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Benzoxazinoids and plant growth-promoting bacteria: A pathway to sustainable agriculture

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ABSTRACT

Grass plants influence the composition of their rhizobiome through the secretion of metabolites, such as benzoxazinoids (BXs), which shape microbial communities. Paramount to plant health, the root associated microbiome may confer plant growth-promoting effects and tolerance to pathogens and herbivorous insects. Specifically, the BX derivative 6-methoxy-2-benzoxazolinone (MBOA), exhibits prolonged effects on soil microbiota and plant defense mechanisms by sustained biosynthesis and its relatively stable molecular structure. Leveraging Plant Growth-Promoting Rhizobacteria (PGPR) offers a sustainable strategy to enhance soil fertility and crop yield while reducing reliance on chemical inputs. However, the efficacy of microbial inoculants is contingent upon various factors, including cultivar and environmental conditions, necessitating tailored approaches for successful implementation. The ecological impact BXs as plant signaling molecules can have on microbial ecology is demonstrated by experiments on *Fusarium* strains. Conditioning soil with MBOA may offer a promising strategy to enhance the efficacy of microbial inoculation, thus improving environmental conditions and crop cultivation outcomes. In this review, we discuss how BXs can be used as a tool in sustainable agricultural practices. Therefore, the biochemistry of BXs; the mechanisms of PGPR involved in root colonization; and plant-soil feedback are discussed, offering insights into optimizing crop management for enhanced sustainability, yield and pest tolerance.

1. Introduction

To optimize benefits gained from a healthy rhizobiome, plants naturally manipulate the composition of microorganisms in the soil by secreting a plethora of primary and specialized metabolites (Bais et al., 2006; Bever et al., 2013a; Bulgarelli et al., 2013). In various grasses, the release of benzoxazinoids (BXs) in the soil fulfills an important role in shaping the root microbiome (Cadot et al., 2021a; Chen et al., 2010; Cotton et al., 2019a; Hu et al., 2018a). Specifically, the lactam BX derivative 6-methoxy-2-benzoxazolinone (MBOA), is efficient in suppression of some fungal pathogens (Oikawa et al., 2004) and promotes herbivore tolerance by inducing systemic defense through rhizobiome structuring (Hu et al., 2018a). Given the moderate 5.4 days half-life of MBOA (Etzerodt et al., 2008a) and the lasting biosynthesis and presence in the soil (Cambier et al., 2000; Hu et al., 2018a; Macías et al., 2004), the influence of MBOA is sustained throughout the next generation of plant progeny (Hu et al., 2018a). The effect that plants have on biotic and abiotic factors of the soil is termed plant-soil feedback. In the case of positive plant-soil feedback, this may improve growth conditions of seedlings from the next generations. Plant-soil feedback can be the result of alterations in resource availability, accumulation of allelopathic molecules or by dynamics in the soil microbiome, which are all strongly influenced by one another (Kulmatiski et al., 2017; Smith-Ramesh and Reynolds, 2017).

The term "rhizosphere" was introduced for the first time in 1904 by Lorenz Hiltner (Hartmann et al., 2008; Hiltner, 1904), stating that the rhizosphere or "soil influenced by roots" creates the capacity for bacteria to fix nitrogen. Furthermore, it was noted that exudates of legume plants attract different bacteria to the rhizosphere than mustard or oats, in respect to their specific nutritional needs. Preceding elaborate studies on symbioses of nodule forming bacteria in legume plants, development of the first microbial inoculant was launched in 1891 (Nobbe et al., 1891; Nobbe and Hiltner, 1893). Those studies elaborated on the specificity of the host plant to enable symbiosis with the microbial inoculant and specific handling and preparation methods for keeping the inoculant viable.

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A compelling amount of evidence demonstrates how the plant microbiome in its whole forms a protective network able to repel pathogens (Ahmad et al., 2011a; Copaja et al., 2006; Glenn et al., 2001a, 2003; Glenn and Bacon, 2009; Meihls et al., 2013; Niemeyer, 2009a; Oikawa et al., 2004; Śmist et al., 2016; Søltoft et al., 2008); enhances abiotic stress tolerance and improves water and nutrient absorption (Aloo et al., 2022; Dehghani and Mostajeran, 2020; Gond et al., 2015; Kumar et al., 2019; Liu et al., 2020; Marques et al., 2020; Schütz et al., 2018; Subiramani et al., 2020; Vurukonda et al., 2016), eventually leading to the overall biomass increase of the host plant (Hungria et al., 2010, 2015, 2018; Mishra et al., 2011; Oliveira et al., 2017; Quecine et al., 2012). Most importantly, microbial inoculation of crops grants a buffer capacity to withstand various adverse abiotic and biotic stress factors, abolishing the need for energy demanding fertilizers and agrochemicals (Daramola and Hatzell, 2023). In the long term, depletion of soil nutrients by over application of fertilizers can be evaded by intelligent and accurate inoculation of Plant Growth-Promoting Rhizobacteria (PGPR) aiming at sustainable agriculture in hand with environmental stability (Mohanty et al., 2021; Shah et al., 2021). Hence, manipulating the plant microbiome can provide significant increases in yield gain especially in more challenging and heterogeneous terrain (Schütz et al., 2018; Teste et al., 2017a).

Indeed, maize exudated BXs can have profound effects on microbiome structuring (Cadot et al., 2021b; Cotton et al., 2019b; Gfeller et al., 2023b; Hu et al., 2018a; Kudjordjie et al., 2019a; Schandry et al., 2021; Thoenen et al., 2023a). The BX influence on the microbiome organization can improve crop yield (Gfeller et al., 2023b), and provokes a jasmonic acid (JA)-dependent enhanced pest tolerance, persisting into the next generation (Hu et al., 2018a). Zeroing in on the individual PGPR strain level, two cases, *P. putida* KT2440 (Neal and Ton, 2013a) and *A. brasilense* Ab-V5 (Baatsen et al., 2025) reportedly exhibited a chemotactic response to BXs. Interestingly, colonization of the roots and leaves by *A. brasilense* and *P. fluorescens* respectively, stimulate BX metabolism in the plant (Walker et al., 2011a; Zhou et al., 2020a). This demonstrates that BXs can impact the PGPR-plant interaction at the strain and microbiome level, and can possibly be involved in the initial colonization process by establishing recruitment of bacteria by evoking a chemotactic response. In return, successful plant colonization, in some cases, can set in motion a positive feedback loop by inducing plant BX metabolism, underpinning its ecological relevance and potential.

The efficacy of microbial inoculants however, depends on many factors such as cultivar, environment (Pacheco da Silva et al., 2022) and inoculation level (Renoud et al., 2022). Inoculating crops with PGPR has proven to be challenging, due to unsuitable environmental conditions or the inability to compete with the native microbiome (Catroux et al., 2001), which depend on the soil type and cultivar (Martinez-Viveros et al., 2010). The complex nature of the soil, defined by many abiotic and biotic factors, makes discriminating relevant players in plant-microbe interactions a compelling task. To analyze the position of BXs in this intricate network environmental variables, in this review we provide an elaborate overview of the biosynthesis and biochemistry of BXs, to understand their diversity; in what conditions and where they are biosynthesized; and to demonstrate how their molecular structure relates to reactivity and their dynamics in a soil environment. The impact of MBOA on soil ecology is demonstrated by an experiment on *Fusarium* strains, showing how host adaptation leads to MBOA tolerance. We further explore what bacterial mechanisms are involved in root colonization and the influence of BXs on plant-soil feedback. At last, to what extent BXs have been tested in agricultural settings is discussed and where future research can improve implementation of BXs on sustainable crop cultivation.

2. Biochemistry of benzoxazinoids

Many plants have the ability to condition the soil by modifying local environmental parameters that in turn influence the plants' performance. Metabolites in plant root exudates contribute to establishing plant-soil feedback, which determine plant diversity and succession (Teste et al., 2017a), particularly by influencing the root microbiome (Bever et al., 2013a; Kudjordjie et al., 2019b). A substantial number of specialized metabolites deposited by maize roots exists of BXs, a highly toxic group of specialized metabolites in Poaceae.

Even though BXs govern the main pathogen defense during early plant development, maize plants produce a range of other specialized metabolites that act in plant immunity. The diversity of defense metabolites origins from ancient duplications of bifunctional diterpene synthases (diTPSs) and cytochrome P450 monooxygenase (P450), leading to functional redundancy and space for diversification of terpene scaffold products (Jia et al., 2022). The kauralexin type of diterpinoids obstructs digestion of plant tissue by pest species, and acts as antimicrobial agent against several fungal pathogens (Ding et al., 2019; Schmelz et al., 2011), in addition to the *in vitro* antifungal activity of dolabralexins, epoxydolabranol and trihydroxydolabrene diterpenoids (Mafu et al., 2018). Mixtures of volatile terpenoids, upon release, contribute to pest control indirectly by attracting predators of the herbivorous insects. Such mixtures can contain linalool, β-caryophyllene and 4,8,12-trimethyltrideca-1,3,7,11- tetraene (TMTT) (Yactayo-Chang and Block, 2023). In a similar fashion, derived from membrane lipids, green leaf volatiles compose a different class of specialized defense metabolites that mediate long distance defense against insect invasion. Akin to green leaf volatiles, oxylipins also derived from membrane lipids, accumulate in local plant tissue upon structural damage and pathogen attack, effectively blocking herbivorous insects and fungal pathogens (Huang et al., 2023; Yang et al., 2023). Furthermore, a third class of strong defense metabolites are flavonoids, which are diverse phenolic compounds with varying bioactivity. For instance, apigenin release in the soil improves nitrogen acquisition and promotes plant growth indirectly, via enrichment of the soil with oxalobacteraceae (Yu et al., 2021), while maysins and coumarates confer pest tolerance (Block et al., 2020; Casas et al., 2016; Förster et al., 2022). On top of that, flavonoid release is triggered in N-poor conditions leading to the recruitment of N-fixing bacteria, and acts as an important signaling molecule stimulating nodule formation by rhizobia (Weston and Mathesius, 2013).

Among this wide range of specialized metabolites, principally during early developmental stages, BXs constitutes the majority of specialized metabolites in maize and stands out for their versatile and system-wide functionality (de Bruijn et al., 2018; Hu et al., 2018a; Köhler et al., 2015a; Niemeyer, 2009b). While the main known function of BXs in plant defense, is limiting the growth of microbial and herbivorous pest species (Ahmad et al., 2011a; Neal and Ton, 2013b; Niemeyer, 2009a), root associated bacterial and fungal communities are strongly affected by BXs, aiding in plant growth and defense for successive generations (Hu et al., 2018a) and can attract certain PGPR to the root surface (Baatsen et al., 2025; Neal et al., 2012). In this chapter, we outline the chemistry, biosynthesis and biological function of BXs on the rhizosphere, modulating the "second plant genome" (Ahmad et al., 2011b; Neal and Ton, 2013a; Niemeyer, 2009b).

2.1. Discovery, occurrence and reactivity

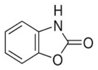
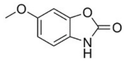
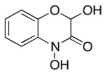
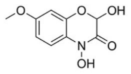
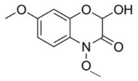
BXs compose a group of specialized metabolites widely spread in grass species including maize, wheat and rye (Niemeyer, 1988b), and also produced by some dicotyledonous species within the *Ranunculaceae, Acanthaceae, Plantaginaceae* and *Lamiaceae* families (Baumeler et al., 2000; Schullehner et al., 2008), that possess the 2-hydroxy-2H-1, 4-benzoxazin-3,4-one (HBOA) base structure. The earliest studies on BXs date back from 1955, in which BXs were isolated form rye seedlings (Virtanen and Hietala, 1955a, 1955b)'. In contrast to phytoalexins, which are *de novo* synthesized specialized defense metabolites after infection or stress that serve as an inducible defense response (we refer to(Ahuja et al., 2012) for a review), BXs are phytoanticipins, constitutively produced specialized metabolites that are pre-formed and sequestered in an inactive, glycosylated form in the vacuole (VanEtten et al., 1994). In their pioneering studies, Virtanen and Hietala demonstrated how cleavage of the glucoside moiety of 2,4-dihydroxy-1,4-benzoxazin-3-one-glucoside (DIBOA-glc) only happened in unheated disrupted plant tissue, while from boiled plant material and hence containing denatured β-glucosidases, only the glucoside form (DIBOA-glc) was obtained (Virtanen and Hietala, 1960). Upon herbivore attack, hydroxylation by vacuole bound β-glucosidases allows activation of the bioactive aglycone benzoxazinones, which are spontaneously converted in benzoxazolinones and formic acid (Niemeyer, 1988b) (both benzoxazinones and benzoxazolinones are referred to as BXs). Despite being constitutively produced, BX biosynthesis is boosted in response to insect herbivory in maize seedlings (Köhler et al., 2015b) and in mature leaves (Maag et al., 2016).

BX content varies in its composition of derivatives and their concentrations according to plant organs or tissue (Cambier et al., 1999; Villagrasa et al., 2006), age (Cambier et al., 1999; Köhler et al., 2015b) and plant species (Copaja et al., 2006; Eljarrat and Barceló, 2001; Schulz et al., 2013). For instance, in wheat and maize 2,4-dihydroxy-7-methoxy-2H-1,4-benzoxazin-3(4H)-one (DIMBOA) is the most abundant BX (Köhler et al., 2015b; Villagrasa et al., 2006), while DIBOA is the most prevalent in rye (Oikawa et al., 2004; Rakoczy-Trojanowska et al., 2017). In maize, early during plant development BX levels are the highest while they decline and stabilize over the first months (Ebisui et al., 1998; Hu et al., 2018a). DIMBOA-glc is predominantly found in aerial parts and in the roots shortly after germination but diminishes fast during the first and second week after germination respectively (Cambier et al., 2000). After that period, in the roots 2-hydroxy-4,7-dimethoxy-1,4-benzoxazin-3-one-glucoside (HDMBOA-glc) and its more stable breakdown product 6-methoxy-benzoxazolin-2-one (MBOA) become more dominant, while in aerial parts of the maize plant DIMBOA-glc is still the most prevalent BX derivative (Cambier et al., 2000; Hu et al., 2018a).

Abiotic factors like pH (Niemeyer et al., 1982) and chemical solvents (Bravo and Niemeyer, 1985) can facilitate the closure of the open ring benzoxazinone intermediate, lowering its reactivity. Stability of benzoxazinones highly depends on the functional group bound to the N atom: lactam forms (N-H) do not convert into benzoxazolinone forms, while hydroxamic acids (N-OH) are rapidly converted and *N-O*-methyl derivatives even faster. For example, the hydroxamic acid DIBOA has a half-life of 25 h, while the half-life of the *N-O*-methyl derivative HDMBOA is only 1.8 h in pH 5.5 (Maresh et al., 2006a) (Table 1).

Once DIMBOA and DIBOA are degraded into the benzoxazolinones MBOA and BOA, they undergo microbial transformation into 5-methoxy-2-aminophenoxazin-3-one (AMPO) (Kumar et al., 1993) and APO (Gagliardo and Chilton, 1992), and decompose further into 2-acetylamino-7-methoxy-phenoxazin-3-one (AAMPO) (Etzerodt et al., 2006) and 2-acetylamino-phenoxazin-3-one (AAPO) (Understrup et al., 2005a) respectively. In degradation experiments with start concentrations of 2400 nmol g^{-1} and pH 6.8, the half-life of MBOA was 5.4 days (Etzerodt et al., 2008a). At the same time, degradation experiments with a start concentration of 3000 nmol g^{-1} and pH 6.8, a half-life of 3.1 days was determined for BOA (Understrup et al., 2005a) (Table 1).

Table 1
Overview of half-life and the molecular structure of selected BX derivatives. The half-time strongly depends on pH, which is indicated between brackets.

IUPAC	Half-life	2D structure	References
3*H*-1,3-benzoxazol-2-one (BOA)	3,1 days (pH 6,8)		Undertrup et al. (2005)
6-methoxy-3*H*-1,3-benzoxazol-2-one (MBOA)	5,4 days (pH 6,8)		Etzerodt et al. (2008)
2,4-dihydroxy-1,4-benzoxazin-3-one (DIBOA)	25 h (pH 5,5)		Maresh et al. (2006)
2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one (DIMBOA)	20 h (pH 6,0)		Woodward et al. (1978)
2-hydroxy-4,7-dimethoxy-1,4-benzoxazin-3-one (HDMBOA)	1,8 h (pH 5,5)		Maresh et al. (2006)

2.2. BX biosynthesis

The first step in BX biosynthesis is mediated by the BX1 enzyme, converting indole-3-glycerolphosphate (IGP) into indole (Fig. 1). This first step forms a shared branch point with tryptophan and auxin synthesis via the shikimate pathway, the conversion in this case by tryptophan synthase is performed in conjunction with the tryptophan synthase beta-subunit, whereas BX1 acts as a monomer (Frey et al., 2000). Free indole can also be formed by indole-3-glycerol phosphate lyase (IGL) induced by herbivory attack, and set free for defense priming (Erb et al., 2015; L Hu et al., 2018), besides serving as a metabolic intermediate. The conversion of indole into DIBOA is carried out by the cytochrome P450 dependent monooxygenases BX2 - BX5 by successively adding four oxygen atoms, which are all substrate specific (Frey et al., 1995) (Fig. 1). Glycosylation of BXs catalyzed by the two UDP-glucosyltransferases BX8 and BX9 (Von Rad et al., 2001), prevents ring opening and self-toxicity, since hydroxylation and *O*-methylation by BX6 and BX7 respectively, takes place in the cytoplasm (Frey et al., 2003; Jonczyk et al., 2008) (Fig. 1). BX6 and BX7 convert DIBOA-Glc into DIMBOA-Glc, and are both stored in the vacuole. Possibly, synthesis of DHBOA-Glc, HDMBOA-Glc and HM$_2$BOA-Glc is mediated by the same enzymes for DIBOA production, however, metabolic pathways of lactam forms remain to be uncovered. Upon pathogen and herbivory insect invasion, glycosylated BX species are hydrolyzed by β-glucosidases GLU1 and GLU2, converting their substrates into highly reactive forms (Czjzek et al., 2001) (Fig. 1).

The exact amount of BX produced by plants is often compromised by sample handling due to the activity of β-glucosidases in the samples and the short half-life of the resulting benzoxazinone aglucons (Cambier et al., 1999; Grambow et al., 1986). Between species the difference in BX production is substantial: in the grains of wheat and rye respectively around 4,8 and 95 μg g^{-1} dry weight is found (Tanwir et al., 2013); in the shoots of rye 1900 μg g^{-1} dry weight (Schulz et al., 2013) and maize can accumulate up to 1700 μg^{-1} of leaf fresh weight depending on the BX derivative (Köhler et al., 2015b; Meihls et al., 2013).

2.3. BX biological function

The aglucon benzoxazinones are cyclic hydroxamic acids that contain a highly reactive α-oxo-aldehyde group upon ring opening (Atkinson et al., 1992). The instability of the metabolic intermediate makes benzoxazinones react with thiols (Atkison et al., 1991) and amines (Pérez and Niemeyer, 1989) in amino acid residues of proteins; with catalytic centers of enzymes which interrupts their functionality (Cuevas et al., 1990) and disrupt metabolic processes such as electron transport (Massardo et al., 1994). In general, hydroxamic acids are more phytotoxic than lactams, DIBOA being the strongest allelopathic natural occurring BX (Macías et al., 2005, 2006). Apart from their allelopathic effect on plants, BXs are toxic for various insects and microorganisms (Ahmad et al., 2011a; Copaja et al., 2006; Meihls et al., 2013; Niemeyer, 2009a; Søltoft et al., 2008). Again, hydroxamic acids are more toxic than lactams and increasingly more potent the higher the level of methylation (Søltoft et al., 2008). However, despite being a BX lactam derivative, MBOA is superior to DIMBOA-glc and HDMBOA-glc (both hydroxamic acids) in suppressing conidia germination and germ tube growth of

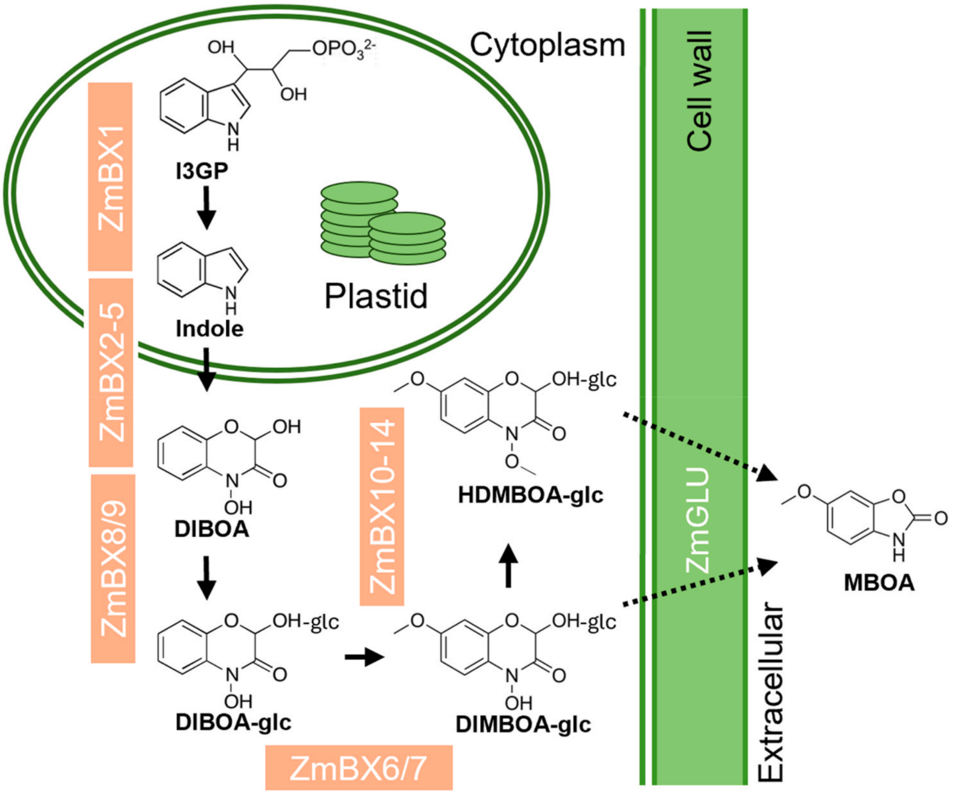


Fig. 1. Benzoxazinoid (BX) biosynthesis pathway in maize. Constitutive BX compounds are in black and related enzymes are in white. 2,4-dihydroxy-7-methoxy-2H-1,4-benzoxazin-3(4H)-one (DIMBOA) and 2-hydroxy-4,7-dimethoxy-1,4-benzoxazin-3-one (HDMBOA) are rapidly converted into 6-methoxy-2-benzoxazolinone (MBOA) in extracellular aqueous milieu.

Bipolaris maydis, *Curvularia lunata* and *Alternaria alternate* (Oikawa et al., 2004). Therefore, the conversion of DIMBOA-glc to HDMBOA-glc is

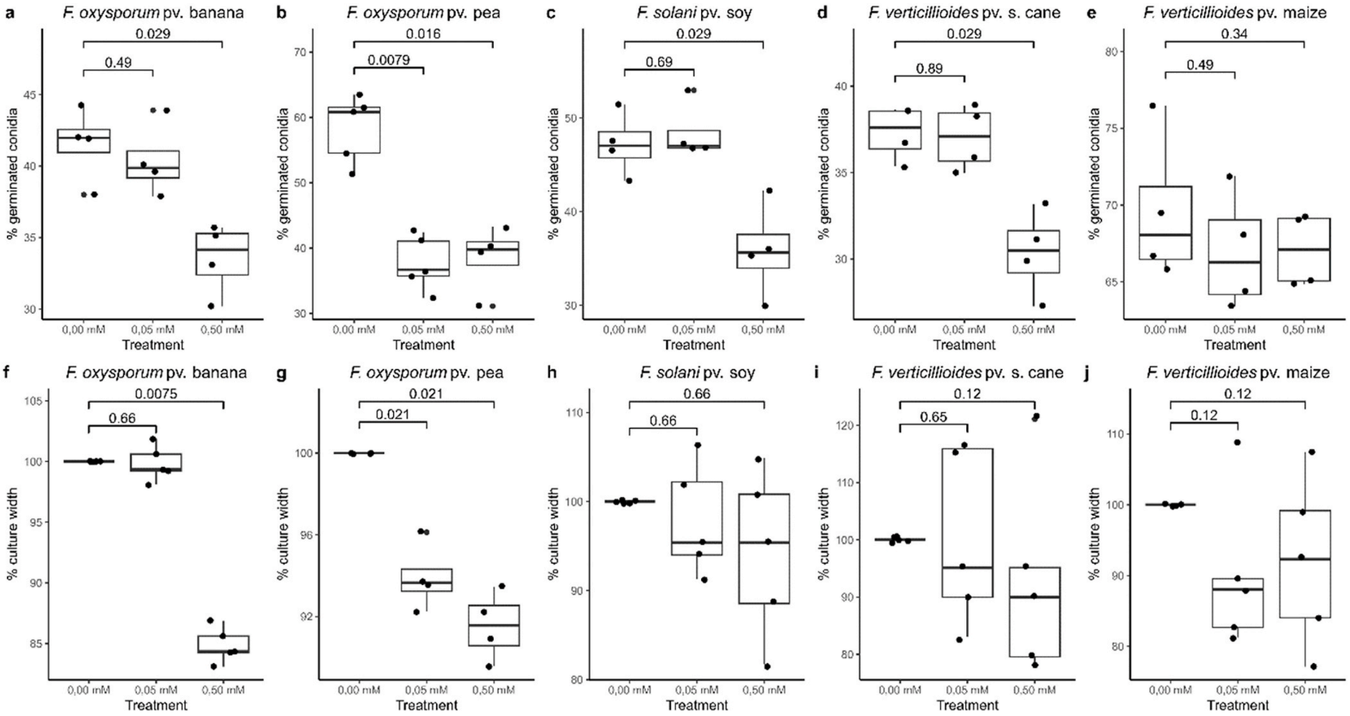


Fig. 2. Assessment of *Fusarium* spp. tolerance to ambient concentrations of 6-methoxy-2-benzoxazolinone (MBOA). Tolerance of *Fusarium* spp. was assessed by germinating conidia in liquid culture, and by growing *Fusarium* on MBOA amended plates. *F. oxysporum* (**a, b, f, g**) was the most sensitive species, while *F. solani* from soybean (**c and h**) and *F. verticillioides* from sugarcane (**d and i**) were more tolerant. *F. verticillioides* from maize (**e and j**) was completely tolerant to MBOA. Data was analyzed by a Wilcoxon rank sum exact test with p-values indicated. Error bars in the charts represent standard deviation.

possibly a mechanism for increasing MBOA content in the soil by spontaneous degradation.

BX metabolites have a strong fungistatic effect on *Fusarium, Phytophtora, Rhizoctonia, Phoma, Alternaria, Blumeria,* and *Botrytis* (Glenn et al., 2001a, 2003; Glenn and Bacon, 2009; Oikawa et al., 2004; Śmist et al., 2016). In the case of *F. verticillioides,* the selective pressure exerted by maize-derived BXs, has led to the retention of the *FDB1* and *FDB2* gene clusters, which are essential for detoxifying the benzoxazolinons MBOA and 2-benzoxazolinone (BOA) (Glenn et al., 2001a; Glenn and Bacon, 2009), These gene clusters were likely acquired through horizontal gene transfer events from *Colletotrichum* and *Aspergillus* (Glenn et al., 2016). An arylamine N-acetyltransferase *NAT1* within the *FDB2* cluster can convert the BOA breakdown product 2-aminopheno (2-AP) into the non-toxic (2-hydroxyphenyl) malonamic acid (HPMA) (Glenn et al., 2003; Glenn and Bacon, 2009). The detoxification of BX metabolites by BX tolerant fungal endophytes was demonstrated by the survival of BX sensitive endophytes after colonization by BX tolerant *Fusarium* (Saunders and Kohn, 2008). Interestingly, the biocontrol agent PGPR *Bacillus mojavensis* is able to neutralize the ability of *F. verticillioides* to convert 2-amino-3H-phenoxazin-3-one (APO), which is toxic for *F. verticillioides* (Bacon et al., 2007), into the less toxic N-(2-hydroxyphenyl) malonamic acid (HPMA).

Our group showed that MBOA suppresses germination of conidia in several *Fusarium* spp. with the exception of *F. verticillioides* T4 isolated from maize and diminished biomass of *F. oxysporum* isolates (Baatsen, 2024) (supporting experimental details are described in Supplementary Material). Interestingly, when comparing *F. verticillioides* species, tolerance to MBOA of T4 from maize was observed, while *F. verticillioides* from sugarcane was susceptible (Fig. 2). Comparable results were obtained in a study of Richardson et al. (1995), where *F. verticillioides* isolated from maize converted up to 2.5 mM BOA and MBOA, while rice isolates did not catabolize any of the benzoxazolinones (Richardson and Bacon, 1995). In contrast to rice, banana, pea, soy and sugarcane that do not produce BX, maize plants produce substantial amounts of BXs and hence, our results strongly suggest that *Fusarium* spp. demonstrate adaptive responses to the host's BX production levels. In general, *Fusarium* species associated with grasses exhibit higher tolerance to BXs, enabling *F. verticillioides* to live as a symptomless endophyte (Bacon and Hinton, 2011; Glenn et al., 2001b). *F. verticillioides* establishes tolerance by bioconversion of BOA and MBOA into N-(2-hydroxy-phenyl)-malonamic acid and N-(2-hydroxy-4-methoxyphenyl)-malonamic acid respectively (Richardson and Bacon, 1995; Yue et al., 1998a). Considering the susceptibility to BXs of pathogens with non-BX producing hosts, BX content in the soil maybe an interesting avenue for disease suppression in non-BX producing crops by crop rotation or combining different crops (Xu et al., 2015a). Besides disease tolerance caused by fungal pathogens, BX enables the plant to withstand negative plant-soil feedback from competing plants, which acts via the soil associated microbiota (Gfeller et al., 2023a).

In some instances, the production of BXs may have a negative side effect, e.g. in respect to its effect on the crown rootworm. DIMBOA has iron chelating properties (Bigler et al., 1996) and is enriched in maize crown roots (Robert et al., 2012). As opposed to generalist herbivores, the crown rootworm is resistant and can sequester DIMBOA (Robert et al., 2012). Moreover, its larvae exploit DIMBOA-Fe complexes for foraging on nutrient rich crown roots (L Hu et al., 2018). In Fe poor soils, growth of the fall armyworm is suppressed by DIMBOA, while in Fe-rich soils, the average biomass of the fall armyworm is increased (Hu et al., 2021). However, this effect may be caused by the elevated Fe content in the plants that the army fall armyworm feeds on. Apart from this example, BXs were proven effective against a number of other nematodes, fungus, aphids and other herbivorous insects (Ahmad et al., 2011a; Cambier et al., 2000; Hu et al., 2018a; Niemeyer, 2009a) (Fig. 3).

3. Benzoxazinoids and root colonization mechanisms

Important to many PGPR for exerting the abilities that improve plant performance, is proper plant or rhizosphere colonization (Compant et al., 2010). Rhizosphere competent bacteria profit from root colonization by occupying a protective ecological niche that provides stable environmental conditions and nutrients (Senthilkumar et al., 2011). In order to establish an intimate relation with the host plant, PGPR communicate for simultaneously undertaken actions within the bacterial community via quorum sensing; they need to be recruited by chemotaxis from the bulk soil and anchor themselves on the root surface by production of biofilm. The selection of microorganisms in the soil associated with a specific plant is orchestrated by the release of a plethora of metabolites by the roots. This plant-specific conditioning of the soil, impacting biotic and abiotic factors, is referred to as plant-soil feedback.

3.1. Quorum sensing

Quorum sensing (QS) is a means of chemical communication, widely

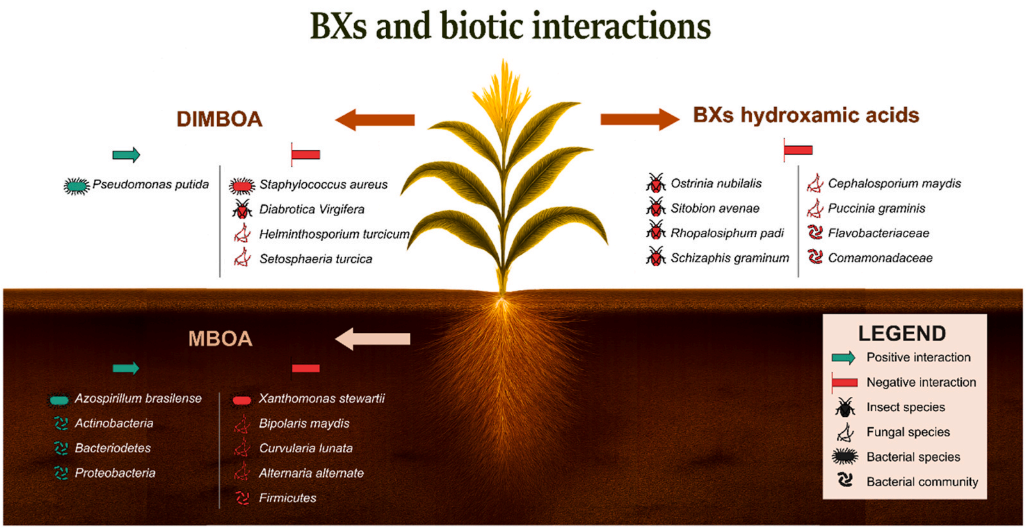


Fig. 3. Biotic effects of benzoxazinoids (BXs) on the environment. In maize, 2,4-dihydroxy-7-methoxy-2H-1,4-benzoxazin-3 (4H)-one (DIMBOA) is the BXs derivate most abundant in the aerial parts, while 6-methoxy-2-benzoxazolinone (MBOA) is most abundant in the roots. Hydroxamic acids are more reactive than lactam BX derivatives. Positive effects are indicated in green, while negative interactions are marked in red.

used among bacteria to monitor their population density and regulate gene expression (Fuqua and Winans, 1994a). QS enables synchronized behavior, and regulates a wide variety of processes falling into four classes: cell behavior; cell maintenance; horizontal gene transfer and microbe-host interactions (Fuqua and Winans, 1994b; Jimenez et al., 2012; Monnet et al., 2014; Whitehead et al., 2001). In this section we will limit ourselves to processes regulated by QS that pertain to root colonization and microbe-host interactions.

A wide range of bacteria produce auto inducer (AI) molecules that are perceived by other individual cells and stimulate the biosynthesis of their own AI. Proportional to the level of environmental AI, bacteria are able to monitor their population density and act accordingly (Fuqua and Winans, 1994b). The threshold to be reached for AI to regulate a certain process, depends on the QS system as well as the regulators involved. *N*-acylhomoserine lactones (AHLs) are synthesized from S-adenosyl-methionine (SAM) by the LuxI synthase (Schaefer et al., 1996) in α-, β- and γ-proteobacteria (Churchill and Chen, 2011) with varying acyl chain lengths donated by acyl chain carrying proteins. Sensing of AHLs happens via interaction with the N-terminal receptor domain of LuxR proteins, while its C-terminal domain has DNA-binding properties allowing regulation of gene expression (Koch et al., 2005). Some Gram-positive bacteria and Gram-negative bacteria make use of the AI-2 system which is a mixture of compounds resulting from cyclization of 4, 5-dihydroxy-2,3-pentanedione mediated by LuxS synthase, also found in the pathogens *Salmonella typhimurium* and *Vibrio cholerae* (Surette et al., 1999). Several other QS molecules are derived from fatty acids (He and Zang, 2008); from amino acids and peptides (Holden et al., 1999; Monnet et al., 2014).

Several fundamental abilities and processes involved in bacterial-host interactions, are controlled by QS. Amongst these are chemotaxis and biofilm formation, which are inextricable parts of the bacterial root colonization process. Both are often regulated by QS (Fukami et al., 2018; Jani et al., 2017; Solano et al., 2014; Zhang et al., 2020), via highly intertwined regulatory mechanisms (Bahlawane et al., 2008; Berne and Brun, 2019; Jani et al., 2017). In *Sinorhizobium meliloti*, the AHL regulator protein ExpR inhibits visNR expression by binding in its operon region, which is a regulator of the flagellation gene set (Bahlawane et al., 2008). Furthermore, flagellar independent movement of bacteria is promoted by ExpR through production of extracellular polymeric substances (EPS) reducing friction with the contact surface and allows bacteria to spread by passive movement through sliding (Nogales et al., 2012). Concerning root colonization mechanisms, the biocontrol strain *P. fluorescens* 2P24 harbors the LuxR/LuxI family PcoR/PcoI system which is involved in colonization of the rhizosphere (Wei and Zhang, 2006). Interestingly, production of the antimicrobial metabolite 2.4-diacetylphoroglucinol (DAPG) by *P. fluorescens* is regulated in a density dependent manner, though not under control of any QS mechanism (Delany et al., 2000; Schnider-Keel et al., 2000). Consequently, when the *pcoI* gene has been knocked-out, DAPG is produced as normal, though biofilm formation and colonization of wheat roots is strongly impaired (Wei and Zhang, 2006). Similarly, in *Serratia plymuthica* AHL signaling is indispensable for colonization of bean roots; for biocontrol of the phytopathogen *P. aphanedermatum* and for activation of induced systemic resistance (ISR) (Pang et al., 2009). In rhizobia-legume symbiosis, QS has a significant impact on the intimate host-symbiont relation in several cases, but is not always required. For example, the *Rizobium elite* CNPAF512 mutant defect in the LuxI-type AHL synthesis gene *cinI* or LuxR-type AHL regulator gene *cinR,* displayed decreased N fixation and aberrant bacteroid development in nodules (Daniels et al., 2002). In contrast, in *R. leguminosarum* bv. *viciae,* mutants of the *cinI* or *cinR* genes did not impair symbiosis and did even increase the number of nodules (Rosemeyer et al., 1998; Wisniewski-Dyé et al., 2002).

How AI molecules affect bacterial biofilm depends on the natural history of the bacteria and the environment it is adapted to. In *V. cholerae* and *Staphylococcus aureas,* accumulation of AI represses biofilm formation, while in *P. aruginosa* biofilm production is stimulated in the presence of high AI concentrations (Bronesky, 2016; de Kievit and Iglewski, 2000). When exposed to fluid flow, the produced AIs in the environment are carried away, consequently, biofilm production in *V. cholerae* and *S. aureus* is stimulated (Kim et al., 2016). After establishment of biofilm, cells that are shielded form fluid flow by neighboring cells experience a buildup in AI which represses biofilm formation. Thus, bacteria with a different special distribution within a biofilm adapt different roles based on AI levels (Kim et al., 2016).

Because QS is a widespread mechanism in prokaryotes and archaea, some eukaryotes exploit QS for perceiving bacteria and to compromise their communication. The diverse effects bacterial AI have on their plant host, correlate with the length of the acyl chain. In general, AHL containing short acyl chains have plant growth stimulating properties, while AHL with long acyl chains stimulate ISR and pathogen defense (Calatrava-Morales et al., 2018; Schenk et al., 2014; Schikora et al., 2011, 2016; Zarkani et al., 2013). In the other way around, plants can produce compounds that perturb QS (Koh et al., 2013; Rasmussen et al., 2005), for example found in garlic (Rasmussen et al., 2005); grapefruit-seed (Heggers et al., 2002), broccoli (Ganin et al., 2013) or nutmeg (Chong et al., 2011) extracts. Likewise, inside the human gut epithelial cells can produce AI-2 mimics as a response to interaction with bacteria. Those mimics interact with the AI-2 receptor LuxP/LsrB in *Salmonella typhimurium* and control QS dependent gene regulation (Ismail et al., 2016). Fungal derived QS molecules play important roles in fungal morphogenesis, biofilm formation and pathogenicity (reviewed in Wongsuk et al. 2016; Wongsuk et al., 2016)). Moreover, some mycotoxins also suppress QS such as fusaric acid from *Fusarium* species, which on top of that inhibits antibiotic production of biocontrol bacteria (Manefield et al., 1999; Quecine et al., 2016; Van Rij et al., 2005).

3.2. Chemotaxis

To support a rich microbiome in the soil, plants release large amounts of fixed carbon and nitrogen in the form of primary and specialized metabolites, mucilage and proteins (Bais et al., 2006). The majority of root exudates are primary metabolites such as carbohydrates, amino acids and organic acids while specialized metabolites like flavonols, lignins, coumarins, and indole compounds make up a smaller moiety (Bardi and Vivanco, 2009). One percent of exudated specialized metabolites are small organic compounds with a lipophilic character and a low boiling point, grouped in volatile organic compounds (VOCs) (Schmidt et al., 2015; Venturi and Keel, 2016). Their physiochemical characteristics allow them to spread easily and have a wide area of influence in the surrounding soil, making them suitable chemo-attractants (Ali et al., 2010; Schulz-bohm et al., 2018; Van Dam et al., 2016). Many plants of the grass family release BXs, significantly altering the microbial composition of the soil microbiome (Cadot et al., 2021a; Cotton et al., 2019a; Hu et al., 2018a) and enhancing pathogen defense (Ahmad et al., 2011a; Neal and Ton, 2013b; Niemeyer, 2009a). To manifest those ecological effects, the BX derivative DIMBOA, attracts *P. putida* to the rhizosphere of maize roots (Neal et al., 2012), while MBOA induces a chemotactic response in *A. brasilense* Ab-V5 (Baatsen et al., 2025).

Low molecular weight compounds are released by passive transport over the plasma membrane via concentration driven diffusion, vesicle transport and through ion channels (Bardi and Vivanco, 2009; Dreyer et al., 2012). Alternatively, metabolites are translocated via transporter proteins in the plasma membrane by an active transport mechanism (Baetz and Martinoia, 2014). Two families of membrane bound transporter proteins can be distinguished: ATP-Binding Cassette (ABC) and Multidrug and toxic compound extrusion (MATE) transporters. ABC transporters are called primary transporters that harness biochemical energy from ATP hydrolysis for transport of various substrates (Orelle et al., 2018), while MATE are secondary transporters which make use of the electrochemical differential over the plasma membrane to facilitate transport (Weston et al., 2012).

Detection of carbon and nitrogen rich components in the soil steers bacteria towards nutrient rich environments by sensing chemical gradients in the circumference. This directed movement is referred to as chemotaxis, a well-studied bacterial behavior (Bi and Sourjik, 2018; Colin and Sourjik, 2017). Locomotion in *E. coli* is established by rotating bundle forming flagella in the same direction, leading to a short linear movement, until the bacterium tumbles by rotating flagella in the opposite direction. Chemotaxis manipulates the duration of straight runs along chemical gradients, resulting in a net directed diffusion of the bacteria over a certain time span (Larsen et al., 1974).

Bacteria can sense chemical gradients by sensory protein complexes that are mainly located at the poles in case of *E. coli* (Yang and Briegel, 2020), existing of the receptor proteins CheW and CheA. CheW contains a scaffolding domain and modulates the activity of CheA upon ligand binding, and CheA is a histidine kinase (Parkinson et al., 2015). The mobile regulatory protein CheY is phosphorylated by CheA and switches the rotation direction of the flagellar motor. Dephosphorylation of CheY-P is carried out by CheZ, CheC or CheX, causing signal termination (Silversmith, 2010). In *A. brasilense* Ab-V5, the transcription of *cheZ* gene is induced by MBOA treatment, which causes movement in longer uninterrupted runs by inhibition of CheY activity, and exhibits a positive chemotactic response *in vitro* (Baatsen et al., 2025).

Another chemotaxis regulatory mechanism is constituted by methylation and demethylation of receptor proteins by the methyltransferase and methylesterase CheR and CheB respecively, altering its affinity for ligands by conformational changes (Kehry and Dahlquist, 1982). CheR transfers methyl groups to glutamate residues in the C-terminal domain of chemotaxis signal transducers, while CheB is able to remove them in the form of methanol (Kehry et al., 1984). The CheR and CheB system is much slower than the CheW, CheA and CheY mediated mechanism, allowing the modulation of bacterial movement according to temporal changes in environments (Kalinin et al., 2009; Yi et al., 2000).

Amino acids are principally perceived by Tsr and Tar receptors that show overlap in their downstream signaling pathway, via CheA mediated CheY phosphorylation (Berg, 2003). Besides being coupled by signalization pathway, those receptors also influence each other by a neighbor assisted mechanism and have similar methylation sites in receptor clusters (Li and Hazelbauer, 2005). Consequently, the combination of the stimulation of both receptors results in different responses than when stimulated separately. More specifically, for instance raising aspartate concentrations does not influence the time interval of tumbling by *E. coli*, also referred to as ‘perfect adaptation’ (Alon et al., 1999). Because ambient serine causes *E. coli* to switch its course slower by tumbling according to the concentration increase, the serine response is therefore not perfectly adapted (Berg and Brown, 1972). Now, when a background, constant serine concentration is applied, increase in aspartate makes *E. coli* tumble slower and hence the response to aspartate is no longer perfectly adapted (Wong-Ng et al., 2016). Perfect adaptation is of ecological relevance for bacteria when encountering swiftly altering peak concentrations of compounds while dwelling in aqueous environments (Celani and Vergassola, 2010).

3.3. Root attachment and biofilm

Once in close proximity to the roots, *Rhizobium, Pseudomonas, Azospirillum, Agrobacterium* and *Salmonella* share a similar two-step root attaching mechanism for anchoring to the root surface (Wheatly and Poole, 2018). The first step is characterized by reversible, loose binding of bacteria to the surface, where after bacteria tightly adhere and form aggregates in the second step of attachment. This second phase is marked by biofilm formation starting from 8 h after initial contact and taking up to five days for developing a mature biofilm (Viruega-Góngora et al., 2020a). This protective coating, mainly composed of a polymeric matrix of EPS (Costerson et al., 1995), provides PGPR with an advantage over free-living bacteria by being anchored in a nutrient rich and protective environment. Biofilms can contain diverse communities, which it grants protection against drought, ultraviolet radiation, extreme pH, pressure, antibiotics and more (Yin et al., 2019). In the following we will summarize the colonization mechanisms by those two phases in *A. brasilense, P. putida* and *P. fluorescens.*

Because both bacterial cells and root epidermal cells carry a net negative charge, bacteria need to overcome electrostatic repulsion in order to physically reach the root surface (Berne et al., 2015). Therefore, during the first phase, *A. brasilense* propels itself towards the root and makes contact with the surface using its polar flagellum, a non-specific and reversible interaction (Croes et al., 1993; Mora et al., 2008). Mutagenesis of the flagellin modification genes *flmA* and *flmB* of the strain *A. brasilense* Cd, resulted in non-motile cells that were incompetent in maize root adsorption and EPS and lipopolysaccharides (LPS) production, as a result of impaired polar flagellum assembly and hence defect in both attachment phases (Rossi et al., 2016). Similarly, in *A. brasilense* Sp245, bacteria with a non-functional polar flagellum and lateral flagella accumulated less biofilm biomass (Shelud'ko et al., 2019). In both the first and second phase of attachment, the polar flagella and outer membrane proteins on the cell surface of *Azospirillum* are involved in absorption onto the root and in aggregation with other bacteria (Burdman et al., 2001). When *Azospirillum* successfully attached to the root surface in the first phase, it is stimulated to proceed to the second phase which is marked by production of polysaccharide fibrils and aggregation of bacteria (Jofré et al., 2004). Factors that involve adherence in the irreversible second step in *Azospirillum* are polysaccharides rich in arabinose, LPS, outer membrane proteins and lectines (De Troch and Vanderleyden, 1996; Michiels et al., 1991). *A. brasilense* Sp245 mutated in the *mmsB1* and *fabG1* genes, were impaired in LPS production and showed reduced hydrophobicity, cell aggregation and mature biofilm biomass (Shumilova et al., 2016). In general, aggregated bacteria start forming biofilm producing micro colonies in the first two days after initial colonization. After 3–5 days a mature biofilm is established, with an average thickness of 28–39 μm on the surface of a glass coverslip, depending on the strain (Viruega-Góngora et al., 2020a). Root colonization patterns are remarkably different among *A. brasilense* strains. While Sp245 is able to penetrate the root epidermis and internally colonize root hairs and vasculature, colonization by *A. brasilense* Sp7 is limited to the root surface (Schloter and Hartmann, 1998; Vande Broek et al., 1998a).

Native soil bacteria may exploit MBOA as a cue associated with roots of nearby grass plants, for identifying relevant plant hosts. For instance, in the common cereal colonizing *A. brasilense* Ab-V5, MBOA enhanced biofilm formation on *A. thaliana* roots, besides exhibiting a chemotactic response *in vitro* (Baatsen et al., 2025). In contrast with more elaborate biofilm formation of Ab-V5 when treated with 0.05 mM MBOA (Fig. 4), Pf-5 biofilm formation in MBOA treatment was not significantly different from the control treatment (Fig. 5) (Baatsen, 2024) (supporting experimental details are described in *Supplementary Materials*) and did not display a chemotactic response (Baatsen et al., 2025).

In *P. putida* and *P. fluorescens*, pili have a role in motility and primary attachment. Another protein, the outer membrane porin F (OprF), partakes in both steps of root attachment. Mutagenesis of the *oprF* gene reduced the capacity to loosely adhere to roots (Crespo and Vervalde, 2009; De Mot and Vanderleyden, 1991; Vesper, 1987). Both species possess two large adhesion proteins LapA and LapF that irreversibly attach the bacteria to the root and mark the onset of colony formation (Fuqua, 2010). Furthermore, biosynthesis of cellulose fibrils ensures surface colonization, strengthening the biofilm by interaction of the LPSs and the cellulose matrix, a characteristic widely spread among *Pseudomonas* species (Spiers et al., 2003; Ude et al., 2006). Despite the similarities in root attachment mechanisms, *P. putida* and *P. fluorescens* differ in the way they occupy the surface of the root. *P. putida* produces a thick continuous biofilm spreading over the entire root, while biofilm from *P. fluorescens* and *P. protegens* is thinner and localized around

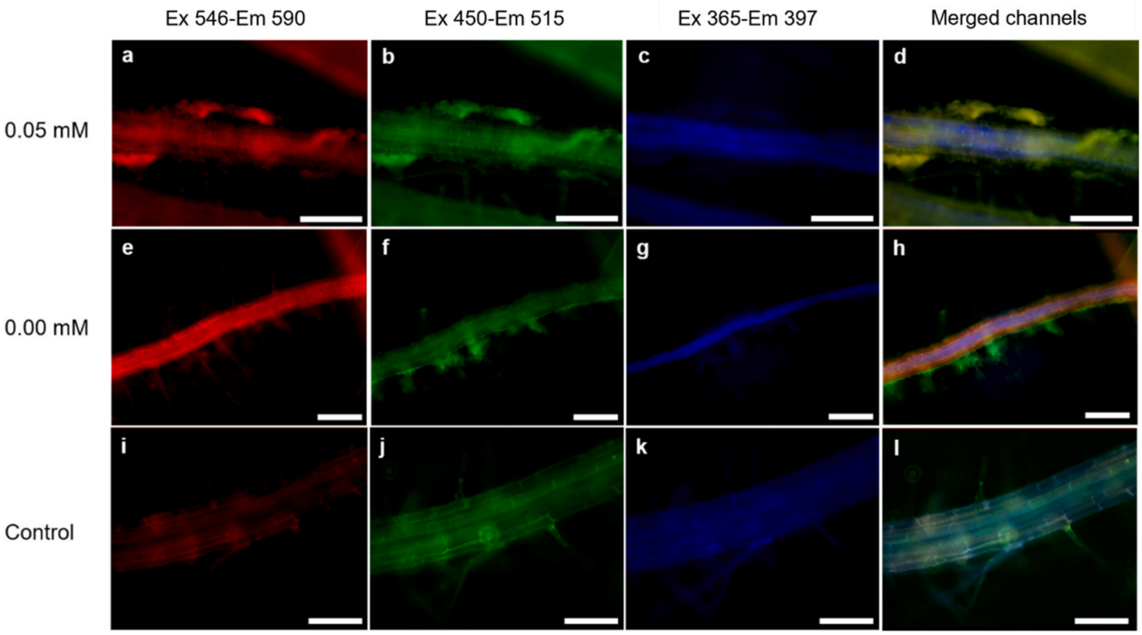


Fig. 4. Epifluorescence microscopy of *A. thaliana* roots inoculated with *Azospirillum brasilense* Ab-V5. **a - d**: 0.05 mM 6-methoxy-2-benzoxazolinone (MBOA) treatment. **e - h**: 0.00 mM MBOA treatment; **i - l**: control treatments without bacteria. *Arabidopsis* roots were treated with 2 μg/mL Nile Red prior microscopic analysis. Nile Red is a lipophilic stain that has an emission wave length of around 540 nm when bound to neutral lipids and around 650 nm when bound to polar lipids. Autofluorescence caused by lignin emission is observed in the blue channel (Ex. 365 – Em. 397). Scale bars indicate 100 μm (**a - h**), and 50 μm (**i - l**).

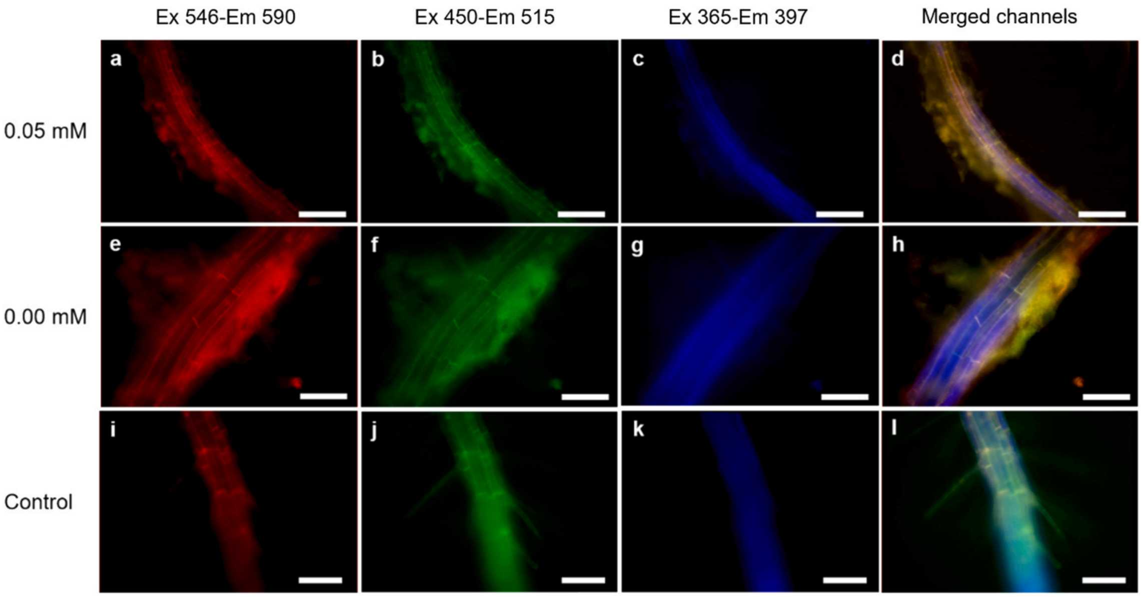


Fig. 5. Epifluorescence microscopy of *A. thaliana* roots inoculated with *Pseudomonas protegens* Pf-5. **a - d**: 0.05 mM 6-methoxy-2-benzoxazolinone (MBOA) treatment; **e - h**: 0.00 mM MBOA treatment; **i - l**: control treatments without bacteria. *Arabidopsis* roots were treated with 2 μg/mL Nile Red prior microscopic analysis. Nile Red is a lipophilic stain that has an emission wave length of around 540 nm when bound to neutral lipids and around 650 nm when bound to polar lipids. Autofluorescence caused by lignin emission is observed in the blue channel (Ex. 365 – Em. 397). Scale bars indicate 100 μm (**a - d**) and 50 μm (**e - l**).

fissures (Baatsen et al., 2025; Bloemberg et al., 2000; Bloemberg and Lugtenberg, 2004). The environmental conditions that stimulate biofilm formation in *Pseudomonas* is strain dependent: where *P. protegens* produces biofilm in nutrient rich environments, *P. fluoresens* and *P. putida* are stimulated to form biofilm in nutrient poor conditions (Baatsen et al., 2025; Ueda and Saneoka, 2015).

Colonizing host tissue, PGPR undergo a transition from a motile lifestyle in bulk soil, to a sessile one when adhering to the root surface. Despite root colonization being a complex process clearly marked by elaborate regulatory mechanisms, there does not seem to be a genetic reprogramming behind the transition to growth in biofilms (Sauer et al., 2002; Whiteley et al., 2001). The bacteria rather seem to adapt cellular motility and adhesion in function of environmental parameters, and the production of biofilm is dependent on nutrient availability (Arruebarrena Di Palma et al., 2013; Shelud'ko et al., 2020a; Ueda and Saneoka, 2015; Wang et al., 2017). As intrinsic features of root colonization, chemotaxis, motility and biofilm formation are highly interconnected and subject to antagonistic regulation (Besharova et al., 2016;

Guttenplan and Kearns, 2013; Prüß, 2017). For example, the highly conserved Che1 chemotaxis signal transduction pathway regulates rotation direction of the flagellar motor (Wuichet and Zhulin, 2010). Apart from chemotaxis, Che1 also regulates flocculation and cell adhesion (Bible et al., 2008, 2012; Siuti et al., 2011a). Mutants in the response regulator CheY, which is a component of the Che1 chemotaxis system, clump and flocculate more and produce more biofilm which enhances attachment on wheat roots (Bible et al., 2008, 2012; Siuti et al., 2011a). Hence, upregulation of the suppressor CheZ, phosphatase of CheY, has a positive response on both chemotaxis (Baatsen et al., 2025) and on cell adherence. In conclusion, chemotaxis signaling regulation is besides chemotaxis responses involved in other bacterial behaviors.

3.4. Plant-soil feedback

Considering the relatively large amount of plant metabolites released in the soil, plant hosts are main drivers for soil community structuring. Up to 11 % of the host net fixed carbon plus 10–16 % of fixed nitrogen metabolites are set free by rhizodeposition (Jones et al., 2009; Pausch and Kuzyakov, 2018; Sasse et al., 2018). Apart from metabolites, in maize plants, root cap border cells are detached that remain active for at least a week in the soil (Vermeer and McCully, 1982). After a substrate-driven accumulation of a candidate population for rhizosphere colonization, follows a host genotype dependent selection of epiphytes and endophytes competent for colonizing the rhizoplane and interior of the host plant (Bulgarelli et al., 2013). This stringent filtering determines the difference in the bacterial density between the rhizosphere containing around 10^7–10^9 colony forming units (CFU) g^{-1} (Benizri et al., 2001) and 10^5–10^7 CFU g^{-1} (Bais et al., 2006; Benizri et al., 2001) in the rhizoplane. The genotype specific selection is based on the innate immune system of plants which blocks pathogen invasion upon recognition of microbial-associated molecular patterns (MAMPs) by pattern recognition receptors at the cell surfaces (Jones and Dangl, 2006). To engage in a symbiotic relation, PGPR need to be able to evade or suppress the host immune response, similar to pathogenic microbes (Boller and He, 2009). One way to achieve this is by production of auxin by PGPR which inhibits salicylic acid (SA) signaling, and suppresses innate immune response (Kunkel and Harper, 2018). In *Bacillus velezensis,* auxin production is indispensable for suppressing plant immune response and reactive oxygen species (ROS) production, which is induced at the onset of root colonization (Tzipilevich et al., 2021). Yet a lot remains to be uncovered regarding the exact mechanisms of evading the plant immune response by PGPR.

Plants help bacteria navigate the complex soil matrix via release of metabolites in the soil. BXs for instance, have a strong selective effect on bacterial strains in the rhizosphere. Thoenen and co-workers correlated the MBOA tolerance of soil bacteria to their abundance in the rhizosphere and identified this relation as potentially an important mechanism for determining the root microbiome organization (Thoenen et al., 2023b). At the same time, *Azospirillum* improves yield of BX producing grass species the bacterium is often associated with (Camilios-Neto et al., 2014; Dehghani and Mostajeran, 2020; Dobbelaere et al., 2001; Hungria et al., 2010; Marques et al., 2020; Mehnaz and Lazarovits, 2006; Michiels et al., 1991; Oliveira et al., 2017; Pereg et al., 2016; Renoud et al., 2022; Rossi et al., 2016; Vande Broek et al., 1998a; Walker et al., 2011b) and emerged as the most sensitive PGPR to MBOA in our studies (Baatsen et al., 2025). Hence, in this bacterium the sensitivity to MBOA may reflect its role in cell signaling. The latter statement was supported by the high proportion of differentially expressed genes related to signal transduction and gene regulation when *A. brasilense* Ab-V5 was treated with MBOA (Baatsen et al., 2025). Furthermore, BX production in maize plants promotes the prevalence of methylophylic, *Proteobacteria* such as Ab-V5, and generally represses the bacterial genera *Flavobacteriaceae* and *Comamonadaceae* (Cadot et al., 2021a; Cotton et al., 2019a; Hu et al., 2018a).

Somewhat similar to the relation between MBOA tolerance and bacterial abundance (Thoenen et al., 2023b), also is a positive correlation between the capacity to detoxify MBOA and pathogenicity in fungal pathogens (Yue et al., 1998b), with MBOA being the most effective BX derivative for suppressing conidia germination of *Bipolaris maydis, Curvularia lunata* and *Alternaria alternata* (Oikawa et al., 2004). BX release in the soil has a strong influence on root-associated fungal communities and contributes to disease suppression by affecting plant pathogens such as *S. cylindrosporus* and *I. macrodidyma* (Cotton et al., 2019a). Fungal communities were remarkably different from BX-producing and BX-deficient maize plants, particularly in their abundance of fungal species belonging to the genera *Ascomycota* and *Glomeromycota* (Cotton et al., 2019a; Hu et al., 2018a). Furthermore, BX producing maize plants harbor more BX tolerant fungal endophytes and other more potentially harmful fungal pathogens (Cadot et al., 2021a) than BX deficient maize plants (Saunders and Kohn, 2008), suggesting in concert with results from our studies (Fig. 2), that BX production may stimulate tolerance in fungal endophytes.

Apart from the toxic effect on several bacterial, fungal and insect species, in maize plants, BXs supposedly evoke a resistance inducing soil microbiome against the fall armyworm (*Spodoptera frugiperda*). Hu et al. (Hu et al., 2018a) achieved restoration of resistance inducing activity by complementation of soil from *bx-1* mutants with MBOA. Resistance against the fall armyworm was achieved through MBOA-correlated structuring of the microbiome, and lasted for subsequent generations of maize plants. Being composed of an enormous number of microbial species, it is however hard to prove that this effect stems from MBOA application alone which may possibly stimulate the release of other organic compounds in other organisms, by acting as a signaling molecule.

Recently, we showed that MBOA treatment has a substantial impact on bacterial physiological processes. Based on transcriptomic data and *in vitro* studies, it was demonstrated that *A. brasilense* Ab-V5 is attracted to MBOA via a positive chemotactic response by stimulation of a response regulatory protein CheZ within the Che1 chemotaxis signal transduction pathway (Baatsen et al., 2025). Interestingly, the regulator protein CheZ, at the same time reportedly promotes clustering and adherence (Bible et al., 2008, 2012; Siuti et al., 2011a), though our transcriptomic analysis points out that biofilm synthesis is downregulated in concert with other genes related to symbiotic processes. Many genes related to signal transduction, gene regulation and cellular respiration were affected, leading to the conclusion that in this case MBOA treatment causes metabolic rewiring and that MBOA acts as a signaling molecule triggering this process. Pf-5, which is a PGPR isolated from cotton which does not produce BX in contrast to cereals host to Ab-V5, allowed the identification of few genes and was little affected by MBOA treatment (Baatsen et al., 2025). Hence, it seems that MBOA production sensitizes and evokes physiological responses in bacteria adapted to MBOA, which can promote recruitment to the rhizosphere.

Interestingly, once *Azospirillum* manages to colonize maize roots, it inflicts a strain specific effect on the secondary metabolism of the host plant, increasing the relative content of BX derivatives according to the *Azospirillum* strain of the inoculum (Walker et al., 2011c). Similarly, inoculation of maize with *P. fluorescence* MZ05 augments DIMBOA content in the leaves by stimulating BX biosynthesis genes, which significantly impacts disease tolerance against the foliar pathogen *Setosphaeria turcica* (Zhou et al., 2020b). Thus, plants can manipulate the soil microbiome with specialized metabolites such as BX, while PGPR in turn influence metabolism of those host synthesized metabolites. Furthermore, *A. brasilense* Ab-V5 displayed a positive chemotactic response to MBOA (Baatsen et al., 2025) and possibly sets in motion a positive feedback loop. In consequence, release of BX metabolites by plants harbors the potential to establish a circular feedback response by recruiting PGPR and indirectly stimulating its own biosynthesis.

4. Benzoxazinoids in agricultural applications

The increase of atmospheric carbon dioxide and global average temperatures each year account for more frequent extreme weather events that lead to decreasing crop yield and productivity (Mirón et al., 2023). With a 5 % decrease of arable land yearly (Borrelli et al., 2020), increasing the efficiency of land use and crop cultivation pose viable solutions for keeping up with the current and future food demands, in concert with implementing complementary socio-political measures.

Host plant genetic factors account for only about 5 % of the variation in rhizosphere microbial communities, with physicochemical factors being the main drivers of root-associated microbiome structure (Bulgarelli et al., 2013; Hacquard et al., 2015). Therefore, plants manipulate soil characteristics in favor of PGPR by secretion of root exudates, which has a genotype specific influence of the secreting plant on the soil (Sasse et al., 2018). Release of BXs accounts for the same amount of variation on soil microbial community composition as the genetic aspect, and exerts a strong effect on soil fungi (Cadot et al., 2021a). BX biosynthesis imposes major changes in root metabolic readout, with emphasis on flavonoid anabolism and regulates root associated microbes (Cotton et al., 2019a). Since the composition of the root associated microbiome is strongly dependent physiochemical factors, ectopically introducing a MBOA regime can imply a harsh disturbance of ecological interactions in microbiomes that are not adapted to BXs. Therefore, elaborate assessments on biosafety are paramount to implementing BXs in agricultural scenarios, which requires the acquisition of relevant data and expertise.

4.1. Methods for studying BX-PGPR interactions

Regardless of successful endeavors aiming to understand BX metabolite interactions and metabolic pathways, many questions remain unanswered in relation to the mode of action and genetic regulatory mechanisms. Furthermore, scientific understanding of BX–PGPR interactions is only at its onset. Undoubtedly, the challenge in exploring this field lays in the enormous amount of biotic and abiotic factors present in the soil. Therefore, powerful resources for scrutinizing BX–PGPR interactions can be found within omics data, enabling the analysis of genetic and phenotypic plasticity within bacterial communities exposed to BX treatments.

To decipher bacterial communities, metataxomics and metagenomics allow the identification, quantification and functionality of bacterial communities, surpassing the limitation of analyzing strains exclusively cultivable under laboratory conditions (Chetty and Blekhman, 2024). For analyzing microbiome community structure, either shotgun metagenomic sequencing or 16S rRNA sequencing are commonly used (Sharpton, 2014). In case of shotgun sequencing, the total DNA from environmental samples is first extracted, then digested and sequenced. Via computational software, fragments are aligned with reference genomes to identify and quantify microbes present in the environmental sample (Sharpton, 2014). During 16S rRNA sequencing, only the variable region of the 16S rRNA amplicon is sequenced for identification and quantification of bacterial taxa. The comparison of taxa present in different treatments can be computed using various programs executable via R or Python (Knight et al., 2018).

Along metagenomics data, integration of other layers of omics data forms a solid foundation for studying microbiomes. For example, metatranscriptomics data relays information about the abundance of gene transcripts, offering insight in the functional roles present in environmental samples (Shakya et al., 2019). Furthermore, metabolomics data generated by mass spectrometry by matching the mass-to-charge readout with reference databases, is indicative of cellular processes (Chong and Xia, 2017), while metaproteomics, typically analyzed by mass spectrometry as well, allows the functional characterization of the microbiome sample. By comparing with metagenomic and metatranscriptomic data, proteomics data reveals translational and post-translational regulation (Peters et al., 2019). Different layers of omics data offer complimentary information, allowing to uncover relationships among data sets, for instance correlating the abundance of strains, biological functions and cellular processes. Integration of different data sets can occur at various steps during data processing, for instance while inferring bacterial taxon abundancies (Heintz-Buschart et al., 2016) or during data preprocessing (Ugidos et al., 2022). Yet, many bioinformatics tools exist for assisting this computationally complex task (Muller et al., 2024; Subramanian et al., 2020).

From meta-omics data, the ecological relevance of Operational Taxonomic Units (OUT) can be assessed by network interference (Katherine and Jose, 2022; Moscardó García et al., 2025). Leveraging computational models, this allows the identification of keystone species, the prediction of relations between taxa and alternative community configurations (Faust and Raes, 2012, Ferrarezi et al., 2023). Moreover, existing microbial interaction networks can be modified, or new interaction networks can be established, through dynamic network modeling. This approach accounts for adaptive changes in microbiome structure and reduces environmental heterogeneity, thereby facilitating the design of synthetic microbial consortia (Garcia and Kao-Kniffin, 2020). Finally, microbial interaction networks can be validated using physiological assays prior to testing synthetic consortia in field trials.

Most relevant data is generated from greenhouse experiments, or even from field trails. Exactly because of the many varying components the soil naturally possesses, such experiments render pertinent data that can be extrapolated easier (Brunetti and Hageman, 1976; Khorasani et al., 2010; Mahalmani et al., 2022). Another interesting tool for uncovering BX signaling mechanisms in bacteria is the application of transposon insertion sequencing (Fabian et al., 2020; Sivakumar et al., 2019). In short, bacteria able to survive on medium supplemented with a lethal dose of BXs after being subjected to random transposon mutagenesis across the genome, are subsequently sequenced. Key components leading to BX tolerance can then be identified by pinpointing genomic regions consistently lacking mutations in the sequenced population.

Characterization of PGPR by studying bacterial characteristics related to plant-microbe interactions are summarized in Table 2. To study bacterial morphology and spatial organization, microscopy-based analyses can deliver ultra-high-resolution images using scanning electron microscopy or enable the identification of specific bacteria expressing fluorescent markers through confocal laser scanning microscopy (Shelud'ko et al., 2020b; Viruega-Góngora et al., 2020b). An overview of microscopic techniques for studying bacterial motility with advantages and disadvantages are summarized in Palma et al. (2022); Palma et al. (2022). Additionally, bacterial motility and morphology can be assessed by plate assays and capillary assays offering straight forward quantitative data (Abe et al., 2016; Adler, 1972; Luu et al., 2013). To analyze chemical signaling, metabolite exchange and cross-feeding, mass spectrometry imaging can provide high-end data, specifically when coupled with transcriptome studies (Dunham et al., 2017).

4.2. BX implementation strategies

From a practical point of view, the gathered knowledge preferably mounts to field application of BXs to be leveraged as a versatile supplement for boosting crop productivity. After careful assessment of the ecological risks BX supplementation or conditioning in agricultural systems can cause, different strategies may be adopted for implementing BXs for crop cultivation purposes. An interesting line of thought is to bring MBOA application in practice by inoculation of biofertilizers with MBOA encapsulated in alginate, permitting slow release through diffusion or erosion in the environment (Flores Céspedes et al., 2013; Young et al., 2006). The advantage is, that over time MBOA release will diminish, mimicking the decay of BX production in maize (Cambier et al., 2000; Köhler et al., 2015a). Strategies for BX application in agricultural settings are summarized in Fig. 6.

Table 2
Summary of methods for studying bacterial features related to plant-microbial interactions.

Bacterial feature	Bacteria	Method	Reference
Motility	*Pseudomonas putida*	Swim plate assay	Luu et al. (2013)
Chemotaxis	*Pseudomonas putida*	Gradient plate assay	Luu et al. (2013)
Chemotaxis	*Escherichia coli*	Capillarary assay	Adler (1972)
Chemotaxis	*Salmonella enteriac*	Capilary assay combined with video microsocpy	Abe et al. (2016)
Attachment	*Azospirillum brasilense*	Attachment assay	Siuti et al. (2011b)
Biofilm	Various	96-Well plate assay	Kwasny and Opperman (2010)
Biofilm	*Azospirillum brasilense*	Microscopy-based assays	Shelud'ko et al., 2020b; Viruega-Góngora et al., 2020b
Root colonization	*Azospirillum brasilense*	Histochemical analysis *gusA* reporter plasmid	Vande Broek et al. (1998b)
Quorum sensing	*Agrobacterium tumefaciens*	*A. tumefaciens* NTL4 reporter strain	Tomohiro et al. (2008)

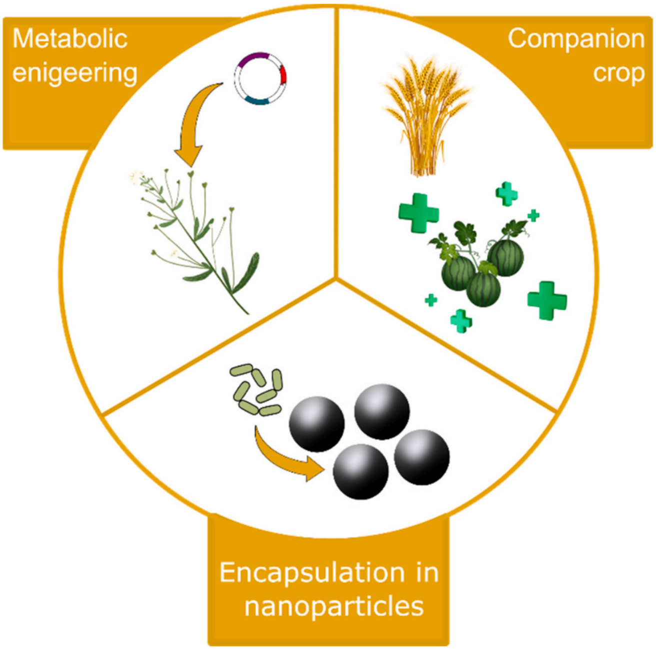


Fig. 6. Strategies for benzoxazinoid (BX) Applications in Agriculture. Three strategies are proposed to apply the use BXs in agricultural settings. Metabolic engineering and encapsulation with BX have so far not been implemented in crop cultivation. Conditioning of the soil by cultivation of crops with a companion crop or via crop rotation with BX-producing cops, has shown beneficent effects.

Alternatively, non-BX-producing crop plants can be metabolically engineered to ectopically synthetize BXs. Evidently, the hallmark for boosting herbivore tolerance was achieved by heterologous biosynthesis of the renowned insecticidal Cry proteins from *B. thuringiensis* in various crop plants (reviewed by Bravo and coworkers (Bravo et al., 2011)). Besides, successful endeavors to integrate transgenic metabolic pathways for improving pest tolerance include the biosynthesis of dhurrin in *Arabidopsis thaliana* and transfer of *A. thaliana* glucosinolates into *Nicotiana benthamiana* (Møldrup et al., 2012; Tattersall et al., 2001). A less successful effort has been made to integrate the DIBOA biosynthetic pathway in *A. thaliana*, by cloning six biosynthesis genes, BX1 – 5 and BX8 (Abramov et al., 2021). Since this pathway branches from indole 3-glycerol phosphate and runs parallel with tryptophan biosynthesis, metabolic stress caused the transgenic *A. thaliana* plants to turn into dwarfed phenotypes by lack of precursor molecules for tryptophan biosynthesis. Hence, in specific cases, promoter activity of transgenic enzymes has to be tightly regulated in order not to compromise yield of transgenic crop plants.

A more traditional yet effective approach that mitigates the metabolic cost for crops to produce BXs, is the implementation of crop rotation. Continuous cultivation of a single crop causes depletion of nutrients and accumulation of species specific phytopathogens in the soil (Dias et al., 2015), while crop rotation profits from plant-soil feedback improving soil microbiota diversity, which in turn enhances nutrient availability, pest control and plant growth (Dias et al., 2015). Hence, plant-soil feedback is of paramount importance to plant health (Teste et al., 2017a) and can be a great resource for improving agricultural efficiency and productivity (Mariotte et al., 2017). Soil conditioning with BXs proved to be effective for biocontrol of *Fusarium oxysporum* f. sp. *niveum* in the soil and controlling *Fusarium* wilt on watermelons by co-cultivating the BX producing wheat as companion crop (Xu et al., 2015b). Similarly, cultivation of maize prior to wheat resulted in a 4 % yield increase of the latter crop, predominantly attributed to repelling insect pests (Gfeller et al., 2023c). Finally, BX production and conditioning of soil with MBOA results in a generation of more tolerant maize plants against the fall armyworm larva which was correlated with restructuring of the soil microbiome (Hu et al., 2018a).

4.3. *Framework for the implementation of BX in agriculture: perspectives and limitations*

Harnessing BXs in agriculture requires going through a series of fundamental steps. Depending on the crop to be cultivated, optionally, suitable PGPR can be selected as bioinput that stimulate BX metabolism in the host plant (Walker et al., 2011a; Zhou et al., 2020a), or that provide health benefits to the crop in addition to BX conditioning. Either commercially available PGPR can serve this purpose, or new PGPR strains can be discovered through rigorous screening in laboratory settings. In the latter case, bacteria from environmental samples are isolated, typically from the plant rhizosphere and extensively tested. The researcher might consider strains that excel consistently in a range of PGP-properties in different soil types. However, one bacterium that outperforms all others in every soil type and crop cultivation condition, does not exist. Nevertheless, it is possible to create a synthetic community in which bacteria adopt specific roles, rendering a versatile and resilient microbial consortium (Anees et al., 2020; Chen et al., 2014). As explained in 4.1., via network interference compatible members can be predicted by computational models, increasing the efficiency of composing a synthetic community. Depending on specific agronomical needs, this can be accurately done by agroecosystem engineering, that enables tailoring agricultural practices to specific agroecological conditions (Bano et al., 2021; Fujiwara et al., 2023). Based on multi-omics data, first a causal network needs to be generated to avoid correlation of data obtained by coincidence. This can be accomplished by LiNGAM software under some assumptions (Shimizu et al., 2006). The outbreak of pathogens in the soil for instance, can in this way be accommodated by introducing keystone species that stimulate bioprotection (Toju et al., 2018).

The second hallmark includes assessing the effect of BXs on the compatibility of crop and microbial inoculum. Keeping other cultivation parameters constant, a BXs gradient must be tested by evaluating the microbial structure of the soil microbiome at regular intervals in greenhouse experiments. When the concentration of BXs to be applied has been adjusted, the effect on crop yield and plant growth must be assessed and the BX concentration can be further improved to ensure a dose that has both a positive impact on the native crop rhizobiome and improves yield (Gómez-Merino et al., 2022; Leitão et al., 2024). As various physio-chemical parameters influence BX activity and composition of the soil microbiome, the BX implementation strategy and PGPR or consortium needs to be tested in various soil types and under different cultivation conditions to yield a robust growth benefit.

Next, the chosen set-up is tested in complex and realistic field trails. This includes evaluating compatibility with chemical inputs, irrigation systems and soil types to comprehend the effectivity and find limitations under field management practices. On top of that, the environmental impact and off-target effect on long-term application must be assessed by conducting field trails over longer periods of sustained BX application. The development of the carrier material must be carefully considered to ensure sufficient nutrition and water retention for improving the viability of the inoculum, and needs to be of a biodegradable material to limit environmental impact (Sivaram et al., 2023). Once the biostimulant formulation has been designed it must be registered to comply with regulatory standards concerning biosafety and effectivity, before being launched in the market and becoming commercially available.

Considering the high reactivity of BX metabolites as discussed in section 2.1 and 2.3, it is imperative that elaborate investigations be conducted on the biosafety of introducing BXs in an agricultural setting. BXs have a strong and long-lasting ecological impact, specifically the impact on the soil microbiome can cause complex soil feedback, altering physio-chemical parameters (Bever et al., 2013b; Cotton et al., 2019b; Gfeller et al., 2023b; Hu et al., 2018a; Teste et al., 2017b). Moreover, despite elaborate evidence of BXs biosynthesis pathways, knowledge about transcription regulation of BX biosynthesis genes is very scarce (Gao et al., 2019; Stahl, 2022). Regulation of BX biosynthesis may relate with the physio-chemical properties of the local soil environment which, on top of that, may interfere with the reactivity and half-time of BX compounds. For instance, the halftime of BXs in strongly influenced by the ambient pH (Table 1), which varies substantially among soil types (Regasa et al., 2025; Zhang et al., 2023).

Another point concerns adaptation of microorganisms to antibiotic compounds such as BXs. Over prolonged application periods spanning many seasons of crop cultivation, this may lead to the evolution of tolerant strains. Such an adaptive response was demonstrated with our experiment on exposure of *Fusarium* strains isolated from different host plants to varying MBOA concentrations, where *Fusarium* from non-BX producing hosts were more susceptible than *Fusarium* isolated from BX-producing maize plants (Fig. 2). Accordingly, the effectivity of BX conditioning of the soil may decrease over time, resulting in a consensus BX-resistant soil-microbiome. In the same line of thought, Thoenen and coworkers (Thoenen et al., 2023a) discovered that root bacteria native to the root environment of maize were more tolerant to BXs than bacteria isolated from the *Arabidopsis* roots, and showed that BX-tolerance was positively correlated with their abundance on BX-producing roots. This illustrates why BX supplementation to non-BX producing crops should be precedented by thorough evaluation of the plants' microbiome at predetermined time intervals, assessing unpredicted disturbances in the soil microbiome equilibrium.

Alongside this, there are many reasons for PGPR not to perform consistently in certain agricultural systems. Starting from the screening of bacterial strains isolated from environmental samples, bacteria may be misjudged because of results from *in vitro* tests that do not translate to potted experiments, or the other way around (Cardinale et al., 2015; Palková, 2004). Furthermore, successful inoculation depends on the survival rate and propagation in the crops' rhizosphere. There are many mechanisms that influence the viability of the inoculum, related to product storage and transportation, and to the suitability of the PGPR. As stipulated before, PGPR performance can be dependent on certain conditions, and consequently, be limited by certain soil parameters such as salinity and pH. Moreover, the soil comprises a highly dynamic ecosystem, sensitive to constantly alternating environmental conditions (Jansson and Hofmockel, 2020). Trailing behind climate induced changes in the soil, bacteria either manage to adapt or perish (Wu et al., 2019). Related to this, PGPR are not always compatible with the native microbiome because of the direct inhibitory effects of metabolites or competitive bacterial strains better adapted to native soil conditions. Additionally, some PGPR exhibit narrow host specificity, resulting in a mediocre performance of top *in vitro* candidates, under field conditions (Tabassum et al., 2017). On top of those reasons for unstable performance, many farmers have a history of excessive use of agrochemicals that affect soil characteristics, or have a direct toxic effect on the inoculum (Dangi et al., 2017).

5. Concluding remarks

The soil is a complex matrix housing an enormous number of microorganisms, unique in every cubic inch of the planet. On top of that, soil types differ in physio-chemical characteristics which influence the soil microbiome. Therefore, the optimization of inoculation conditions for bio-fertilizing bacteria is inherently dependent on the unique abiotic and biotic factors that characterize agricultural environments. On the other hand, the optimal growth conditions for a certain crop, may prove to be suboptimal for another plant species. For instance, BX production by maize enhances soil conditions that promote plant health (Cotton et al., 2019a; Hu et al., 2018a), However, in crops lacking BXs, these benefits may not arise from exogenous BXs, which can exert allelopathic effects on certain species (Rice et al., 2012; Schulz et al., 2013; Tabaglio et al., 2008; Wouters et al., 2016). Hence, each crop requires an individual study to evaluate the effect of MBOA on plant physiology; on its associated microbiome and its feedback on plant productivity.

In essence, bacterial root colonization is a complex event involving various intertwined mechanisms starting from chemotaxis and extending to communication via quorum sensing, root attachment and biofilm production. This sequence of events is essential for many plant-beneficial bacteria to apply their growth promoting properties to the host plant. The success rate of bacterial root colonization is highly dependent on how well the bacteria is suited to abiotic and biotic factors of the soil. Hence, there are many steps within this process where BX application can improve successful microbial inoculation.

Bearing in mind the cumbersome legislative procedures and ethical issues associated with genetically modified crop plants, so far, successful BXs application in agricultural systems has principally been exploited in the form of crop rotation or soil conditioning with BXs (Gfeller et al., 2023c; Hu et al., 2018a) and by co-cultivation with a BX-producing companion crop (Xu et al., 2015b). Those examples are proof of concept that MBOA treatment of the soil can improve crop cultivation by leveraging soil feedback.

However, studies on the effects of BXs on bacterial physiology are still scarce, despite the growing availability and commercial use of PGPR in biofertilizer formulations. In plants however, early studies on BXs primarily focus on their chemistry and their application as an agrochemical, harnessing its allelopathic effect. In the last decade, research on BX has been rejuvenated, shifting its emphasis towards implications for the root microbiome of crops. Despite the substantial unexplored potential of BXs, emerging research shows promise for optimizing sustainable crop management. Recent findings open various avenues for future investigation, such as testing the inoculation success and soil compatibility of microbial inoculants in MBOA-amended coatings; exploring the impact of ectopic MBOA application on crop plant microbiomes alongside metabolic engineering; or conducting fundamental research on diverse PGPR to uncover the core molecular mechanisms influenced by MBOA in bacteria.

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CRediT authorship contribution statement

Jeroen Baatsen: Conceptualization, Formal analysis, Investigation, Methodology, Writing – original draft. **João L. Azevedo:** Funding acquisition, Resources, Supervision. **Maria C. Quecine:** Conceptualization, Data curation, Funding acquisition, Methodology, Resources, Supervision, Writing – review & editing.

Declaration of competing interest

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

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Glossary

Microbiome The community of microorganisms such as bacteria, fungi and viruses living in a specific environment
Rhizobiome The microbiome associated with plant roots
Primary metabolite Compounds that are essential to cell homeostasis and are indispensable for growth, development and reproduction
Specialized metabolite Metabolites with a specific function that are not essential for the organisms' survival. Often playing part in virulence, defense or attraction of symbionts
Benzoxazinoids Plant-produced specialized metabolites, that play a role in plant defense in areal parts and in the roots
Biotic factor The components of an ecosystem that are governed by the living organisms within that ecosystem, their direct and indirect interactions
Abiotic factor All non-living parameters that influence an ecosystem such as temperature, pH, salinity and humidity
Plant-soil feedback The influence of plants on biotic and abiotic factors in the soil and its effect on other plants or the next progeny of plant in return
Allelopathic molecule A plant-derived molecule that has an either positive or negative effect on plant-growth of another plant
Nitrogen fixation The conversion of atmospheric nitrogen into ammonia, which can be metabolized by plants and microbes. Bacteria capable of fixing nitrogen often live in association with plant roots and are termed ‘diazotrophs’
Symbiosis Intimate relationship between organisms, can be of a positive, negative or neutral nature
Pathogen A microorganism that can cause disease
Fertilizer Compounds that have the purpose to enrich the soil in nutrients. They often contain growth limiting nutrients such as nitrogen and phosphor. Biofertilizers can be composed of beneficial microbes
Agrochemical Chemicals used in the agroindustry, including fertilizers, pesticides and more
Cultivar A plant line that has been bred and selected because of a specific set of characteristics that allows better growth in a certain environment, that confers disease tolerance or in general renders higher yield
β-glucosidase Enzyme that hydroxylizes the β-glucosyl bond, breaking down complex sugars into simple sugars
Vacuole Organelle of the plant cell that exerts a positive pressure (turgor pressure) and is used for storage
Defense priming Triggering a state in plants that enables it to respond faster to pathogen attack
Biocontrol Method of controlling pests by the use of other organisms, by introducing predators, herbivores or antagonistic microbes
Endophyte Often bacteria or fungus that manifests at least for part of its lifecycle inside a plant's tissue
Quorum sensing Means of communication common in bacteria, depending on cell density. By being receptive to auto inducer molecules, that induce their own biosynthesis, bacteria can monitor the cell number of their population. Many physiological responses are regulated by quorum sensing such as biofilm formation and release of toxins
Auto inducer molecule A molecule that can be perceived and stimulate its own biosynthesis in bacteria. Several bacterial behaviors are controlled by genetic regulation depending on the concentration of auto inducer molecules, when trespassing a certain threshold
Flagella Proteinaceous appendixes used by bacteria for locomotion. Typically, bacteria can possess several long flagella located at the poles, or they can have many small flagella dispersed over the cell surface
Induced systemic resistance Immune response in plants triggered by bacteria and fungus that leads to an elevated defense response in the whole plant. This immune response is mediated via jasmonic acid and ethylene signaling
Nodules Specialized root structures formed through endosymbiosis with Rhizobia. Nodules contain nitrogen-fixing rhizobia in bacteroid form, sealed from oxygen to provide optimal conditions for the nitrogenase enzyme
Biofilm A matrix rich in polysaccharides, lipids, proteins and external DNA produced by bacteria and fungus that forms a protective film against environmental factors. Biofilms can contain diverse microbial communities and are often an important virulence factor
Mycotoxin A toxin produced by fungus
Chemotaxis Directed movement of bacteria in response to a concentration gradient of a molecule. A positive chemotactic response leads to attraction, while a negative chemotactic response leads to repulsion of a bacteria to a substance
Perfect adaptation The capacity to return to the initial state after being activated by a persistent external stimulus
Rhizodeposition The release of molecules in the soil by plant roots
Rhizoplane The interface between the root surface and the soil
Crop rotation Agricultural system that alternates the cultivation of crop types during different seasons of the year to aim at improving the soils' microbial diversity, the available nutrients and metabolites
Operational taxonomic unit Classification of organisms based on similarity, when exact species identification in not possible
Synthetic microbial consortium An engineered community of multiple microbial species designed to work together for specific purposes
Agroecosystem engineering The study of agricultural systems as ecosystems, focusing on the interactions among plants, animals, microbes, humans and their environment to design and manage sustainable farming

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.

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Data availability

Data will be made available on request.

References

Abe, T., Nakamura, S., Kudo, S., 2016. Bioconvection induced by bacterial chemotaxis in a capillary assay. Biochem. Biophys. Res. Commun. 483, 277–282. https://doi.org/10.1016/j.bbrc.2016.12.152.

Abramov, A., Hoffmann, T., Stark, T.D., Zheng, L., Lenk, S., Hammerl, R., Lanzl, T., Dawid, C., Schön, C.-C., Schwab, W., Gierl, A., Frey, M., 2021. Engineering of benzoxazinoid biosynthesis in arabidopsis thaliana: Metabolic and physiological challenges. Phytochemistry 192, 112947. https://doi.org/10.1016/j.phytochem.2021.112947.

Adler, J., 1972. A method for measuring chemotaxis and use of the method to determine optimum conditions for chemotaxis by Escherichia coli. J. Gen. Microbiol. 74, 77–91. https://doi.org/10.1099/00221287-74-1-77.

Ahmad, S., Veyrat, N., Gordon-weeks, R., Zhang, Y., Martin, J., Smart, L., Erb, M., Flors, V., Frey, M., Ton, J., 2011a. Benzoxazinoid metabolites regulate innate immunity against aphids and Fungi in Maize 1 [W]. Plant Physiol 157, 317–327. https://doi.org/10.1104/pp.111.180224 [OA].

Ahmad, S., Veyrat, N., Gordon-weeks, R., Zhang, Y., Martin, J., Smart, L., Erb, M., Flors, V., Frey, M., Ton, J., 2011b. Benzoxazinoid Metabolites Regulate Innate Immunity against Aphids and Fungi in Maize 1 [W]. Plant Physiol 157, 317–327. https://doi.org/10.1104/pp.111.180224 [OA].

Ahuja, I., Kissen, R., Bones, A.M., 2012. Phytoalexins in defense against pathogens. Trends Plant Sci. 17, 73–90. https://doi.org/10.1016/j.tplants.2011.11.002.

Ali, J.G., Alborn, H.T., Stelinski, L.L., 2010. Subterranean herbivore-induced volatiles released by citrus roots upon feeding by Diaprepes abbreviatus recruit entomopathogenic nematodes. J. Chem. Ecol. 36, 361–368.

Alon, U., Barkai, N., Surette, M.G., Leibler, S., 1999. Adaptation in bacterial chemotaxis. Nature 397, 168–171.

Aloo, B.N., Tripathi, V., Makumba, B.A., Mbega, E.R., 2022. Plant growth-promoting rhizobacterial biofertilizers for crop production: the past, present, and future. Front. Plant Sci. 13, 1–15. https://doi.org/10.3389/fpls.2022.1002448.

Anees, M., Qayyum, A., Jamil, M., Rehman, F. ur, Abid, M., Malik, M.S., Yunas, M., Ullah, K., 2020. Role of halotolerant and chitinolytic bacteria in phytoremediation of saline soil using spinach plant. Int. J. Phytoremediation 22, 653–661. https://doi.org/10.1080/15226514.2019.1707160.

Arruebarrena Di Palma, A., M Pereyra, C., Moreno Ramirez, L., Xiqui Vázquez, M.L., Baca, B.E., Pereyra, M.A., Lamattina, L., Creus, C.M., 2013. Denitrification-derived nitric oxide modulates biofilm formation in Azospirillum brasilense. FEMS Microbiol. Lett. 338, 77–85. https://doi.org/10.1111/1574-6968.12030.

Atkinson, J., Arnason, J., Compos, F., Niemeyer, H.M., Bravo, H.R., 1992. Synthesis and reactivity of cyclic hydroxamic acids. Resistance factors in the Gramineae. In: Baker, D.R., Fenyes, J.G., Steffens, J.J. (Eds.), Synthesis and Chemistry of Agrochemicals III. American Chemical Society, Washinton, DC, pp. 349–360.

Atkison, J., Morand, P., Arnason, J.T., Niemeyer, H.M., Bravo, H.R., 1991. Analogues of the cyclic hydroxamic acid 2,4-dihydroxy- 7-methoxy-1,4-benzoxazin-3-one (DIMBOA): decomposition to benzoxazolinones and reaction with -mercaptoethanol. J. Org. Chem. 56, 1788–1800.

Baatsen, J., 2024. Benzoxazinoids Influence Rhizosphere Establishment and Root Colonization by PGPB Piracicaba 2024. USP. https://doi.org/10.11606/T.11.2024.tde-06062024-083116. Piracicaba.

Baatsen, J., Hosaka, G.K., Mondin, M., Azevedo, J.L., Hungria, M., Quecine, M.C., 2025. Benzoxazinoids stimulate chemotaxis and act as a signaling molecule in Azospirillum brasilense Ab-V5, while showing minor effects on Pseudomonas protegens Pf-5. mBio. https://doi.org/10.1128/mbio.01414-25.

Bacon, C.W., Hinton, D.M., Glenn, A.E., Macías, F.A., Marin, D., 2007. Interactions of Bacillus mojavensis and Fusarium verticillioides with a benzoxazolinone (BOA) and its transformation product, APO. J. Chem. Ecol. 33, 1885–1897. https://doi.org/10.1007/s10886-007-9347-5.

Bacon, C.W., Hinton, D.M., 2011. Symptomless endophytic colonization of maize by Fusarium moniliforme. Can. J. Bot. 74, 1195–1202. https://doi.org/10.1139/b96-144.

Baetz, U., Martinoia, E., 2014. The hidden part of plant defense. Trends Plant Sci. 19, 90–98.

Bahlawane, C., McIntoch, M., Krol, E., Becker, A., 2008. Sinorhizobium meliloti regulator MucR couples exopolysaccharide synthesis and motility. Mol. Plant Microbe Interact. 21, 1498–1509.

Bais, H.P., Weir, T.L., Perry, L.G., Gilroy, S., Vivanco, J.M., 2006. The role of root exudates in rhizosphere interactions with plants and other organisms. Annu. Rev. Plant Biol. 57, 233–266. https://doi.org/10.1146/annurev.arplant.57.032905.105159.

Bano, S., Wu, X., Zhang, X., 2021. Towards sustainable agriculture: rhizosphere microbiome engineering. Appl. Microbiol. Biotechnol. https://doi.org/10.1007/s00253-021-11555-w.

Bardi, D.V., Vivanco, J.M., 2009. Regulation and function of root exudates. Plant Cell Environ. 32, 666–681.

Baumeler, A., Hesse, M., Werner, C., 2000. Benzoxazinoids-cyclic hydroxamic acids, lactams and their corresponding glucosides in the genus Aphelandra. Phytochemistry 53, 213–222.

Benizri, E., Baudoin, E., Guckert, A., 2001. Root colonization by inoculated plant growth-promoting rhizobacteria. Biocontrol Sci. Technol. 11, 557–574.

Berg, H.C., 2003. E. coli in Motion. Springer, New York.

Berg, H.C., Brown, D.A., 1972. Chemotaxis in Escherichia coli analyzed by three-dimensional tracking. Nature 239, 500–504.

Berne, C., Ducret, A., Hardy, G.G., Brun, Y.V., 2015. Adhesins involved in attachment to abiotic surfaces by gram-negative bacteria. Microbiol. Spectr. 3.

Berne, C., Brun, Y.V., 2019. The two chemotaxis clusters in caulobacter crescentus play different roles in chemotaxis and biofilm regulation. J. Bacteriol. 201, 1–16. https://doi.org/10.1128/JB.00071-19.

Besharova, O., Suchanek, V.M., Hartmann, R., Drescher, K., Sourjik, V., 2016. Diversification of gene expression during formation of static submerged biofilms by Escherichia coli. Front. Microbiol. 7, 1–17. https://doi.org/10.3389/fmicb.2016.01568.

Bever, J.D., Platt, T.G., Morton, E.R., 2013a. Microbial population and community dynamics on plant roots and their feedbacks on plant communities. Annu. Rev. Microbiol. 265–283. https://doi.org/10.1146/annurev-micro-092611-150107. Microbial.

Bever, J.D., Platt, T.G., Morton, E.R., 2013b. Microbial population and community dynamics on plant roots and their feedbacks on plant communities. Annu. Rev. Microbiol. 265–283. https://doi.org/10.1146/annurev-micro-092611-150107. Microbial.

Bi, S., Sourjik, V., 2018. Stimulus sensing and signal processing in bacterial chemotaxis. Curr. Opin. Microbiol. 45, 22–29.

Bible, A., Russell, M.H., Alexandre, G., 2012. The Azospirillum brasilense Che1 chemotaxis pathway controls swimming velocity, which affects transient cell-to-cell clumping. J. Bacteriol. 194, 3343–3355. https://doi.org/10.1128/JB.00310-12.

Bible, A.N., Stephens, B.B., Ortega, D.R., Xie, Z., Alexandre, G., 2008. Function of a chemotaxis-like signal transduction pathway in modulating motility, cell clumping, and cell length in the alphaproteobacterium Azospirillum brasilense. J. Bacteriol. 190, 6365–6375. https://doi.org/10.1128/JB.00734-08.

Bigler, L., Baumeler, A., Werner, C., Hesse, M., 1996. Detection of noncovalent complexes of hydroxamic-acid derivatives by means of electrospray mass spectrometry. Helv. Chim. Acta 79, 1701–1709.

Block, A.K., Hunter, C.T., Sattler, S.E., Rering, C., McDonald, S., Basset, G.J., Christensen, S.A., 2020. Fighting on two fronts: elevated insect resistance in flooded maize. Plant Cell Environ. 43, 223–234. https://doi.org/10.1111/pce.13642.

Bloemberg, G.V., Wijfjes, A.H., Lamers, G.E., 2000. Simultaneous imaging of Pseudomonas fluorescens WCS365 populations expressing three different autofluorescent proteins in the rhizosphere: new perspectives for studying microbial communities. Mol. Plant Microbe Interact. 13, 1170–1176.

Bloemberg, G.V., Lugtenberg, B.J., 2004. Bacterial biofilms on plants: relevance and phenotypic aspects. In: Ghannoum, M., O' Tool, G.A. (Eds.), Microbial Biofilms. American Society of Microbiology, Washinton, DC, pp. 141–159.

Boller, T., He, S.Y., 2009. Innate immunity in plants: an arms race between pattern recognition receptors in plants and effectors in microbial pathogens. Science (1979) 324, 742–744.

Borrelli, P., Robinson, D.A., Panagos, P., Emanuele, L., Yang, J.E., Alewell, C., Montanarella, L., Ballabio, C., 2020. Land use and climate change impacts on global soil erosion by water (2015-2070). Proc. Natl. Acad. Sci. USA 117, 21994–22001.

Bravo, A., Likitvivatanavong, S., Gill, S.S., Soberón, M., 2011. Bacillus thuringiensis: a story of a successful bioinsecticide. Insect Biochem. Mol. Biol. 41, 423–431. https://doi.org/10.1016/j.ibmb.2011.02.006.

Bravo, H.R., Niemeyer, H.M., 1985. Decomposition in aprotic solvents of 2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one, a hydroxamic acid from cereals. Tetrahedron 21, 4983–4986.

Bronesky, D., 2016. Staphylococcus aureas RNAIII and its regulon lonk quorum sensing, stress responses, metabolic adaptation and regulation of virulence gene expression. Annu. Rev. Mircobiol. 70, 299–316.

Brunetti, N., Hageman, R.H., 1976. Comparison of in vivo and in vitro assays of nitrate reductase in wheat (Triticum aestivum L.) seedlings 1. Plant Physiol 58, 583–587. https://doi.org/10.1104/pp.58.4.583.

Bulgarelli, D., Schlaeppi, K., Spaepen, S., van Themaat, E.V.L., Schulze-Lefert, P., 2013. Structure and functions of the bacterial microbiota of plants. Annu. Rev. Plant Biol. 64, 807–838. https://doi.org/10.1146/annurev-arplant-050312-120106.

Burdman, S., Dulguerova, G., Okon, Y., 2001. Purification of the major outer membrane protein of Azospirillum brasilense, its affinity to plant roots, and its involvement in cell aggregation. Mol plant Microbe Interactl 14, 555–561.

Cadot, S., Guan, H., Bigalke, M., Walser, J.C., Jander, G., Erb, M., van der Heijden, M.G.A., Schlaeppi, K., 2021a. Specific and conserved patterns of microbiota-structuring by maize benzoxazinoids in the field. Microbiome 9. https://doi.org/10.1186/s40168-021-01049-2.

Cadot, S., Guan, H., Bigalke, M., Walser, J.C., Jander, G., Erb, M., van der Heijden, M.G.A., Schlaeppi, K., 2021b. Specific and conserved patterns of microbiota-structuring by maize benzoxazinoids in the field. Microbiome 9. https://doi.org/10.1186/s40168-021-01049-2.

Calatrava-Morales, N., McIntosh, M., Soto, M.J., 2018. Regulation mediated by N-acyl homoserine lactone quorum sensing signals in the rhizobium-legume symbiosis. Genes 9. https://doi.org/10.3390/genes9050263.

Cambier, V., Hance, T., de Hoffmann, E., 1999. Non-injured maize contains several 1,4-benzoxazin-3-one related compounds but only as glucoconjugates. Phytochem. Anal. 10, 119–126.

Cambier, V., Hance, T., Hoffmann, E. De, 2000. Variation of DIMBOA and related compounds content in relation to the age and plant organ in maize. Phytochemistry 53, 223–229.

Camilios-Neto, D., Bonato, P., Wassem, R., Tadra-Sfeir, M.Z., Brusamarello-Santos, L.C. C., Valdameri, G., Donatti, L., Faoro, H., Weiss, V.A., Chubatsu, L.S., Pedrosa, F.O., Souza, E.M., 2014. Dual RNA-seq transcriptional analysis of wheat roots colonized by Azospirillum brasilense reveals up-regulation of nutrient acquisition and cell cycle genes. BMC Genom. 15, 1–13. https://doi.org/10.1186/1471-2164-15-378.

Cardinale, M., Ratering, S., Suarez, C., Zapata Montoya, A.M., Geissler-Plaum, R., Schnell, S., 2015. Paradox of plant growth promotion potential of rhizobacteria and their actual promotion effect on growth of barley (Hordeum vulgare L.) under salt stress. Microbiol. Res. 181, 22–32. https://doi.org/10.1016/j.micres.2015.08.002.

Casas, M.I., Falcone-Ferreyra, M.L., Jiang, N., Mejía-Guerra, M.K., Rodríguez, E., Wilson, T., Engelmeier, J., Casati, P., Grotewold, E., 2016. Identification and characterization of maize salmon silks genes involved in Insecticidal Maysin Biosynthesis. Plant Cell 28, 1297–1309. https://doi.org/10.1105/tpc.16.00003.

Catroux, G., Hartmann, A., Revellin, C., 2001. Trends in rhizobial inoculant production and use. Plant Soil 230, 21–30.

Celani, A., Vergassola, M., 2010. Bacterial strategies for chemotaxis response. Plant Soil. 107, 1391–1396.

Chen, K.J., Zheng, Y.Q., Kong, C.H., Zhang, S.Z., Li, J., Liu, X.G., 2010. 2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one (DIMBOA) and 6-methoxy-benzoxazolin-2-one (MBOA) levels in the wheat rhizosphere and their effect on the soil microbial community structure. J. Agric. Food Chem. 58, 12710–12716. https://doi.org/10.1021/jf1032608.

Chen, Y., Li, C., Zhou, Z., Wen, J., You, X., Mao, Y., Lu, C., Huo, G., Jia, X., 2014. Enhanced biodegradation of Alkane hydrocarbons and crude oil by mixed strains and bacterial community analysis. Appl. Biochem. Biotechnol. 172, 3433–3447. https://doi.org/10.1007/s12010-014-0777-6.

Chetty, A., Blekhman, R., 2024. Multi-omic approaches for host-microbiome data integration. Gut Microbes 16, 2297860. https://doi.org/10.1080/19490976.2023.2297860.

Chong, Y.M., Yin, W.F., Ho, C.Y., Mustafa, M.R., Hadi, A.H.A., Awang, K., Narrima, P., Koh, C.-L., Appleton, D.R., Chan, K.-G., 2011. Malabaricone C from Myristica cinnamomea exhibits anti-quorum sensing activity. J Nat Prod 74, 2261–2264.

Chong, J., Xia, J., 2017. Computational approaches for integrative analysis of the metabolome and microbiome. Metabolites 7. https://doi.org/10.3390/metabo7040062.

Churchill, E.A.M., Chen, L., 2011. Structural basis of acyl-homoserine lactone-dependent signaling. Chem Rev 111, 68–85.

Colin, R., Sourjik, V., 2017. Emergent properties of bacterial chemotaxis pathway. Curr. Opin. Microbiol. 39, 24–33.

Compant, S., Clément, C., Sessitsch, A., 2010. Plant growth-promoting bacteria in the rhizo- and endosphere of plants: their role, colonization, mechanisms involved and prospects for utilization. Soil Biol. Biochem. 42, 669–678. https://doi.org/10.1016/j.soilbio.2009.11.024.

Copaja, S.V., Villarroel, E., Bravo, H.R., Pizarro, L., Argandona, V.H., 2006. Hydroxamic acids in Secale cereale L. and the relationship with their antifeedant and allelopathic properties. Biosci 61, 670–676.

Costerson, J.W., Lewandowski, Z., Caldwell, D.E., Korber, D.R., Lappin-Scott, H.M., 1995. Microbial biofilms. Ann Rev Microbio 49, 711–745.

Cotton, T.E.A., Pétriacq, P., Cameron, D.D., Meselmani, M. Al, Schwarzenbacher, R., Rolfe, S.A., Ton, J., Rolfe, S.A., 2019a. Metabolic regulation of the maize rhizobiome by benzoxazinoids. ISME J. https://doi.org/10.1038/s41396-019-0375-2.

Cotton, T.E.A., Pétriacq, P., Cameron, D.D., Meselmani, M. Al, Schwarzenbacher, R., Rolfe, S.A., Ton, J., Rolfe, S.A., 2019b. Metabolic regulation of the maize rhizobiome by benzoxazinoids. ISME J. https://doi.org/10.1038/s41396-019-0375-2.

Crespo, M.C.A., Vervalde, C., 2009. A single mutation in the oprF mRNA leader confers strict translational control by the Gac/Rsm system in Pseudomonas fluorescens CHA0. Curr. Microbiol. 58, 182–188.

Croes, C.L., Moens, S., Van Bastelaere, E., Vanderleyden, J., Michiels, K.W., 1993. The polar flagellum mediates Azospirillum brasilense adsorption to wheat roots. Microbiology (N. Y.) 139.

Cuevas, L., Niemeyer, H.M., Pérez, F.J., 1990. Reaction of DIMBOA, a resistance factor from cereals, with R-chymotrypsin. Phytochemistry 29, 1429–1432.

Czjzek, M., Cicek, M., Zamboni, V., Burmeister, W.P., Bevan, D.R., Henrissat, B., Esen, A., 2001. Crystal structure of a monocotyledon (maize ZMGlu1) beta-glucosidase and a model of its complex with p-nitrophenyl beta-dthioglucoside. Biochem. J. 354, 37–46.

Dangi, S.R., Tirado-Corbalá, R., Gerik, J., Hanson, B.D., 2017. Effect of long-term continuous fumigation on soil microbial communities. Agronomy 7. https://doi.org/10.3390/agronomy7020037.

Daniels, R., De Vos, D.E., Desair, J., Raedschelders, G., Luyten, E., Rosemeyer, V., Verreth, C., Schoeter, E., Vanderleyde, J., Michiels, J., 2002. The cin quorum sensing locus of Rhizobium etli CNPAF512 affects growth and symbiotic nitrogen fixation. J. Biol. Chem. 277, 462–468.

Daramola, D.A., Hatzell, M.C., 2023. Energy demand of nitrogen and phosphorus based fertilizers and approaches to circularity. ACS Energy Lett. 8, 1493–1501. https://doi.org/10.1021/acsenergylett.2c02627.

de Bruijn, W.J.C., Gruppen, H., Vincken, J.P., 2018. Structure and biosynthesis of benzoxazinoids: plant defence metabolites with potential as antimicrobial scaffolds. Phytochemistry 155, 233–243. https://doi.org/10.1016/j.phytochem.2018.07.005.

de Kievit, T.R., Iglewski, B.H., 2000. Bacterial quorum sensing in pathogenic relationships. Infect. Immun. 68, 4839–4849.

De Mot, R., Vanderleyden, J., 1991. Purification of a root-adhesive outer membrane protein of root-colonizing Pseudomonas fluorescens. FEMS Microbiol. Lett. 81, 323–327.

De Troch, P., Vanderleyden, J., 1996. Surface properties and motility of Rhizobium and Azospirillum in relation to plant root attach- ment. Microb. Ecol. 32, 149–169.

Dehghani, I., Mostajeran, A., 2020. Does compatibility of wheat cultivars with Azospirillum brasilense strains affect drought tolerance? Cereal Res. Commun. 48, 121–129. https://doi.org/10.1007/s42976-019-00001-3.

Delany, I., Sheetian, M.M., Fenon, A., Bardin, S., Aarons, S., O'Gara, F., 2000. Regulation of production of the antifungal metabolite 2,4-diacetylphloroglucinol in Pseudomonas fluorescens F113: genetic analysis of phlF as a transcriptional repressor. Microbiology (N. Y.) 146, 537–546.

Dias, T., Dukes, A., Antunes, P., 2015. Accounting for soil biotic effects on soil health and crop productivity in design of crop rotations. J. Sci. Food Agric. 95, 447–454.

Ding, Y., Murphy, K.M., Poretsky, E., Mafu, S., Yang, B., Char, S.N., Christensen, S.A., Saldivar, E., Wu, M., Wang, Q., Ji, L., Schmitz, R.J., Kremling, K.A., Buckler, E.S., Shen, Z., Briggs, S.P., Bohlmann, J., Sher, A., Castro-Falcon, G., Hughes, C.C., Huffaker, A., Zerbe, P., Schmelz, E.A., 2019. Multiple genes recruited from hormone pathways partition maize diterpenoid defences. Nat. Plants 5, 1043–1056. https://doi.org/10.1038/s41477-019-0509-6.

Dobbelaere, S., Croonenborghs, A., Thys, A., Ptacek, D., Vanderleyden, J., Dutto, P., Landanbera-Gonzalez, C., Caballero-ellado, J., Aguirre, J.F., Kapulnik, Y., Brener, S., Burdman, S., Kadouri, D., Sarig, S., Okon, Y., 2001. Responses of agronomically important crops to inoculation with Azospirillum. Aust. J. Plant Physiol. 871–879.

Dreyer, I., Gomez-Porras, J.L., Reaño-Pachón, D.M., Hendrich, R., Grieger, D., 2012. Molecular evolution of slow and quick anion channels (SLACs and QUACs/ALMTs). Front. Plant Sci. 3, 263.

Dunham, S.J.B., Ellis, J.F., Li, B., Sweedler, J.V., 2017. Mass spectrometry imaging of complex microbial communities. Acc. Chem. Res. 50, 96–104. https://doi.org/10.1021/acs.accounts.6b00503.

Ebisui, K., Ishihara, A., Hirai, N., Iwamura, H., 1998. Occurrence of 2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one (DIMBOA) and a b-glucosidase specific for its glucoside in maize seedlings. Naturforsch 53c, 793–798.

Eljarrat, E., Barceló, D., 2001. Sample handling and analysis of allelochemical compounds in plants. Trend Anal Chem 20, 584–590.

Erb, M., Veyrat, N., Robert, C.A.M., Xu, H., Frey, M., Ton, J., Turlings, T.C.J., 2015. Indole is an essential herbivore-induced volatile priming signal in maize. Nat. Commun. 6, 1–10. https://doi.org/10.1038/ncomms7273.

Etzerodt, T., Mortensen, A.G., Fomsgaard, I.S., 2008a. Transformation kinetics of 6-methoxybenzoxazolin-2-one in soil. J Environ Sci Health B 43, 1–7. https://doi.org/10.1080/03601230701734774.

Etzerodt, T., Mortensen, A.G., Fomsgaard, I.S., 2008b. Transformation kinetics of 6-methoxybenzoxazolin-2-one in soil. J Environ Sci Health B 43, 1–7. https://doi.org/10.1080/03601230701734774.

Etzerodt, T., Nielsen, S.T., Mortensen, A.G., Christophersen, C., Formsgaard, I.S., 2006. Elucidating the transformation pattern of the cereal allelochemical 6-Methoxy-2-benzoxazolinone(MBOA) and the trideuteriomethoxy analogue [D3]-MBOA in soil. J Agri Food Chem 54, 1075–1085.

Fabian, B.K., Tetu, S.G., Paulsen, I.T., 2020. Application of transposon insertion sequencing to agricultural science. Front. Plant Sci. https://doi.org/10.3389/fpls.2020.00291.

Faust, K., Raes, J., 2012. Microbial interactions: from networks to models. Nat. Rev. Microbiol. 10, 538–550. https://doi.org/10.1038/nrmicro2832.

Ferrarezi, Jessica Aparecida, Defant, Heloísa, de Souza, Leandro Fonseca, Azevedo, João Lúcio, Hungria, Mariangela, et al., 2023. Meta-omics integration approach reveals the effect of soil native microbiome diversity in the performance of inoculant Azospirillum brasilense. Frontiers in Plant Science 14, 1172839. https://doi.org/10.3389/fpls.2023.1172839. https://www.frontiersin.org/articles/10.3389/fpls.2023.1172839/full. (Accessed 29 June 2023).

Flores Céspedes, F., Pérez García, S., Villafranca Sánchez, M., Fernández Pérez, M., 2013. Bentonite and anthracite in alginate-based controlled release formulations to reduce leaching of chloridazon and metribuzin in a calcareous soil. Chemosphere 92, 918–924. https://doi.org/10.1016/j.chemosphere.2013.03.001.

Frey, M., Huber, K., Park, W.J., Sicker, D., Lindberg, P., Meeley, R.B., Simmons, C.R., Yalpani, N., Gierl, A., 2003. A 2-oxoglutarate-dependent dioxygenase is integrated in DIMBOA-biosynthesis. Phytochemistry 62, 371–376.

Frey, M., Kliem, R., Saedler, H., Gierl, A., 1995. Expression of a cytochrome P450 gene family in maize. Mol. Gen. Genet. 24, 100–109.

Frey, M., Stettner, C., Pare, P.W., Schmelz, E.A., Tumlinson, J.H., Gierl, A., 2000. An herbivore elicitor activates the gene for indole emission in maize. Proc. Natl. Acad. Sci. 97, 14801–14806.

Förster, C., Handrick, V., Ding, Y., Nakamura, Y., Paetz, C., Schneider, B., Castro-Falcón, G., Hughes, C.C., Luck, K., Poosapati, S., Kunert, G., Huffaker, A., Gershenzon, J., Schmelz, E.A., Köllner, T.G., 2022. Biosynthesis and antifungal activity of fungus-induced O-methylated flavonoids in maize. Plant Physiol 188, 167–190. https://doi.org/10.1093/plphys/kiab496.

Fujiwara, F., Miyazawa, K., Nihei, N., Ichihashi, Y., 2023. Agroecosystem engineering extended from plant-microbe interactions revealed by multi-omics data. Biosci. Biotechnol. Biochem. https://doi.org/10.1093/bbb/zbac191.

Fukami, J., Abrantes, J.L.F., del Cerro, P., Nogueira, M.A., Ollero, F.J., Megías, M., Hungria, M., 2018. Revealing strategies of quorum sensing in Azospirillum brasilense strains Ab-V5 and Ab-V6. Arch. Microbiol. 200, 47–56. https://doi.org/10.1007/s00203-017-1422-x.

Fuqua, C., 2010. Passing the baton between laps: adhesion and cohesion in Pseudomonas putida biofilms. Mol. Microbiol. 77, 533–536.

Fuqua, W.C., Winans, S.C., 1994a. A LuxR-LuxI type regulatory System activates agrobacterium Ti plasmid conjugal transfer in the presence of a plant tumor metabolite. J. Bacteriol. 1734, 2796–2806.

Fuqua, W.C., Winans, S.C., 1994b. A LuxR-LuxI type regulatory System activates agrobacterium Ti plasmid conjugal transfer in the presence of a plant tumor metabolite. J. Bacteriol. 1734, 2796–2806.

Gagliardo, R.W., Chilton, W.S., 1992. Soil transformation of 2(3H)- benzoxazolone of rye into phytotoxic 2-amino-3H-phenoxazin- 3-one. J. Chem. Ecol. 18, 1683–1691.

Ganin, H., Rayo, J., Amara, N., Levy, N., Krief, P., Meijler, M.M., 2013. Sulforaphane and erucin, natural isothiocyanates from broccoli, inhibit bacterial quorum sensing. Medchemcomm 4, 175–179.

Gao, L., Shen, G., Zhang, L., Qi, J., Zhang, C., Ma, C., Li, J., Wang, L., Malook, S.U., Wu, J., 2019. An efficient system composed of maize protoplast transfection and HPLC–MS for studying the biosynthesis and regulation of maize benzoxazinoids. Plant Methods 15, 144. https://doi.org/10.1186/s13007-019-0529-2.

Garcia, J., Kao-Kniffin, J., 2020. Can dynamic network modelling be used to identify adaptive microbiomes? Funct. Ecol. 34, 2065–2074. https://doi.org/10.1111/1365-2435.13491.

Gfeller, V., Thoenen, L., Erb, M., 2023a. Root-exuded benzoxazinoids can alleviate negative plant-soil feedbacks. New Phytol. https://doi.org/10.1111/nph.19401.

Gfeller, V., Waelchli, J., Pfister, S., Deslandes-Hérold, G., Mascher, F., Glauser, G., Aeby, Y., Mestrot, A., Robert, C.A.M., Schlaeppi, K., Erb, M., 2023b. Plant secondary metabolite-dependent plant-soil feedbacks can improve crop yield in the field. eLife 12, e84988. https://doi.org/10.7554/eLife.84988.

Gfeller, V., Waelchli, J., Pfister, S., Deslandes-Hérold, G., Mascher, F., Glauser, G., Aeby, Y., Mestrot, A., Robert, C.A.M., Schlaeppi, K., Erb, M., 2023c. Plant secondary metabolite-dependent plant-soil feedbacks can improve crop yield in the field. eLife 12, e84988. https://doi.org/10.7554/eLife.84988.

Glenn, A.E., Davis, C.B., Gao, M., Gold, S.E., Mitchell, T.R., Proctor, R.H., 2016. Two horizontally transferred xenobiotic resistance gene clusters associated with detoxification of benzoxazolinones by Fusarium species. PLoS One 11, e0147486.

Glenn, A.E., Hinton, D.M., Yates, I.E., Bacon, C.W., 2001a. Detoxification of corn antimicrobial compounds as the basis for isolating. Society 67, 2973–2981. https://doi.org/10.1128/AEM.67.7.2973.

Glenn, A.E., Hinton, D.M., Yates, I.E., Bacon, C.W., 2001b. Detoxification of corn antimicrobial compounds as the basis for isolating. Society 67, 2973–2981. https://doi.org/10.1128/AEM.67.7.2973.

Glenn, A.E., Meredith, F.I., Bacon, C.W., 2003. Identification of intermediate and branch metabolites resulting in the biotransformation of 2-benzoxazolinone by Fusarium verticillioides. Appl. Environ. Microbiol. 3165–3169.

Glenn, A.E., Bacon, C.W., 2009. FDB2 encodes a member of the arylamine N-acetyltransferase family and is necessary for biotransformation of benzoxazolinones by Fusarium verticillioides. J. Appl. Microbiol. 107, 657–671. https://doi.org/10.1111/j.1365-2672.2009.04246.x.

Gómez-Merino, F., Gómez-Trejo, L., Ruvalcaba-Ramírez, R., Trejo-Téllez, L.I., 2022. Application of phosphite as a biostimulant in agriculture, 135–153. https://doi.org/10.1016/B978-0-323-85581-5.00002-1.

Gond, S.K., Torres, M.S., Bergen, M.S., Helsel, Z., White, J.F., 2015. Induction of salt tolerance and up-regulation of aquaporin genes in tropical corn by rhizobacterium Pantoea agglomerans. Lett. Appl. Microbiol. 60, 392–399. https://doi.org/10.1111/lam.12385.

Grambow, H.J., Lückge, J., Klausener, A., Müller, E., 1986. Occurrence of 2-(2-hydroxy-4,7-dimethoxy-2H-1,4-benzoxazin-3-one)-β-D-glucopyranoside in Triticum aestivum leaves and its conversion into 6-methoxy-benzoxazolinone. Z. Naturforsch. 41, 684, 60.

Guttenplan, S.B., Kearns, D.B., 2013. Regulation of flagellar motility during biofilm formation. FEMS Microbiol. Rev. 37, 849–871. https://doi.org/10.1111/1574-6976.12018.

Hacquard, S., Garrido-Oter, R., González, A., Spaepen, S., Ackermann, G., Lebeis, S., 2015. Microbiota and host nutrition across plant and animal kingdoms. Cell Host Microbe 17, 603–616.

Hartmann, A., Rothballer, M., Schmid, M., 2008. Lorenz Hiltner, a pioneer in rhizosphere microbial ecology and soil bacteriology research. Plant Soil 312, 7–14. https://doi.org/10.1007/s11104-007-9514-z.

He, Y.-W., Zang, L.-H., 2008. Quorum sensing and virulence regulation in Xanthomonas campestris. FEMS Microbiol. Rev. 32, 842–857.

Heggers, J.P., Cottingham, J., Gusman, J., Reagor, L., McCoy, L., Carino, E., Cox, R., Zhao, J.-G., 2002. The effectiveness of processed grapefruit-seed extract as an antibacterial agent: II. Mechanism of action and in vitro toxicity. J. Alternative Compl. Med. 8, 333–340.

Heintz-Buschart, A., May, P., Laczny, C.C., Lebrun, L.A., Bellora, C., Krishna, A., Wampach, L., Schneider, J.G., Hogan, A., de Beaufort, C., Wilmes, P., 2016. Integrated multi-omics of the human gut microbiome in a case study of familial type 1 diabetes. Nat. Microbiol. 2, 16180. https://doi.org/10.1038/nmicrobiol.2016.180.

Hiltner, L., 1904. Ueber neuere Erfahrungen and Probleme auf dem Gebiete der Bodembakteriologie und unter besonderer Berucksichtingung der Grundungung und Brache. Arb. Deut. Landw. Gesell 98, 59–78.

Holden, M.T.G., Chhabra, S.R., de Nys, R., 1999. Quorum-sensing cross talk: isolation and chemical characterization of cyclic dipeptides from Pseudomonas aeruginosa and other Gram-negative bacteria. Mol. Microbiol. 33, 1254–1266.

Hu, L., Mateo, P., Ye, M., Zhang, X., Berset, J.D., Handrick, V., Radisch, D., Grabe, V., Gershenzon, J., Robert, C.A.M., Erb, M., 2018. Plant iron acquisition strategy exploited by an insect herbivore. Plant Sci. 697, 694–697.

Hu, L., Wu, Z., Robert, C.A.M., Ouyang, X., Züst, T., Mestrot, A., Xu, J., Erb, M., 2021. Soil chemistry determines whether defensive plant secondary metabolites promote or suppress herbivore growth. Proc. Natl. Acad. Sci. U. S. A. 118. https://doi.org/10.1073/pnas.2109602118.

Hu, Lingfei, Robert, C.A.M., Cadot, S., Zhang, X., Ye, M., Li, B., Manzo, D., Chervet, N., Steinger, T., Van Der Heijden, M.G.A., Schlaeppi, K., Erb, M., 2018a. Root exudate metabolites drive plant-soil feedbacks on growth and defense by shaping the rhizosphere microbiota. Nat. Commun. 9, 1–13. https://doi.org/10.1038/s41467-018-05122-7.

Huang, P.-C., Grunseich, J.M., Berg-Falloure, K.M., Tolley, J.P., Koiwa, H., Bernal, J.S., Kolomiets, M.V., 2023. Maize OPR2 and LOX10 mediate defense against fall armyworm and Western corn rootworm by tissue-specific regulation of Jasmonic acid and Ketol metabolism. Genes 14. https://doi.org/10.3390/genes14091732.

Hungria, M., Campo, R.J., Souza, E.M., Pedrosa, F.O., 2010. Inoculation with selected strains of Azospirillum brasilense and A . lipoferum improves yields of maize and wheat in Brazil 413–425. https://doi.org/10.1007/s11104-009-0262-0.

Hungria, M., Nogueira, M.A., Araujo, R.S., 2015. Soybean Seed Co-Inoculation with Bradyrhizobium spp . and Azospirillum brasilense : a New Biotechnological Tool to Improve yield and Sustainability. https://doi.org/10.4236/ajps.2015.66087.

Hungria, M., Ribeiro, A., Nogueira, A., 2018. Crossm V5 and Ab-V6 , Commercially Used in Inoculants for Grasses 5–6.

Ismail, A.S., Valastyan, J.S., Bassier, B.L.A., 2016. Host- produced autoinducer-2 mimic activates bacterial quorum sensing. Cell Host Microbe 19, 470–480.

Jani, S., Seely, A.L., Peaboy, V.G.L., Jayaraman, A., Manson, M.D., 2017. Chemotaxis to self-generated AI-2 promotes biofilm formation in Escherichia coli. Microbiology. Microbiology (N Y) 163, 1778–1790.

Jansson, J.K., Hofmockel, K.S., 2020. Soil microbiomes and climate change. Nat. Rev. Microbiol. 18, 35–46. https://doi.org/10.1038/s41579-019-0265-7.

Jia, Q., Brown, R., Köllner, T.G., Fu, J., Chen, X., Wong, G.K.-S., Gershenzon, J., Peters, R.J., Chen, F., 2022. Origin and early evolution of the plant terpene synthase family. Proc. Natl. Acad. Sci. 119, e2100361119. https://doi.org/10.1073/pnas.2100361119.

Jimenez, P.N., Koch, G., Thompson, J.A., 2012. The multiple signaling systems regulating virulence in Pseudomonas aeruginosa. Microbiol Molr Biol R 76, 46–65.

Jofré, E., Lagares, A., Mori, G., 2004. Disruption of dTDP-rhamnose biosyn- thesis modifies lipopolysaccharide core, exopolysaccharide production, and root colonization in Azospirillum brasilense. FEMS Microbiol. Lett. 231, 267–275.

Jonczyk, R., Schmidt, H., Osterrieder, A., Fiesselmann, A., Schullehner, K., Haslbeck, M., Sicker, D., Hofmann, D., Yalpani, N., Simmons, C., Frey, M., Gierl, A., 2008. Elucidation of the final reactions of DIMBOA-glucoside biosynthesis in maize: characterization of Bx6 and Bx7. Plant Physiol 146, 1053–1063.

Jones, D.L., Nguyen, C., Finlay, R.D., 2009. Carbon flow in the rhizosphere: carbon trading at the soil-root interface. Plant Soil 321, 5–33.

Jones, D.L., Dangl, J.L., 2006. The plant immune system. Nature 444, 323–329.

Kalinin, Y.V., Jiang, L., Tu, Y., 2009. Logarithmic sensing in Escherichia coli bacterial chemotaxis. Biophys. J. 96, 2439–2448.

Katherine, J., Jose, M.-M., 2022. Computational network inference for bacterial interactomics. mSystems 7. https://doi.org/10.1128/msystems.01456-21 e01456-21.

Kehry, M.R., Doak, T.G., Dahlquist, F.W., 1984. Stimulus-induced changes in methylesterase activity during chemotaxis in Escherichia coli. J. Biol. Chem. 259, 11828–11835. https://doi.org/10.1016/s0021-9258(20)71286-x.

Kehry, M.R., Dahlquist, F.W., 1982. The methyl-accepting chemotaxis proteins of Escherichia coli - identification of the multiple methylation sites on methyl-accepting chemotaxis protein-I. J. Biol. Chem. 257, 378–386.

Köhler, A., Maag, D., Veyrat, N., Glauser, G., Wolfender, J.L., Turlings, T.C.J., Erb, M., 2015a. Within-plant distribution of 1,4-benzoxazin-3-ones contributes to herbivore niche differentiation in maize. Plant Cell Environ. 38, 1081–1093.

Köhler, A., Maag, D., Veyrat, N., Glauser, G., Wolfender, J.L., Turlings, T.C.J., Erb, M., 2015b. Within-plant distribution of 1,4-benzoxazin-3-ones contributes to herbivore niche differentiation in maize. Plant Cell Environ. 38, 1081–1093.

Khorasani, A., Sani, W., Philip, K., Mat Taha, R., Rafat, A., 2010. Antioxidant and antibacterial activities of ethanolic extracts of Asparagus officinalis cv. Mary Washington: comparison of in vivo and in vitro grown plant bioactivities. Afr. J. Biotechnol. 9, 8460–8466.

Kim, M.K., Ingremeau, F., Zhao, A., Bassler, B.L., Stone, H.A., 2016. Local and global consequences of flow on bacterial quorum sensing. Nat. Microbiol. 1, 15005.

Knight, R., Vrbanac, A., Taylor, B.C., Aksenov, A., Callewaert, C., Debelius, J., Gonzalez, A., Kosciolek, T., McCall, L.-I., McDonald, D., Melnik, A.V., Morton, J.T., Navas, J., Quinn, R.A., Sanders, J.G., Swafford, A.D., Thompson, L.R., Tripathi, A., Xu, Z.Z., Zaneveld, J.R., Zhu, Q., Caporaso, J.G., Dorrestein, P.C., 2018. Best practices for analysing microbiomes. Nat. Rev. Microbiol. 16, 410–422. https://doi.org/10.1038/s41579-018-0029-9.

Koch, B., Liljefors, T., Persson, T., Nielsen, J., Kjelleberg, S., Givskov, M., 2005. The LuxR receptor: the sites of interaction with quorum-sensing signals and inhibitors. Microbiology (N. Y.) 151, 3589–3602. https://doi.org/10.1099/mic.0.27954-0.

Koh, C.L., Sam, C.K., Yin, W.F., Tn, L.Y., Chong, Y.M., Chanf, K.G., 2013. Plant derived natural products as sources of anti-quorum sensing compounds. Sensors 13, 6217–6228.

Kudjordjie, E.N., Sapkota, R., Steffensen, S.K., Fomsgaard, I.S., Nicolaisen, M., 2019a. Maize synthesized benzoxazinoids affect the host associated microbiome. Microbiome 1–17.

Kudjordjie, E.N., Sapkota, R., Steffensen, S.K., Fomsgaard, I.S., Nicolaisen, M., 2019b. Maize synthesized benzoxazinoids affect the host associated microbiome. Microbiome 1–17.

Kulmatiski, A., Beard, K.H., Norton, J.M., Heavilin, J.E., Forero, L.E., Grenzer, J., 2017. Live long and prosper: plant–soil feedback, lifespan, and landscape abundance covary. Ecology 98, 3063–3073. https://doi.org/10.1002/ecy.2011.

Kumar, A., Patel, J.S., Meena, V.S., Srivastava, R., 2019. Recent advances of PGPR based approaches for stress tolerance in plants for sustainable agriculture. Biocatal. Agric. Biotechnol. 20, 101271. https://doi.org/10.1016/j.bcab.2019.101271.

Kumar, P., Gagliardo, R.W., Chilton, W.S., 1993. Soil transformation of wheat and corn metabolites MBOA and DIM2BOA into aminophenoxazinones. J. Chem. Ecol. 19, 2453–2461.

Kunkel, B.N., Harper, C.P., 2018. The roles of auxin during interactions between bacterial plant pathogens and their hosts. J. Exp. Bot. 69, 245–254.

Kwasny, S.M., Opperman, T.J., 2010. Static biofilm cultures of Gram-positive pathogens grown in a microtiter format used for anti-biofilm drug discovery. Curr. Protoc. Pharmacol. https://doi.org/10.1002/0471141755.ph13a08s50.

Larsen, S.H., Reader, R.W., Kort, E.N., 1974. Change in direction of flagellar rotation is basis of chemotactic response in Escherichia coli. Nature 249, 74–77.

Leitão, F., Pinto, G., Henriques, I., 2024. Pinus radiata seedlings rhizobiome shifts in response to foliar and root phosphite application. Eur. J. Soil Biol. 123, 103688. https://doi.org/10.1016/j.ejsobi.2024.103688.

Li, M.S., Hazelbauer, G.L., 2005. Adaptational assistance in clusters of bacterial chemoreceptors. Mol. Microbiol. 56, 1617–1626.

Liu, H., Brettell, L.E., Qiu, Z., Singh, B.K., 2020. Microbiome-Mediated stress resistance in plants. Trends Plant Sci. 25, 733–743. https://doi.org/10.1016/j.tplants.2020.03.014.

Luu, R.A., Schneider, B.J., Ho, C.C., Nesteryuk, V., Ngwesse, S.E., Liu, X., Parales, J.V., Ditty, J.L., Parales, R.E., 2013. Taxis of Pseudomonas putida F1 toward phenylacetic acid is mediated by the energy taxis receptor AER2. Appl. Environ. Microbiol. 79, 2416–2423. https://doi.org/10.1128/AEM.03895-12.

Maag, D., Köhler, A., Robert, C.A.M., Frey, M., Wolfender, J.L., Turlings, T.C.J., Glauser, G., Erb, M., 2016. Highly localized and persistent induction of Bx1-dependent herbivore resistance factors in maize. Plant J. 88, 976–991. https://doi.org/10.1111/tpj.13308.

Macías, F.A., Marín, D., Oliveros-Bastidas, A., Castellano, D., Simonet, A.M., Molinillo, J.M.G., 2005. Structure-activity relationships (SAR) studies of benzoxazinones, their degradation products and analogues. Phytotoxicity on standard target species (STS). J. Agric. Food Chem. 53, 538–548.

Macías, F.A., Marín, D., Oliveros-Bastidas, A., Castellano, D., Simonet, A.M., Molinillo, J.M.G., 2006. Structure-activity relationship (SAR) studies of benzoxazinones, their degradation products, and analogues. Phytotoxicity on problematic weeds Avena fatua L. and Lolium rigidum Gaud. J. Agric. Food Chem. 54, 1040–1048.

Macías, F.A., Oliveros-Bastidas, A., Marín, D., Castellano, D., Simonet, A.M., Molinillo, J.M.G., 2004. Degradation studies on benzoxazinoids. Soil degradation dynamics of 2,4-dihydroxy-7-methoxy-(2H)-1,4-benzoxazin-3(4H)-one (DIMBOA) and its degradation products, phytotoxic allelochemicals from gramineae. J. Agric. Food Chem. 52, 6402–6413. https://doi.org/10.1021/jf0488514.

Mafu, S., Ding, Y., Murphy, K.M., Yaacoobi, O., Addison, J.B., Wang, Q., Shen, Z., Briggs, S.P., Bohlmann, J., Castro-Falcon, G., Hughes, C.C., Betsiashvili, M., Huffaker, A., Schmelz, E.A., Zerbe, P., 2018. Discovery, biosynthesis and stress-related accumulation of Dolabradiene-Derived defenses in maize. Plant Physiol 176, 2677–2690. https://doi.org/10.1104/pp.17.01351.

Mahalmani, V., Sinha, S., Prakash, A., Medhi, B., 2022. Translational research: bridging the gap between preclinical and clinical research. Indian J. Pharmacol. 54.

Manefield, M., de, Nys, Rkumar, N., Read, R., Givskov, M., Steinberg, P., Kjelleber, S., 1999. Evidence that halogenated furanones from Delisea pulchra inhibit acylated homoserine lactone mediated gene expression by displacing the AHL signal from its receptor protein. Microbiology (N. Y.) 145, 283–291.

Maresh, J., Zhang, J., Lynn, D.G., 2006a. The innate immunity of maize and the dynamic chemical strategies regulating two-component signal transduction in Agrobacterium tumefaciens. Chem Biol 1, 165–175.

Maresh, J., Zhang, J., Lynn, D.G., 2006b. The innate immunity of maize and the dynamic chemical strategies regulating two-component signal transduction in Agrobacterium tumefaciens. Chem Biol 1, 165–175.

Mariotte, P., Mehrabi, Z., Bezemer, M., De Deyn, G., Kulmatiski, A., Drigo, B., Veen, C., van der Heijden, M., Kardol, P., 2017. Plant-soil feedback: bridging natural and agricultural sciences. Trends Ecol. Evol. 33, 129–142.

Marques, D.M., Magalhães, P.C., Marriel, I.E., Gomes, C.C., Bortolotti, A., 2020. Azospirillum brasilense favors morphophysiological characteristics and nutrient accumulation in maize under two water regimes. Revista Brasileira de Milo e Sorgo 19, 1–17.

Martinez-Viveros, O., Jorquera, M.A., Crowley, D.E., Gajardo, G., Mora, M.L., 2010. Mechanisms and practical considerations involved in plant growth promotion by rhizobacteria. J. Soil Sci. Plant Nutr. 10, 293–319.

Massardo, F., Zúñiga, G.E., Pérez, L.M., Corcuera, L.J., 1994. Effects of hydroxamic acids on electron transport and their cellular location in corn. Phytochemistry 35, 873–876.

Mehnaz, S., Lazarovits, G., 2006. Inoculation effects of Pseudomonas putida, Gluconacetobacter azotocaptans, and Azospirillum lipoferum on corn plant growth under greenhouse conditions. Microb. Ecol. 51, 326–335.

Meihls, L.N., Handrick, V., Glauser, G., Barbier, H., Kaur, H., Haribal, M.M., Lipka, A.E., Gershenzon, J., Buckler, E.S., Erb, M., Köllner, T.G., Jander, G., 2013. Natural variation in maize aphid resistance is associated with 2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one glucoside methyltransferase activity. Plant Cell 25, 2341–2355.

Michiels, K., Croes, C., Vanderleyden, J., 1991. Two different modes of attachment of Azospirillum brasilense Sp7 to wheat roots. J. Gen. Microbiol. 137, 2241–2246.

Mirón, I.J., Linares, C., Díaz, J., 2023. The influence of climate change on food production and food safety. Environ. Res. 216, 114674.

Mishra, A., Chauhan, P.S., Chaudhry, V., Tripathi, M., Nautiyal, C.S., 2011. Rhizosphere competent Pantoea agglomerans enhances maize (Zea mays) and chickpea (Cicer arietinum L.) growth, without altering the rhizosphere functional diversity. Antonie van Leeuwenhoek, International Journal of General and Molecular Microbiology 100, 405–413. https://doi.org/10.1007/s10482-011-9596-8.

Śmist, M., Kwiecień, H., Krawczyk, M., 2016. Synthesis and antifungal activity of 2 H-1, 4-benzoxazin-3 (4 H)- one derivatives. J Environ Sci Heal B 51, 393–401.

Møldrup, M.E., Geu-Flores, F., de Vos, M., Olsen, C.E., Sun, J., Jander, G., Halkier, B.A., 2012. Engineering of benzylglucosinolate in tobacco provides proof-of-concept for dead-end trap crops genetically modified to attract Plutella xylostella (diamondback moth). Plant Biotechnol. J. 10, 435–442.

Mohanty, P., Singh, P.K., Chakraborty, D., Mishra, S., Pattnaik, R., 2021. Insight into the role of PGPR in sustainable agriculture and environment. Front. Sustain. Food Syst. 5. https://doi.org/10.3389/fsufs.2021.667150.

Monnet, V., Juillard, V., Gardan, R., 2014. Peptide conversations in grampositive bacteria. Crit. Rev. Microbiol. 8, 1–13.

Mora, P., Rosconi, F., Fraguas, L.F., 2008. Azospirillum brasilense Sp7 produces an outer-membrane lectin that specifi- cally binds to surface-exposed extracellular polysaccharide produced by the bacterium. Arch. Microbiol. 189, 519–524.

Moscardó García, M., Aalto, A., Montanari, A.N., Skupin, A., Gonçalves, J., 2025. Multi-omic network inference from time-series data. NPJ Syst Biol Appl 11, 114. https://doi.org/10.1038/s41540-025-00591-1.

Muller, E., Shiryan, I., Borenstein, E., 2024. Multi-omic integration of microbiome data for identifying disease-associated modules. Nat. Commun. 15, 2621. https://doi.org/10.1038/s41467-024-46888-3.

Neal, A.L., Ahmad, S., Gordon-Weeks, R., Ton, J., 2012. Benzoxazinoids in root exudates of maize attract pseudomonas putida to the rhizosphere. PLoS One 7. https://doi.org/10.1371/journal.pone.0035498.

Neal, A.L., Ton, J., 2013a. Systemic defense priming by Pseudomonas putida KT2440 in maize depends on benzoxazinoid exudation from the roots. Plant Signal. Behav. 8, 120–124. https://doi.org/10.4161/psb.22655.

Neal, A.L., Ton, J., 2013b. Systemic defense priming by Pseudomonas putida KT2440 in maize depends on benzoxazinoid exudation from the roots. Plant Signal. Behav. 8, 120–124. https://doi.org/10.4161/psb.22655.

Niemeyer, H.M., 1988. Hydroxamic acids (4-hydroxy-1,4-Benzoxazin-3-Ones), defense chemicals in the gramineae. Phytochemistry 27, 3349–3358.

Niemeyer, H.M., Bravo, H.R., Peña, G.F., Corcuera, L.J., 1982. Decomposition of 2,4-dihydroxy-7-methoxy-2H-1,4-benzoxazin- 3(4H)-one, a hydroxamic acid from Gramineae. In: Kehl, H. (Ed.), Chemistry and Biology of Hydroxamic Acid from Gramineae. Karger, A G, Basel, p. 2228.

Niemeyer, H.M., 2009a. Hydroxamic Acids derived from 2-Hydroxy-2 H -1 , 4-Benzoxazin-3 (4 H) -one : Key Defense Chemicals of Cereals. J. Agric. Food Chem. 3, 1677–1696.

Niemeyer, H.M., 2009b. Hydroxamic acids derived from 2-Hydroxy-2 H -1 , 4-Benzoxazin-3 (4 H) -one : Key defense Chemicals of Cereals. J. Agric. Food Chem. 3, 1677–1696.

Nobbe, F., Schmid, E., Hiltner, L., Hotter, E., 1891. Versuche über die Stickstoff - assimilation con Leguminosen. Landwirtsch Vers-Stn 39, 327–359.

Nobbe, F., Hiltner, L., 1893. Impfet den Boden. Sächsische Landwirtschaftliche Zeitschrift 16, 1–5.

Nogales, J., Bernabéu, L., Cuéllar, V., Soto, M.J., 2012. ExpR is not required for swarming but promotes sliding in Sinorhizobium meliloti. J. Bacteriol. 194, 2027–2035.

Oikawa, A., Ishihara, A., Tanaka, C., Mori, N., Tsuda, M., Iwamura, H., 2004. Accumulation of HDMBOA-Glc is induced by biotic stresses prior to the release of MBOA in maize leaves. Phytochem 65, 2995–3001.

Oliveira, A.L.M., Santos, O.J.A.P., Marcelino, P.R.F., Milani, K.M.L., Zuluaga, M.Y.A., Zucareli, C., Gonçalves, L.S.A., 2017. Maize inoculation with Azospirillum brasilense Ab-V5 cells enriched with exopolysaccharides and polyhydroxybutyrate results in high productivity under Low N fertilizer input. Front. Microbiol. 8, 1–18. https://doi.org/10.3389/fmicb.2017.01873.

Orelle, C., Durmont, C., Mathieu, K., Duchêne, B., Aros, S., Fenaile, F., André, F., Junot, C., Vernet, T., Jault, J.M., 2018. A multidrug ABC transporter with a taste for GTP. Sci. Rep. 8 article number 2309.

Pacheco da Silva, M.L., Moen, F.S., Liles, M.R., Feng, Y., Sanz-Saez, A., 2022. The response to inoculation with PGPR plus Orange peel amendment on soybean is cultivar and environment dependent. Plants 11. https://doi.org/10.3390/plants11091138.

Palková, Z., 2004. Multicellular microorganisms: laboratory versus nature. EMBO Rep. 5, 470–476. https://doi.org/10.1038/sj.embor.7400145.

Palma, V., Gutiérrez, M.S., Vargas, O., Parthasarathy, R., Navarrete, P., 2022. Methods to evaluate bacterial motility and its role in bacterial–host interactions. Microorganisms. https://doi.org/10.3390/microorganisms10030563.

Pang, Y., Liu, X., Ma, Y., 2009. Induction of systemic resistance , root colonisation and biocontrol activities of the rhizospheric strain of Serratia plymuthica are dependent on N-acyl homoserine lactones. J. Plant Pathol. 261–268. https://doi.org/10.1007/s10658-008-9411-1.

Parkinson, J.S., Hazelbauer, G.L., Falke, J.J., 2015. Signaling and sensory adaptation in Escherichia coli chemoreceptors. Trends Microbiol. 23, 257–266.

Pausch, J., Kuzyakov, Y., 2018. Carbon input by roots into the soil: quantification of rhizodeposition from root to ecosystem scale. Glob Chang Biol 24, 1–12.

Pereg, L., de-Bashan, L.E., Bashan, Y., 2016. Assessment of affinity and specificity of Azospirillum for plants. Plant Soil 399, 389–414. https://doi.org/10.1007/s11104-015-2778-9.

Peters, D.L., Wang, W., Zhang, X., Ning, Z., Mayne, J., Figeys, D., 2019. Metaproteomic and metabolomic approaches for characterizing the gut microbiome. Proteomics 19, 1800363. https://doi.org/10.1002/pmic.201800363.

Prüß, B.M., 2017. Involvement of two-component signaling on bacterial motility and biofilm development. J. Bacteriol. 199. https://doi.org/10.1128/JB.00259-17.

Pérez, F.J., Niemeyer, H.M., 1989. Reaction of DIMBOA with amines. Phytochemistry 28, 1831–1834.

Quecine, M.C., Araújo, W.L., Rossetto, P.B., Ferreira, A., Tsui, S., Lacava, P.T., Mondin, M., Azevedo, J.L., Pizzirani-Kleiner, A.A., 2012. Sugarcane growth promotion by the endophytic bacterium Pantoea agglomerans 33.1. Appl. Environ. Microbiol. 78, 7511–7518. https://doi.org/10.1128/AEM.00836-12.

Quecine, M.C., Kidarsa, T.A., Goebel, N.C., Shaffer, B.T., Henkels, M.D., Zabriskie, T.M., Loper, J.E., 2016. An interspecies signaling System mediated by fusaric acid has parallel effects on antifungal metabolite production by Pseudomonas protegens strain Pf-5 and antibiosis of fusarium spp. Appl. Environ. Microbiol. 82, 1372–1382. https://doi.org/10.1128/aem.02574-15.

Rakoczy-Trojanowska, M., Orczyk, W., Krajewski, P., Bocianowski, J., Stochmal, A., Kowalczyk, M., 2017. ScBx gene based association analysis of hydroxamate content in rye (Secale cereale L.). J. Appl. Genet. 58, 1–9.

Rasmussen, T.B., Bjarnsholt, T., Skindersoe, M.E., Hentzer, M., P, K., Kote, P., Neilsen, J., Eberl, L., Givskov, M., 2005. Screening for quorum sensing inhibitors (QSI) by use of a novel genetic system. J. Bacteriol. 187, 1799–1814.

Regasa, A., Haile, W., Abera, G., 2025. Variation in soil acidity across different land uses, soil types and altitudinal gradients in Western Oromia, Ethiopia. Sci. Rep. 15, 31565. https://doi.org/10.1038/s41598-025-13597-w.

Renoud, S., Abrouk, D., Prigent-Combaret, C., Wisniewski-Dyé, F., Legendre, L., Moënne-Loccoz, Y., Muller, D., 2022. Effect of inoculation level on the impact of the PGPR Azospirillum lipoferum CRT1 on selected microbial functional groups in the rhizosphere of field maize. Microorganisms 10. https://doi.org/10.3390/microorganisms10020325.

Rice, C.P., Cai, G., Teasdale, J.R., 2012. Concentrations and allelopathic effects of benzoxazinoid compounds in soil treated with rye (Secale cereale) cover crop. J. Agric. Food Chem. 60, 4471–4479. https://doi.org/10.1021/jf300431r.

Richardson, M.D., Bacon, C.W., 1995. Catabolism of 6-methoxy-benzoxazolinone and 2-benzoxazolinone by Fusarium moniliforme. Mycologia 87, 510–517. https://doi.org/10.1080/00275514.1995.12026562.

Robert, C.A.M., Veyrat, N., Glauser, G., Marti, G., Doyen, G.R., Villard, N., Gaillard, M.D. P., Köllner, T.G., Giron, D., Body, M., Babst, B.A., Ferrieri, R.A., Turlings, T.C.J., Erb, M., 2012. A specialist root herbivore exploits defensive metabolites to locate nutritious tissues. Ecol. Lett. 15, 55–64. https://doi.org/10.1111/j.1461-0248.2011.01708.x.

Rosemeyer, V., Michiels, J., Verreth, C., Vanderleyden, J., 1998. luxI- and luxR-homologous genes of Rhizobium etli CNPAF512 contribute to synthesis of autoinducer molecules and nodulation of Phaseolus vulgaris. J. Bacteriol. 180, 815–821.

Rossi, F.A., Medeot, D.B., Liaudat, J.P., Pistorio, M., Jofré, E., 2016. In Azospirillum brasilense, mutations in flmA or flmB genes affect polar flagellum assembly, surface polysaccharides, and attachment to maize roots. Microbiol. Res. 190, 55–62. https://doi.org/10.1016/j.micres.2016.05.006.

Sasse, J., Martinoia, E., Northen, T., 2018. Feed your friends : do plant exudates shape the root microbiome. Trends Plant Sci. 23, 25–41. https://doi.org/10.1016/j.tplants.2017.09.003.

Sauer, K., Camper, A.K., Ehrlich, G.D., Costerton, J.W., Davies, D.G., 2002. Pseudomonas aeruginosa displays multiple phenotypes during development as a biofilm. J. Bacteriol. 184, 1140–1154.

Saunders, M., Kohn, L.M., 2008. Host-synthesized secondary compounds influence the in vitro interactions between fungal endophytes of maize. Appl. Environ. Microbiol. 74, 136–142. https://doi.org/10.1128/AEM.01538-07.

Schaefer, A.L., Val, D.L., Hanzelka, B.L., 1996. Generation of cell-tocell signals in quorum sensing: acyl homoserine lactone synthase activity of a purified Vibrio fischeri LuxI protein. P Natl Acad Sci USA 93, 9505–9509.

Schandry, N., Jandrasits, K., Garrido-Oter, R., Becker, C., 2021. Plant-derived benzoxazinoids act as antibiotics and shape bacterial communities. bioRxiv. https://doi.org/10.1101/2021.01.12.425818.

Schenk, S.T., Hernández-reyes, C., Samans, B., Stein, E., Neumann, C., Schikora, M., Reichelt, M., Mithöfer, A., Becker, A., Kogel, K., Schikora, A., 2014. N -Acyl-Homoserine lactone primes plants for cell Wall reinforcement and induces resistance to bacterial pathogens via the salicylic acid/oxylipin pathway. Plant Cell 26, 2708–2723. https://doi.org/10.1105/tpc.114.126763.

Schikora, A., Schenk, S.T., Hartmann, A., 2016. Beneficial effects of bacteria-plant communication based on quorum sensing molecules of the N-acyl homoserine lactone group. Plant Mol. Biol. 90, 605–612. https://doi.org/10.1007/s11103-016-0457-8.

Schikora, A., Schenk, S.T., Stein, E., Molitor, A., Zuccaro, A., Kogel, K.-H., 2011. N-Acyl-Homoserine lactone confers resistance toward biotrophic and hemibiotrophic pathogens via altered activation of AtMPK6. Plant Physiol 157, 1407–1418. https://doi.org/10.1104/pp.111.180604.

Schloter, M., Hartmann, A., 1998. Endophytic and surface colonization of wheat roots (Triticum aestivum) by different Azospirillum brasilense strains studied with strain-specific monoclonal antibodies. Symbiosis 25, 159–179.

Schmelz, E.A., Kaplan, F., Huffaker, A., Dafoe, N.J., Vaughan, M.M., Ni, X., Rocca, J.R., Alborn, H.T., Teal, P.E., 2011. Identity, regulation, and activity of inducible diterpenoid phytoalexins in maize. Proc. Natl. Acad. Sci. 108, 5455–5460. https://doi.org/10.1073/pnas.1014714108.

Schmidt, R., Cordovez, V., de Boer, W., Raaijmakers, J., Garbeva, P., 2015. Volatile affairs in microbial interactions. ISME J. 9, 2329–2335.

Schnider-Keel, U., Seematter, A., Maurhofer, M., Blumer, C., Duffy, B., Gigot-Bonnefoy, C., Reinmann, C., Notz, R., Défago, G., Haas, D., Keel, C., 2000. Autoinduction of 2,4- diacetylphloroglucinol biosynthesis in the biocontrol agent Pseudomonas fluorescens CHA0 and repression by the bacterial metabolites salicylate and pyoluteorin. J. Bacteriol. 182, 1215–1225.

Schütz, L., Gattinger, A., Meier, M., Müller, A., Boller, T., Mäder, P., Mathimaran, N., 2018. Improving crop yield and nutrient use efficiency via biofertilization—A global meta-analysis. Front. Plant Sci. 8. https://doi.org/10.3389/fpls.2017.02204.

Schullehner, K., Dick, R., Vitzthum, F., Schwab, W., Brandt, W., Frey, M., Gierl, A., 2008. Benzoxazinoid biosynthesis in dicot plants. Phytochemistry 69, 2668–2677. https://doi.org/10.1016/j.phytochem.2008.08.023.

Schulz, M., Marocco, A., Tabaglio, V., Macías, F.A., Molinillo, J.M.G., 2013. Benzoxazinoids in rye allelopathy - from discovery to application in sustainable weed control and organic farming. J. Chem. Ecol. 39, 154–174.

Schulz-bohm, K., Gerards, S., Hundscheid, M., Melenhorst, J., Boer, W. de, Garbeva, P., 2018. Calling from distance : attraction of soil bacteria by plant root volatiles. ISME J. 1252–1262. https://doi.org/10.1038/s41396-017-0035-3.

Senthilkumar, M., Anadham, R., Madhaiyan, M., Venkateswaran, V., Sa, T., 2011. Endophytic bacteria: perspectives and applications in agricultural crop production. In: Bacteria in Aagrobiology: Crop Ecosystems. Springer, pp. 61–96.

Shah, A., Nazari, M., Antar, M., Msimbira, L.A., Naamala, J., Lyu, D., Rabileh, M., Zajonc, J., Smith, D.L., 2021. PGPR in agriculture: a sustainable approach to increasing climate change resilience. Front. Sustain. Food Syst. 5. https://doi.org/10.3389/fsufs.2021.667546.

Shakya, M., Lo, C.-C., Chain, P.S.G., 2019. Advances and challenges in metatranscriptomic analysis. Front. Genet. 10–2019. https://doi.org/10.3389/fgene.2019.00904.

Sharpton, T.J., 2014. An introduction to the analysis of shotgun metagenomic data. Front. Plant Sci. 5–2014. https://doi.org/10.3389/fpls.2014.00209.

Shelud'ko, A.V., Filip'echeva, Y.A., Telesheva, E.M., Yevstigneeva, S.S., Petrova, L.P., Katsy, E.I., 2019. Polar flagellum of the alphaproteobacterium Azospirillum brasilense Sp245 plays a role in biofilm biomass accumulation and in biofilm maintenance under stationary and dynamic conditions. World J. Microbiol. Biotechnol. 35. https://doi.org/10.1007/s11274-019-2594-0.

Shelud'ko, A.V., Mokeev, D.I., Evstigneeva, S.S., Filip'echeva, Y.A., Burov, A.M., Petrova, L.P., Ponomareva, E.G., Katsy, E.I., 2020a. Cell ultrastructure in Azospirillum brasilense biofilms. Microbiology (Russian Federation) 89, 50–63. https://doi.org/10.1134/S0026261720010142.

Shelud'ko, A.V., Mokeev, D.I., Evstigneeva, S.S., Filip'echeva, Y.A., Burov, A.M., Petrova, L.P., Ponomareva, E.G., Katsy, E.I., 2020b. Cell ultrastructure in Azospirillum brasilense biofilms. Microbiology (Russian Federation) 89, 50–63. https://doi.org/10.1134/S0026261720010142.

Shimizu, S., Hoyer, P.O., Hyvärinen, A., Kerminen, A.J., 2006. A linear Non-Gaussian acyclic model for causal discovery. J. Mach. Learn. Res. 7, 2003–2030.

Shumilova, E.M., Shelud'ko, A.V., Filip'echeva, Y.A., Evstigneeva, S.S., Ponomareva, E. G., Petrova, L.P., Katsy, E.I., 2016. Changes in cell surface properties and biofilm formation efficiency in Azospirillum brasilense Sp245 mutants in the putative genes of lipid metabolism mmsB1 and fabG1. Microbiology (Russian Federation) 85, 172–179. https://doi.org/10.1134/S002626171602017X.

Silversmith, R.E., 2010. Auxiliary phosphatases in two-component signal transduction. Curr. Opin. Microbiol. 13, 177–183.

Siuti, P., Green, C., Edwards, A.N., Doktycz, M.J., Alexandre, G., 2011a. The chemotaxis-like Che1 pathway has an indirect role in adhesive cell properties of Azospirillum brasilense. FEMS Microbiol. Lett. 323, 105–112. https://doi.org/10.1111/j.1574-6968.2011.02366.x.

Siuti, P., Green, C., Edwards, A.N., Doktycz, M.J., Alexandre, G., 2011b. The chemotaxis-like Che1 pathway has an indirect role in adhesive cell properties of Azospirillum brasilense. FEMS Microbiol. Lett. 323, 105–112. https://doi.org/10.1111/j.1574-6968.2011.02366.x.

Sivakumar, R., Ranjani, J., Vishnu, U.S., Jayashree, S., Lozano, G.L., Miles, J., Broderick, N.A., Guan, C., Gunasekaran, P., Handelsman, J., Rajendhran, J., 2019. Evaluation of inseq to identify genes essential for pseudomonas aeruginosa PGPR2 corn root colonization. G3: genes, Genomes. Genetics 9, 651–661. https://doi.org/10.1534/g3.118.200928.

Sivaram, A.K., Abinandan, S., Chen, C., Venkateswartlu, K., Megharaj, M., 2023. Chapter two - microbial inoculant carriers: soil health improvement and moisture retention in sustainable agriculture. In: Sparks, D.L. (Ed.), Advances in Agronomy. Academic Press, pp. 35–91. https://doi.org/10.1016/bs.agron.2023.03.001.

Søltoft, M., Jørgensen, L.N., Svensmark, B., Fomsgaard, I.S., 2008. Benzoxazinoid concentrations show correlation with Fusarium Head Blight resistance in Danish wheat varieties. Biochem Syst Ecol 36, 245–259.

Smith-Ramesh, L.M., Reynolds, H.L., 2017. The next frontier of plant–soil feedback research: unraveling context dependence across biotic and abiotic gradients. J. Veg. Sci. 28, 484–494.

Solano, C., Echever, M., Lasa, I., 2014. Biofilm dispersion and quorum sensing. Curr. Opin. Microbiol. 18, 96–104.

Spiers, A.J., Bohannon, J., Gehrig, S.M., 2003. Biofilm formation at the air-liquid interface by the Pseudomonas fluorescens SBW25 wrinkly spreader requires an acetylated form of cellulose. Mol. Microbiol. 50, 15–27.

Stahl, E., 2022. New insights into the transcriptional regulation of benzoxazinoid biosynthesis in wheat. J. Exp. Bot. 73, 5358–5360. https://doi.org/10.1093/jxb/erac244.

Subiramani, S., Ramalingam, S., Muthu, T., Nile, S.H., Venkidasamy, B., 2020. Development of abiotic stress tolerance in crops by plant growth-promoting rhizobacteria (PGPR). In: Kumar, M., Kumar, V., Prasad, R. (Eds.), Phyto-Microbiome in Stress Regulation. Springer Singapore, Singapore, pp. 125–145. https://doi.org/10.1007/978-981-15-2576-6_8.

Subramanian, I., Verma, S., Kumar, S., Jere, A., Anamika, K., 2020. Multi-omics data integration, interpretation, and its application. Bioinform Biol Insights 14, 1177932219899051. https://doi.org/10.1177/1177932219899051.

Surette, M.G., Miller, M.B., Bassler, B.L., 1999. Quorum sensing in Escherichia coli, Salmonella typhimurium, and Vibrio harveyi: a new family of genes responsible for autoinducer production. PNatl Acad Sci USA 96, 1639–1644.

Tabaglio, V., Gavazzi, C., Schulz, M., Marocco, A., 2008. Alternative weed control using the allelopathic effect of natural benzoxazinoids from rye mulch. Agron. Sustain. Dev. 28, 397–401. https://doi.org/10.1051/agro:2008004.

Tabassum, B., Khan, A., Tariq, M., Ramzan, M., Iqbal Khan, M.S., Shahid, N., Aaliya, K., 2017. Bottlenecks in commercialisation and future prospects of PGPR. Appl. Soil Ecol. 121, 102–117. https://doi.org/10.1016/j.apsoil.2017.09.030.

Tanwir, F., Fredholm, M., Gregersen, P.L., Fomsgaard, I.S., 2013. Comparison of the levels of bioactive benzoxazinoids in different wheat and rye fractions and the transformation of these compounds in homemade foods. Food Chem. 141, 444–450.

Tattersall, D.B., Bak, S., Jones, P.R., Olsen, C.E., Nielsen, J.K., Hansen, M.L., Høj, P.B., Møller, B.L., 2001. Resistance to an herbivore through engineered cyanogenic glucoside synthesis. Science (1979) 293, 1826–1828.

Teste, F.P., Kardol, P., Turner, B.L., Wardle, D.A., Zemunik, G., Renton, M., Laliberté, E., 2017a. Plant-soil feedback and the maintenance of diversity in Mediterranean-climate shrublands. Science (1979) 355, 173–176. https://doi.org/10.1126/science.aai8291.

Teste, F.P., Kardol, P., Turner, B.L., Wardle, D.A., Zemunik, G., Renton, M., Laliberté, E., 2017b. Plant-soil feedback and the maintenance of diversity in Mediterranean-climate shrublands. Science (1979) 355, 173–176. https://doi.org/10.1126/science.aai8291.

Thoenen, L., Giroud, C., Kreuzer, M., Waelchli, J., Gfeller, V., Deslandes-Hérold, G., Mateo, P., Robert, C.A.M., Ahrens, C.H., Rubio-Somoza, I., Bruggmann, R., Erb, M., Schlaeppi, K., 2023a. Bacterial tolerance to host-exuded specialized metabolites structures the maize root microbiome. Proc. Natl. Acad. Sci. U. S. A. 120, e2310134120. https://doi.org/10.1073/pnas.2310134120.

Thoenen, L., Giroud, C., Kreuzer, M., Waelchli, J., Gfeller, V., Deslandes-Hérold, G., Mateo, P., Robert, C.A.M., Ahrens, C.H., Rubio-Somoza, I., Bruggmann, R., Erb, M., Schlaeppi, K., 2023b. Bacterial tolerance to host-exuded specialized metabolites structures the maize root microbiome. Proc. Natl. Acad. Sci. U. S. A. 120, e2310134120. https://doi.org/10.1073/pnas.2310134120.

Toju, H., Peay, K.G., Yamamichi, M., Narisawa, K., Hiruma, K., Naito, K., Fukuda, S., Ushio, M., Nakaoka, S., Onoda, Y., Yoshida, K., Schlaeppi, K., Bai, Y., Sugiura, R., Ichihashi, Y., Minamisawa, K., Kiers, E.T., 2018. Core microbiomes for sustainable agroecosystems. Nat. Plants 4, 247–257. https://doi.org/10.1038/s41477-018-0139-4.

Tomohiro, K., Pin, C.Y., Sean, N.R., W, D.A., 2008. Rapid screening of quorum-sensing signal N-Acyl homoserine lactones by an In vitro cell-free assay. Appl. Environ. Microbiol. 74, 3667–3671. https://doi.org/10.1128/AEM.02869-07.

Tzipilevich, E., Russ, D., Dangl, J.L., Benfey, P.N., 2021. Plant immune system activation is necessary for efficient root colonization by auxin-secreting beneficial bacteria. Cell Host Microbe 29, 1507–1520.e4. https://doi.org/10.1016/j.chom.2021.09.005.

Ude, S., Arnold, D.L., Moon, C.D., Timms-Wilson, T., Spiers, A.J., 2006. Biofilm formation and cellulose expression among diverse environmental Pseudomonas isolates. Environ. Microbiol. 8, 1997–2011.

Ueda, A., Saneoka, H., 2015. Characterization of the ability to form biofilms by plant-associated pseudomonas species. Curr. Microbiol. 70, 506–513. https://doi.org/10.1007/s00284-014-0749-7.

Ugidos, M., Nueda, M.J., Prats-Montalbán, J.M., Ferrer, A., Conesa, A., Tarazona, S., 2022. MultiBaC: an R package to remove batch effects in multi-omic experiments. Bioinformatics 38, 2657–2658. https://doi.org/10.1093/bioinformatics/btac132.

Understrup, A.G., Ravnskov, S., Hansen, H.C.B., Fomsgaard, I.S., 2005a. Biotransformation of 2-benzoxazolinone to 2-amino-3Hphenoxazin- 3-one and 2-acetylamino-3H-phenoxazin-3-one in soil. J. Chem. Ecol. 31, 1205–1222.

Understrup, A.G., Ravnskov, S., Hansen, H.C.B., Fomsgaard, I.S., 2005b. Biotransformation of 2-benzoxazolinone to 2-amino-3Hphenoxazin- 3-one and 2-acetylamino-3H-phenoxazin-3-one in soil. J. Chem. Ecol. 31, 1205–1222.

Van Dam, N.M., Weinhold, A., Garbeva, P., 2016. Calling in the dark: the role of volatiles for communication in the rhizosphere. In: Blande, J.D., Glinwood, R. (Eds.), Deciphering Chemical Language of Plant Communication. Springer International Publishing Cham, pp. 175–210.

Van Rij, E.T., Girard, G., Lugtenberg, B.J.J., Bloemberg, G.V., 2005. Influence of fusaric acid on phenazine-1-carboxamide synthesis and gene expression of Pseudomonas chlororaphis strain PCL1391. Microbiology (N. Y.) 151, 2805–2814.

Vande Broek, A., Lambrecht, M., Vanderleyden, J., 1998a. Bacterial chemotactic motility is important for the initiation of wheat root colonization by Azospirillum brasilense. Microbiology (N. Y.) 144, 2599–2606. https://doi.org/10.1099/00221287-144-9-2599.

Vande Broek, A., Lambrecht, M., Vanderleyden, J., 1998b. Bacterial chemotactic motility is important for the initiation of wheat root colonization by Azospirillum brasilense. Microbiology (N. Y.) 144, 2599–2606. https://doi.org/10.1099/00221287-144-9-2599.

VanEtten, H.D., Mansfield, J.W., Bailey, J.A., Farmer, E.E., 1994. Two classes of plant antibiotics: phytoalexins versus "phytoanticipins.". Plant Cell 6, 1191–1192.

Venturi, V., Keel, C., 2016. Signaling in the rhizosphere. Trends Plant Sci. 21, 187–198.

Vermeer, J.H., McCully, M.E., 1982. The rhizosphere in Zea: new insight into its structure and development. Planta 156, 45–61.

Vesper, S.J., 1987. Production of pili (fimbriae) by Pseudomonas fluorescens and correlation with attachment to corn roots. Appl Environ Microb 53, 1397–1405.

Villagrasa, M., Guillamón, M., Labandeira, A., Taberner, A., Eljarrat, E., Barceló, D., 2006. Benzoxazinoid allelochemicals in wheat: distribution among foliage, roots, and seeds. J. Agric. Food Chem. 54, 1009–1015.

Virtanen, I.A., Hietala, P., 1960. Precursors of benzoxazolinone in rye plants. II. Precursor I, the glucoside. Acta Chem. Scand. 499–502.

Virtanen, A.I., Hietala, P.K., 1955a. Benzoxazolinone an anti-fusarium factor in rye seedlings. Acta Chem. Scand. 9, 1543–1544.

Virtanen, A.I., Hietala, P.K., 1955b. The structure of the precursors of benzoxazolinone in rye plants. Suom. Kemistil. A 32, 252.

Viruega-Góngora, V.I., Acatitla-Jácome, I.S., Reyes-Carmona, S.R., Baca, B.E., Ramírez-Mata, A., 2020a. Spatio-temporal formation of biofilms and extracellular matrix analysis in Azospirillum brasilense. FEMS Microbiol. Lett. 367, 1–10. https://doi.org/10.1093/femsle/fnaa037.

Viruega-Góngora, V.I., Acatitla-Jácome, I.S., Reyes-Carmona, S.R., Baca, B.E., Ramírez-Mata, A., 2020b. Spatio-temporal formation of biofilms and extracellular matrix analysis in Azospirillum brasilense. FEMS Microbiol. Lett. 367, 1–10. https://doi.org/10.1093/femsle/fnaa037.

Von Rad, U., Hüttl, R., Lottspeich, F., Gierl, A., Frey, M., 2001. Two glucosyltransferases are involved in detoxification of benzoxazinoids in maize. Plant J. 28, 633–642. https://doi.org/10.1046/j.1365-313x.2001.01161.x.

Vurukonda, S.S.K.P., Vardharajula, S., Shrivastava, M., SkZ, A., 2016. Enhancement of drought stress tolerance in crops by plant growth promoting rhizobacteria. Microbiol. Res. 184, 13–24. https://doi.org/10.1016/j.micres.2015.12.003.

Walker, V., Bertrand, C., Bellvert, F., Moënne-Loccoz, Y., Bally, R., Comte, G., 2011a. Host plant secondary metabolite profiling shows a complex, strain-dependent response of maize to plant growth-promoting rhizobacteria of the genus Azospirillum. New Phytol. 189, 494–506. https://doi.org/10.1111/j.1469-8137.2010.03484.x.

Walker, V., Bertrand, C., Bellvert, F., Moënne-Loccoz, Y., Bally, R., Comte, G., 2011b. Host plant secondary metabolite profiling shows a complex, strain-dependent response of maize to plant growth-promoting rhizobacteria of the genus Azospirillum. New Phytol. 189, 494–506. https://doi.org/10.1111/j.1469-8137.2010.03484.x.

Walker, V., Bertrand, C., Bellvert, F., Moënne-Loccoz, Y., Bally, R., Comte, G., 2011c. Host plant secondary metabolite profiling shows a complex, strain-dependent response of maize to plant growth-promoting rhizobacteria of the genus Azospirillum. New Phytol. 189, 494–506. https://doi.org/10.1111/j.1469-8137.2010.03484.x.

Wang, D., Xu, A., Elmerich, C., Ma, L.Z., 2017. Biofilm formation enables free-living nitrogen-fixing rhizobacteria to fix nitrogen under aerobic conditions. ISME J. 11, 1602–1613. https://doi.org/10.1038/ismej.2017.30.

Wei, H.L., Zhang, L.Q., 2006. Quorum-sensing system influences root colonization and biological control ability in Pseudomonas fluorescens 2P24. Antonie van Leeuwenhoek, International Journal of General and Molecular Microbiology 89, 267–280. https://doi.org/10.1007/s10482-005-9028-8.

Weston, L.A., Ryan, P.R., Watt, M., 2012. Mechanisms for cellular transport and release of allelochemicals from plant roots into the rhizosphere. J. Exp. Bot. 63, 3445–3454.

Weston, L.A., Mathesius, U., 2013. Flavonoids: their structure, biosynthesis and role in the rhizosphere, including allelopathy. J. Chem. Ecol. 39, 283–297. https://doi.org/10.1007/s10886-013-0248-5.

Wheatly, R.M., Poole, S., 2018. Mechanisms of bacterial attachment to roots. FEMS Microbiol. Rev. 42, 448–461.

Whitehead, N.A., L, B.A.M., Slater, H., 2001. Quorum-sensing in gram-negative bacteria. FEMS Microbiol. Rev. 25, 365–404.

Whiteley, M., Bangera, M.G., Bumgarner, R.E., Parsek, M.R., Teitzel, G.M., Lory, S., Greenberg, E.P., 2001. Gene expression in Pseudomonas aeruginosa biofilms. Nature 413, 860–864.

Wisniewski-Dyé, F., Jones, J., Chhabra, S.R., Downie, J.A., 2002. raiIR Genes are part of a quorum-sensing network controlled by cinI and cinR in Rhizobium leguminosarum. J Bacteriol2 184, 2002.

Wong-Ng, J., Melbinger, A., Celani, A., Vergassola, M., 2016. The role of adaptation in bacterial speed races. PLoS Comput. Biol. 397, 168–171.

Wongsuk, T., Pumeesat, P., Luplertlop, N., 2016. Fungal quorum sensing molecules: role in fungal morphogenesis and pathogenicity. J. Basic Microbiol. 56, 440–447. https://doi.org/10.1002/jobm.201500759.

Woodward, M.D., Corcuera, L.J., Helgeson, J.P., Upper, C.D., 1978. Decomposition of 2,4-Dihydroxy-7-methoxy-2H-1,4-benzoxazin-3(4H)-one in Aqueous Solutions 1. Plant Physiol 61, 796–802. https://doi.org/10.1104/pp.61.5.796.

Wouters, F.C., Gershenzon, J., Vassão, D.G., 2016. Benzoxazinoids: reactivity and modes of action of a versatile class of plant chemical defenses. J. Braz. Chem. Soc. 27, 1379–1397. https://doi.org/10.5935/0103-5053.20160177.

Wu, Xiaogang, Li, J., Ji, M., Wu, Q., Wu, Xinxin, Ma, Y., Sui, W., Zhao, L., Zhang, X., 2019. Non-synchronous structural and functional dynamics during the coalescence of two distinct soil bacterial communities. Front. Microbiol. 10–2019. https://doi.org/10.3389/fmicb.2019.01125.

Wuichet, K., Zhulin, I.B., 2010. Origins and diversification of a complex signal transduction system in prokaryotes. Sci. Signal. 3. https://doi.org/10.1126/scisignal.2000724 ra50.

Xu, W., Wang, Z., Wu, F., 2015a. The effect of D123 wheat as a companion crop on soil enzyme activities, microbial biomass and microbial communities in the rhizosphere of watermelon. Front. Microbiol. 6. https://doi.org/10.3389/fmicb.2015.00899.

Xu, W., Wang, Z., Wu, F., 2015b. The effect of D123 wheat as a companion crop on soil enzyme activities, microbial biomass and microbial communities in the rhizosphere of watermelon. Front. Microbiol. 6. https://doi.org/10.3389/fmicb.2015.00899.

Yactayo-Chang, J.P., Block, A.K., 2023. The impact of climate change on maize chemical defenses. Biochem. J. 480, 1285–1298. https://doi.org/10.1042/BCJ20220444.

Yang, Z., Cao, Y., Shi, Y., Qin, F., Jiang, C., Yang, S., 2023. Genetic and molecular exploration of maize environmental stress resilience: toward sustainable agriculture. Mol. Plant 16, 1496–1517. https://doi.org/10.1016/j.molp.2023.07.005.

Yang, W., Briegel, A., 2020. Diversity of bacterial chemosensory arrays. Trends Microbiol. 28, 68–80.

Yi, T.M., Huang, Y., Simon, M.I., 2000. Robust perfect adaptation in bacterial chemotaxis through integral feedback control. Porc Natl Acad Sci USA 97, 4649–4653.

Yin, W., Wang, Y., Liu, L., He, J., 2019. Biofilms: the microbial "Protective Clothing" in extreme environments. Int. J. Mol. Sci. 20, 3423.

Young, C.-C., Rekha, P.D., Lai, W.-A., Arun, A.B., 2006. Encapsulation of plant growth-promoting bacteria in alginate beads enriched with humic acid. Biotechnol. Bioeng. 95, 76–83. https://doi.org/10.1002/bit.20957.

Yu, P., He, X., Baer, M., Beirinckx, S., Tian, T., Moya, Y.A.T., Zhang, X., Deichmann, M., Frey, F.P., Bresgen, V., Li, C., Razavi, B.S., Schaaf, G., von Wirén, N., Su, Z., Bucher, M., Tsuda, K., Goormachtig, S., Chen, X., Hochholdinger, F., 2021. Plant flavones enrich rhizosphere Oxalobacteraceae to improve maize performance under nitrogen deprivation. Nat. Plants 7, 481–499. https://doi.org/10.1038/s41477-021-00897-y.

Yue, Q., Bacon, C.W., Richardson, M.D., 1998a. Biotransformation of 2-benzoxazolinone and 6-methoxy-benzoxazolinone by Fusarium moniliforme. Phytochemistry 48, 451–454.

Yue, Q., Bacon, C.W., Richardson, M.D., 1998b. Biotransformation of 2-benzoxazolinone and 6-methoxy-benzoxazolinone by Fusarium moniliforme. Phytochemistry 48, 451–454.

Zarkani, A.A., Stein, E., Röhrich, C.R., Schikora, M., 2013. Homoserine lactones influence the reaction of plants to Rhizobia. Journal of Molecular Sience 17122–17146. https://doi.org/10.3390/ijms140817122.

Zhang, L., Li, S., Liu, X., Wang, Z., Jiang, M., Wang, R., Xie, X., Shang, D., Li, M., Wei, Z., Wang, Y., Fan, C., Luo, Z.Q., Shen, X., 2020. Sensing of autoinducer-2 by functionally distinct receptors in prokaryotes. Nat. Commun. 11, 5371.

Zhang, S., Zhu, Q., de Vries, W., Ros, G.H., Chen, X., Muneer, M.A., Zhang, F., Wu, L., 2023. Effects of soil amendments on soil acidity and crop yields in acidic soils: a world-wide meta-analysis. J Environ Manage 345, 118531. https://doi.org/10.1016/j.jenvman.2023.118531.

Zhou, C., Ma, Z., Lu, X., Zhu, L., Yan, C., 2020a. Pseudomonas fluorescens MZ05 enhances resistance against Setosphaeria turcica by mediating benzoxazinoid metabolism in the maize inbred line Anke35. agriculture 10, 1–14. https://doi.org/10.3390/agriculture10020032.

Zhou, C., Ma, Z., Lu, X., Zhu, L., Yan, C., 2020b. Pseudomonas fluorescens MZ05 enhances resistance against Setosphaeria turcica by mediating benzoxazinoid metabolism in the maize inbred line Anke35. agriculture 10, 1–14. https://doi.org/10.3390/agriculture10020032.