where it is transformed into the 2,4-dihydroxy-1,4-benzoxazin-3-one (DIBOA) aglycone product through the sequential action of four monooxygenase enzymes (BX2-BX5). Subsequently, this product is glycosylated by UDP-glucosyltransferases (BX8/BX9), yielding the compound DIBOA-Glc (von Rad et al., 2001). DIBOA-Glc can follow two distinct metabolic routes:

the first involves transport to the vacuole of this compound, whereas the second route uses DIBOA-Glc as a substrate for cytoplasmic enzymes BX6, BX7, BX10/11/12, resulting in the formation of the final product HDMBOA-Glc. However, the production of this compound appears to be primarily induced by herbivory or pathogen attack (Glauser et al., 2011), as HDMBOA-Glc is more toxic than 2,4-dihydroxy-7-methoxy-2H-1,4-benzoxazin-3(4H)-one (DIMBOA)-Glc, even in the producing plant (Meihls et al., 2013). Due to their toxicity these compounds accumulate in the vacuole. The induction and release of the different glycosylated BXs depend on the severity of the infection. DIBOA-Glc and DIMBOA-Glc are considered constitutive, or basal defense molecules, whereas HDMBOA-Glc and HDM₂BOA-Glc represent high-level defense molecules (Oikawa et al., 2001; Handrick et al., 2016) (Figure 1). However, deglycosylation is required to generate the active forms of BX compounds stored in the vacuole and may occur either before or after their release into the rhizosphere in roots exudates.

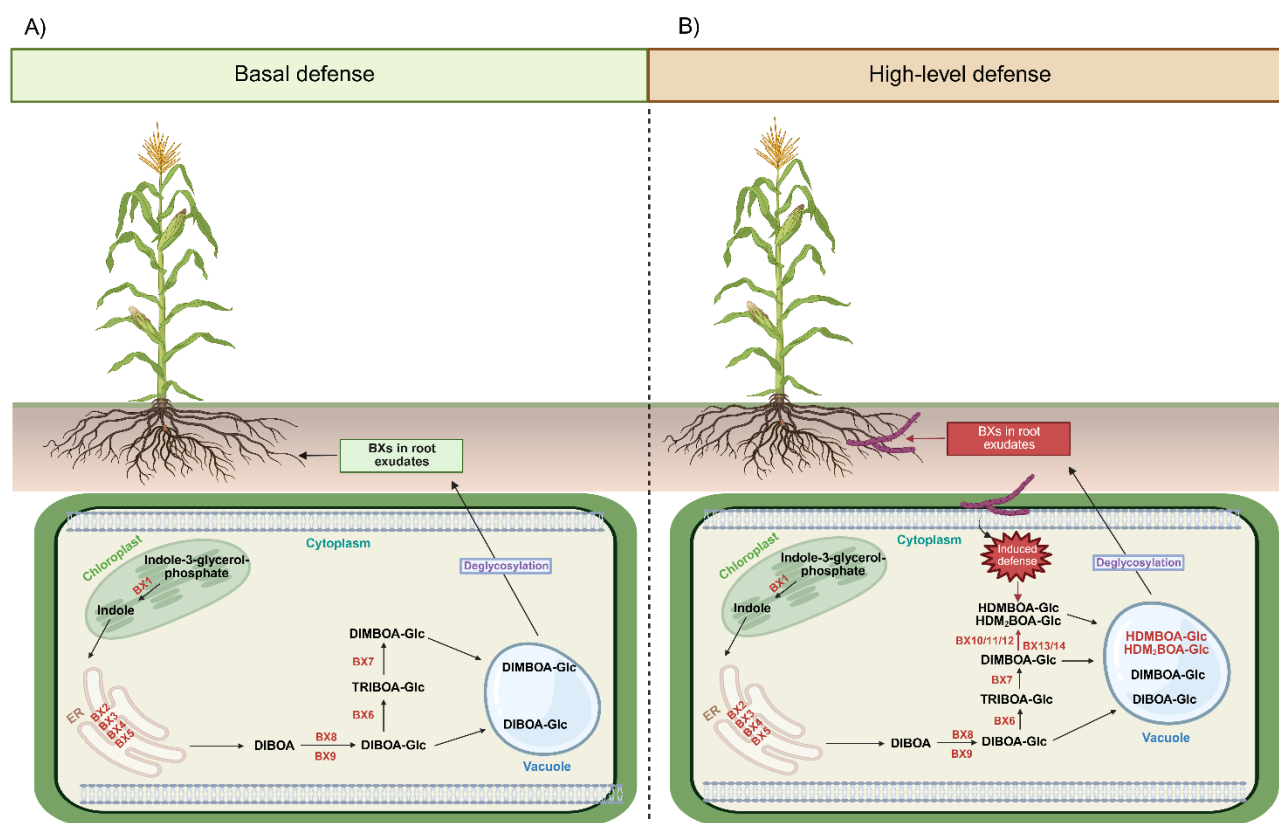


Figure 1. BXs biosynthesis model in A) basal and B) high-level defense against fungi. In response to pathogenic fungal attack, plants can induce the production of BX compounds, which exhibit increased antifungal activity. BioRender was used for the illustration.

Extensive studies have investigated the effects of BXs on phytopathogenic fungi, including reductions of *in vitro* mycelial growth of *Gaeumannomyces graminis* var. *graminis* and *Fusarium culmorum* when MBOA is used as a substrate (Martyniuk et al., 2006). Likewise, a reduction in the pathogenicity of *F. oxysporum* f. sp. *fabae* has been observed using DIMBOA and MBOA treatment (Ma et al., 2024).

Transcriptomic analyses have shown that BXs-related genes are induced in resistant wheat cultivars (04 Zhong 36) infected with *F. pseudograminearum*, and wheat metabolomic profiles mainly detected the accumulation of BOA and MBOA (Duan et al., 2022).

BXs are widely distributed in the Poaceae family species. However, the presence and amounts of each compound vary across plant species. For example, BXs are found in wheat grains but absent in mature maize seeds (Hanhineva et al., 2011). The presence of BXs in different tissues is also related to the production of their methylated products, such as DIBOA and DIMBOA (Rice et al., 2005). Cambier et al. (2000) detected high concentrations of DIMBOA-Glc and DIM₂BOA-Glc during maize seed germination, but the main BX product in roots was HDMBOA-Glc (N-O-methylated DIMBOA-Glc). Xu et al. (2021) demonstrated that benzoxazinoid biosynthetic pathway genes were differentially expressed between WT wheat and the quick development mutant (*qd*), which affects stem elongation. The results indicate that the mutant exhibits alterations in the BX biosynthesis pathway, with *bx1*, *bx3*, *bx4*, *bx5*, *bx8*, and *bx9* being differentially expressed between *qd* and WT, suggesting that this pathway plays an important role in stem regulation, which associates BX with the elongation phenotype. Park et al. (2004) found that BXs are released around the emerging lateral and crown roots of maize, suggesting that BXs are produced during maize growth to protect the plant against fungi. Furthermore, benzoxazolinones can inhibit auxin-induced growth in roots and coleoptiles by auxin-receptor binding affinity (Hasegawa et al., 1992), suggesting that they can control plant growth indirectly. BXs also function as chelator compounds of iron, aluminum, and molybdenum; and it has been demonstrated that BX, especially DIMBOA-Glc and DIBOA-Glc, form complexes with Fe(III) (Farkas et al., 1998). In addition, Poschenrieder et al. (2005) investigated the potential involvement of BX compounds in aluminum tolerance in maize, finding that BX may contribute to aluminum resistance by forming complexes with Al³⁺, reducing its phytotoxicity in root tissues. Therefore, BXs cannot be considered solely as metabolites involved in plant defense, but they can also play a role in maize nutrition, growth, and development.

ALLELOPATHIC PROCESSES INVOLVED IN BENZOXAZINOID PRODUCTION

BXs are primarily considered as defense metabolites (Niemeyer, 2009). As we have pointed out before, the main benzoxazinoid products, DIBOA and DIMBOA, are synthesized by enzymatic glycosylation, and can reach the extracellular environment or be stored in the vacuole (Frey et al., 2009). Upon plant root tissue damage or fungal attack, the aglycone forms are released as root exudates, where they act as potent allelochemicals. Allelopathy is a well-studied mechanism involving chemical interactions between plants or between plants and fungi, and can be mediated by secondary metabolites, which may negatively affect neighboring organisms (Meiners et al., 2012). Likewise, soil bacteria play a major role in controlling certain invasive species. Some bacteria can degrade allelochemicals that

accumulate in the soil, primarily released by invasive plants of the genus *Argeratina*. These bacteria can adapt and mitigate the effects of these allelochemicals (Li et al., 2015).

The potential of BXs to control weed growth in maize (Jabran, 2017) and wheat (Hussain et al., 2022) has been investigated. Similarly, this allelopathic mechanism has also been analyzed in various plant-microbe interactions. For example, arbuscular mycorrhizal fungi (AMF) colonization in maize has been shown to induce the production of diverse metabolites in root exudates, thereby reducing infection by *F. graminearum*, *F. oxysporum*, and *Rhizoctonia solani* (Ma et al., 2022). Belz and Hurle et al. (2005) demonstrated variations in the proportion of DIBOA and DIMBOA production in root exudates of different Triticeae species, which can inhibit the growth of the white mustard (*Sinapis alba* L.). The release and modification of BXs can mediate communication between plants and microorganisms by regulating plant growth and interactions with neighboring plants through altering the dynamics of the soil microbial community (Li et al., 2025b). Soil microbiota plays an important role in modifying BXs to produce various derivatives, such as phenoxazinones, acetamides, and malonic acids (Schulz et al., 2013).

Communication between plants and soil microorganisms is highly complex; however, root exudates are among the main mediators acting as signal molecules. These exudates strongly influence the rhizosphere microbiota, which, in turn, affects the release and composition of specific root exudates (Dowarah et al., 2025). These compounds enable the plant to recruit different bacterial species to its benefit; for example, leguminous plants can release exudates such as isoflavonoids, which, in turn, promote symbiotic relationships with nitrogen-fixing bacteria (Santoyo, 2022). Another important group of bacteria that directly interacts with plants is plant growth-promoting rhizobacteria (PGPR), which are recruited by plant root exudates. This communication is mediated by the exudates and by bacterial derived responses, such as movement towards the rhizoplane mediated by bacterial flagella and/or pili, as well as the production of extracellular proteins and lipopolysaccharides (Chen; Liu, 2024). PGPR-plant interactions are dynamic and possibly strain-specific, as plants modify the compound release patterns in their root exudates. Ankati et al. (2019) demonstrated that two PGPR strains, *Bacillus sonorensis* RS4 and *Pseudomonas aeruginosa* RP2, induced the production of diverse root exudate compounds in groundnut plants when inoculated either individually or in consortium. In the latter case, metabolites such as serine, pentanoic acid, glucopyranoside, tartaric acid, and 2-pyrrolidinone were detected by gas chromatography (GC) coupled to mass spectrometry (MS) [GC-MS], or MS analyses compared with the uninoculated control, indicating that PGPR have a significant influence on the release of metabolites in root exudates.

PRODUCTION OF BENZOXAZINOIDS IS NOT SUFFICIENT TO CONTROL *FUSARIUM VERTICILLIOIDES* INFECTION IN MAIZE

Fungal infections are one of the main problems affecting agriculturally important crops, including maize, rice, and wheat. It is estimated that around 3.5 million tons of maize grain are lost due to biotic

factors (Ávila et al., 2023). Among infectious agents of maize, *Fusarium* species are important. The life cycle of *Fusarium* in maize has been well studied (Ajmal et al., 2022; Li et al., 2025c). *Fusarium* spp. can survive in soil for up to 10 years as highly resistant conidia. It is considered a cosmopolitan organism, found in various regions of the world, primarily in soil, plant debris, seeds, and inside living plants. Furthermore, it is not exclusive to maize, as these fungi can infect various agriculturally important crops, including wheat, tomato, and potato (Alisaac et al., 2023; Srinivas et al., 2019; Xue et al., 2023).

However, the main problem with *Fusarium* is not its presence in the soil or its easy entry into the plant, but rather its potential to act as an endophytic fungus in maize cells, since it can colonize the root epidermis and vascular vessels (Leyva-Madriral et al., 2014). Therefore, one of the main control methods is the use of chemical fungicides; however, these compounds can accumulate in soils, affecting microbial diversity and enzymatic activity (Wang et al., 2025). *Fusarium verticillioides* (*Fv*) has maintained a long-standing interaction with maize for thousands of years, co-evolving to become able to evade several plant defense mechanisms, including salicylic acid and jasmonate signaling (Wang et al., 2016), PAMP (Pathogen-Associated Molecular Patterns) recognition (Li et al., 2025d), modification of chitinases (Naumann et al., 2011), and benzoxazinoid detoxification (Gao et al., 2022) (Figure 2).

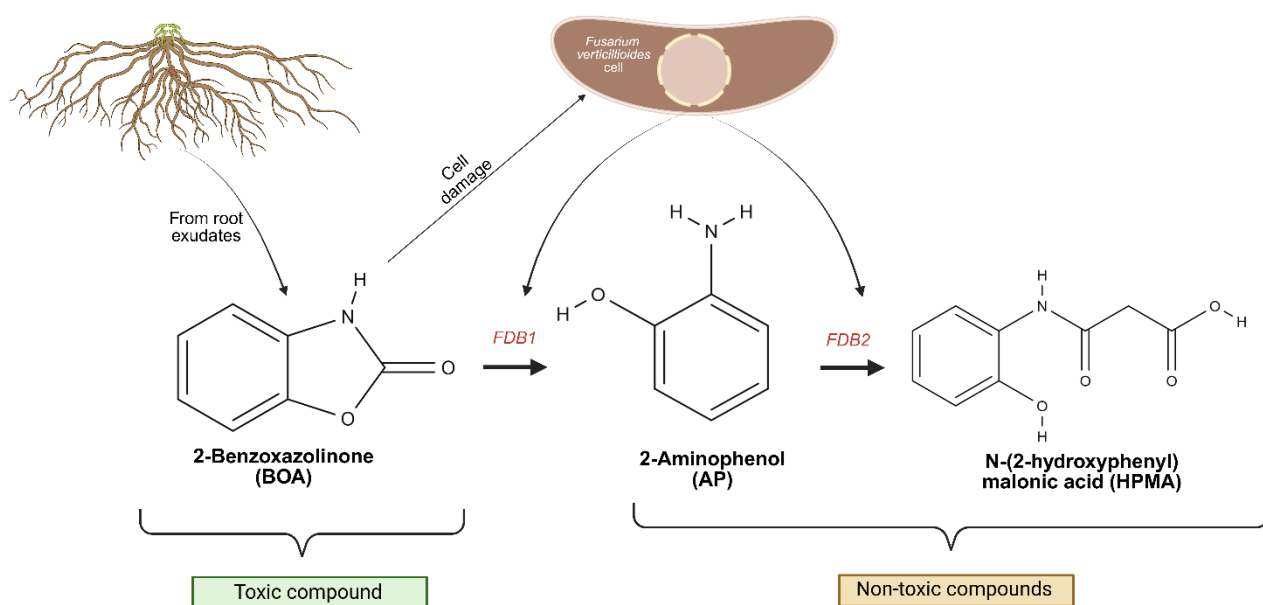


Figure 2. Detoxification pathway of maize BOA in *Fusarium verticillioides*. The first step involves the *FDB1* locus, which produces 2-aminophenol, a non-toxic compound. Furthermore, the *FDB2* locus participates in the transformation of 2-AP into malonic acids. BioRender was used for the illustration.

Fusarium verticillioides has demonstrated high tolerance to MBOA and BOA, transforming these compounds into non-toxic metabolites (Glenn et al., 2001). However, detoxification capacity varies among *Fusarium* species; *F. verticillioides*, *F. subglutinans*, *F. cerealis*, and *F. graminearum* are the most tolerant. The genes involved in BOA detoxification in *Fv* are in two major loci, *FDB1* and *FDB2* (Glenn et al.,

2002). These loci are not physically linked, but most of their genes are essential for detoxification. Among them, the *MBL1* gene (β -lactamase, *FVEG_08291*) from the *FDB1* locus and the *NAT1* gene (arylamine N-acetyltransferase, *FVEG_12636*) from the *FDB2* locus (Glenn; Bacon, 2009) are particularly important during BOA exposure (Glenn et al., 2016). Primarily, *FDB1* catalyzes the first step of BOA detoxification by producing 2-AP, followed by the involvement of *FDB2*, which leads to the production of malonamic acids (HPMA) [see Figure 2].

BENEFICIAL BACTERIA CAN INDUCE THE PRODUCTION OF MORE TOXIC BX COMPOUNDS TO CONTROL PHYTOPATHOGENIC FUNGI

From an ecological perspective, root exudation plays a key role in shaping interactions among rhizosphere organisms. Due to the high abundance of microorganisms and fungi in soil, plants can selectively recruit different microbial species to their benefit through root exudates. However, the interactions between rhizosphere bacteria and root-secreted benzoxazinoids remain poorly understood. BXs significantly influence soil microbial and fungal community composition (Kudjardjie et al., 2019), and their presence in the rhizosphere has enabled some microbial species to become tolerant to these compounds. For example, *Azospirillum brasilense* strain A-V5 can induce several genes in response to MBOA *in vitro*. These genes are primarily involved in transport, signal transduction, transcriptional regulation, and cellular respiration. Additionally, MBOA enhances biofilm formation, resulting in increased biomass associated with the *Arabidopsis thaliana* roots (Baatsen et al., 2025). Furthermore, rhizosphere bacteria adapt to the soil environment surrounding plant roots by metabolizing BXs. For instance, the *bxdA* gene of *Microbacterium*, which encodes an N-acyl homoserine lactonase, catalyzes the conversion of MBOA to AMPO *in vitro* (Thoenen et al., 2024). Notably, enzymes of this family are generally characterized by degrading N-acyl homoserine lactones, key quorum-sensing signaling molecules in bacteria (Morohoshi et al., 2009). Likewise, Neal et al. (2012) demonstrated that *Pseudomonas putida* is tolerant of DIMBOA and possesses the metabolic capacity to detoxify BXs. In addition, transcriptomic analyses revealed the induction of genes associated with benzoate catabolism and chemotaxis. The bacterial BX detoxification pathway is not yet fully elucidated; however, based on analyses of N-acyl homoserine lactonase enzymes, this gene family may be involved in bacterial adaptations to the rhizosphere environment. Such adaptations could occur through potential enzymatic coordination with multicopper laccases, as these enzymes have been reported to oxidize o-aminophenols (Sousa et al., 2021). During the maize-*Fv* interaction, the *BX6* and *BX8* genes are induced (Tran et al., 2021), along with other relevant BX-related genes, suggesting that this pathway plays an important role in controlling *Fv* infection.

Plant growth-promoting rhizobacteria (PGPR) have an important effect on plant growth and the control of *Fv* in maize. Species of the genera *Bacillus* (Cavaglieri et al., 2005), *Pseudomonas* (Nayaka et al.,

2009), and *Enterobacter* (Omotayo et al., 2023) have been reported to inhibit mycelial growth and reduce *Fusarium* root rot. *Bacillus cereus sensu lato* B25 is a rhizosphere bacterium that has been reported to act as a PGPR and to exhibit antagonistic activity against *Fv* (Lizárraga-Sánchez et al. 2015). Furthermore, during direct interactions between B25 and *Fv*, B25 induces several genes associated with antagonism, including chitinases, antibiotics, and siderophores (Báez-Astorga et al., 2022).

Transcriptomic analyses of root samples inoculated with either the bacterium *Bacillus cereus sensu lato* B25 or the fungus *Fusarium verticillioides*, or both at 7 days post inoculation, demonstrated that several BX biosynthetic genes are induced, mainly *bx2* (*Zm00001eb165620*), *bx5* (*Zm00001eb165580*), *bx8* (*Zm00001eb165590*), and *bx13* (*Zm00001eb116010*) (Báez-Astorga et al., 2025) (Table 1).

Table 1. Differentially Expressed Genes (DEGs) involved in the BX biosynthesis were identified in transcriptomic analyses of maize root samples in interaction with the PGPR B25, the fungal pathogen *Fv*, and both simultaneously.

ID	Name	FC (Fold change)		
		Maize- <i>B25</i>	Maize- <i>Fv</i>	Maize- <i>B25</i> - <i>Fv</i>
<i>Zm00001eb165620</i>	BX2	2.55	2.85	4
<i>Zm00001eb165580</i>	BX5	2.53	2.04	2.45
<i>Zm00001eb165590</i>	BX8	14.12	10.78	4.79
<i>Zm00001eb116010</i>	BX13	2.38	2.48	2.68

NE: not expressed gene

It is noteworthy that the *Zm00001eb165620* gene (BX2) was highly induced in the tripartite interaction, suggesting that maize responds more rapidly to *Fv* infection. In contrast, the remaining BX-related genes were also induced across the other treatments, suggesting that the BX biosynthesis pathway is activated during the early stages of root development. Consistent with previous reports (Tran et al., 2021), a strong induction of *bx8* was observed in maize-*Fv* treatment. Notably, a similarly high level of *bx8* expression was detected in the maize-B25 interaction. This response may be attributed to the plant growth-promoting rhizobacteria activity of the B25 strain, which could prepare the plant by activating defense-related mechanisms in anticipation of potential pathogen attack. These findings suggest that BXs are involved in tripartite plant-microbial interactions. The study of BXs in these interactions may help elucidate novel mechanisms of molecular crosstalk between plants and their microbial partners when they interact simultaneously.

CONCLUSIONS

Interactions within the plant rhizosphere are highly complex. Hundreds or thousands of microorganisms may co-exist and compete for survival and reproduction in this environment. Root

exudates are an essential resource for many, particularly for bacteria that can colonize root tissues. Plant-bacteria communication has been extensively studied over the past decade; however, important questions remain regarding more complex interactions involving plants, beneficial bacteria, and pathogenic fungi.

Benzoxazinoids are secondary metabolites that play a crucial role in the early stages of plant-microbe communication. These compounds may contribute to the suppression of fungal infections, the recruitment and selection of beneficial bacteria, and possibly to plant growth and development. Nevertheless, the mechanisms by which PGPR perceive and respond to BX compounds remain poorly understood. Given their roles in plant defense against pathogenic fungi and in the induction of bacterial antagonistic genes, future research should explore whether bacterial detoxification of BX functions as a mechanism of plant-microbe communication and a strategy for fungal biocontrol.

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