



作物化感作用类型: 中国研究现状及其展望

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Crop allelopathy types: Current research status and prospects in China^{*}

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Abstract: In this review, we present details of recent advances in research on different types and action modes of crop allelopathy in China. In particular, we focus not only on direct and indirect allelopathy but also on intra- and interspecific interactions, with the aim of informing international peers of the ongoing developments in this field. The term crop allelopathy was first defined in 1984, and since that time, substantial progress has been made in this area, during which the concept of crop allelopathy has been broadened to encompass plant-soil-microbial interactions, including amensalism, autotoxicity, and facilitation in cropping systems. Recent studies have revealed that donor plants are able to trigger the expression of defense-related genes, resulting in the release of specific metabolites (allelochemicals) into the environment. In particular, allelopathic crops have been found to secrete these chemicals into the soil environment via root exudation in response to stresses induced by target plants (such as weeds), which in turn results in allelopathic amensalism and allelopathic commensalisms in cropping systems. The amensalistic and commensalistic components of crop allelopathy can be further divided into intra- and interspecific interactions based on mode of action. Interspecific interactions involve the inhibitory or facilitative effects of donors on recipient plants, depending on the types, concentrations, and bio-activity of allelochemicals; whereas intraspecific interactions include auto-promotive and auto-toxic effects, which can be either positive or negative. The current consensus indicates that both positive and negative allelopathic interactions are mediated via changes in rhizosphere soil microbial composition and structure in response to root allelopathic secretions. In this regard, however, there is often an imbalance in the composition of soil microbial communities, which is largely attributable to an increase in pathogen populations and reduction in those of beneficial bacteria as a consequence of consecutive monoculture cropping. Such imbalances inevitably lead to three undesirable outcomes in continuous cropping systems, namely, soil nutrient sequestration, soil acidification, and the outbreak of soil-borne diseases, thereby resulting in reduced crop yields and quality. Conversely, in the case of positive allelopathic interactions, continuous cropping can contribute to promoting increases in microbial diversity mainly as a consequence of increments in the populations of beneficial bacteria and corresponding reductions in pathogenic microorganisms, thereby enhancing soil micro-habitats, and thus increasing crop yield and quality. Given these responses, a key priority for future research is more in-depth studies of the structure and function of rhizosphere microbial communities, and appropriate modification of rhizosphere habitats, with the aim of producing high-yielding good quality crops for sustainable agricultural development.

Keywords: Crop allelopathy; Amensalism; Commensalism; Action mode; Soil microorganism

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作物化感作用类型：中国研究现状及其展望^{*}

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摘 要: 本文从作物种内互作和种间互作以及直接化感作用和间接化感作用两个维度重点阐述了近年来中国在作

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物化感作用类型的研究及其新进展,以期与同行分享该领域的研究成果和经验。早在 1984 年就有作物化感作用的相关报道,近年来取得了很大的进展。作物化感作用的概念也延伸到植物-土壤-微生物相互之间的化感作用,作物种植体系中存在的偏害、自毒和促进等现象均与此有关。最近的研究表明,供体植物通过触发防御基因的表达,使代谢产物(化感物质)释放到环境中,尤其是土壤环境中作物的根系等对靶标植物(如杂草)的胁迫做出响应,从而在栽培系统中产生化感偏害或化感偏利现象。根据作用对象的不同,作物化感偏害和偏利现象分为种间和种内的相互作用两种类型。种间作用包括抑制和互惠作用,化感物质的种类、含量及其生物效应决定了其对邻近物种的化感效应;种内作用包括促进和自毒作用,即化感正效应和化感负效应。化感正效应或负效应均与根系分泌物介导的根际土壤微生物组成和结构的变化有关。连续单一化种植导致的病原菌增多、有益菌减少,土壤微生物结构失衡可引起化感负效应。这种微生物结构失衡不可避免地导致土壤养分封存、土壤酸化和土传病害发生等,从而导致作物产量和品质下降。化感正效应则与之相反,连作促进了有益菌群的增加和致病微生物的减少,提高了微生物多样性,从而改善土壤微生境,提高作物产量和品质。因此,研究根际土壤微生物的结构与功能,合理调控作物根际生境以保证其高产优质,促进农业可持续发展,将是今后研究的重点。

关键词: 作物化感作用; 偏害; 偏利; 作用模式; 土壤微生物

As early as 77 AD, the Roman natural scientist Pliny Elder described the toxic effects of black walnut (*Juglans nigra*) on neighboring plants (Duke, 2010), a phenomenon that the German scientist Molisch (1937) first described as allelopathy. The first formal definition of allelopathy was that proposed by Rice in 1983, who described this concept as a chemical ecological phenomenon, in which plants affect the growth and development of neighboring plants (including microorganisms) by releasing allelochemicals into the surrounding environment (Rice, 1983). Since that time, there has been considerable progress regarding research on different aspects of crop allelopathy, notably the findings of more recent studies, which have revealed that soil microorganisms are vital determinants of plant allelopathic capacity (Inderjit, 2005). Moreover, the findings of an increasing number of studies have indicated that crop allelopathy results from a complex web of interactions between plants and soil microbes, which are mediated via root exudates released into rhizosphere ecosystem. The different types of crop allelopathy and their modes of action have been extensively investigated in China, and substantial progress has been made in this regard (Lin et al., 2007; Wang et al., 2013). In this review, we focus primarily on recent advances made in Chinese research on the types of crop allelopathy and their modes of action, with the aim of bringing ongoing developments in this field to the attention of a wider international audience.

1 Crop allelopathy types and modes of action

It is well documented that ecologically, crop allelo-

pathy is a particularly complex chemical process (Einhellig, 1988, 1996). Since its original definition, the concept of crop allelopathy has been broadened to encompass a spectrum of plant-soil-microbial interactions, including amensalism, autotoxicity, and facilitation in cropping systems. Moreover, on the basis of mode of action, crop allelopathy can be further divided into either intra- or interspecific interactions (Duke, 2010; Molisch, 1937; Rice, 1984; Lin et al., 2007; Wang et al., 2013).

1.1 Interspecific allelopathic amensalism

By releasing a diverse range of root exudates, different plant species can inhibit the growth of neighboring plants, thereby limiting the competition for resources, a process referred to as allelopathic amensalism (Wang et al., 2013). In cropping systems, allelopathic amensalism can be found in both intra- and interspecific interactions. An example of the latter is allelopathic rice (*Oryza sativa*), accessions of which can inhibit growth of the target weed barnyard grass (*Echinochloa crus-galli*) in the absence of any herbicide use (Kim et al., 1998; Fang et al., 2013; Xu et al., 2003). In our studies, we have found that allelopathic rice has survival strategies that differ from those non-allelopathic counterparts. Whereas when co-cultured with its competitor barnyard grass under conditions of limited nitrogen resources, non-allelopathic rice struggles to survive by strengthening its nutrient up-take ability, allelopathic rice shows better growth by enhancing its allelopathic potential to suppress barnyard grass (Xiong et al., 2005; He et al., 2012; Song et al., 2008).

1.2 Allelochemicals in allelopathic amensalism

Although allelochemicals play a key role in the de-

velopment of rice allelopathy (Olofsdotter et al., 1999; Olofsdotter, 2001; Kong et al., 2006; Kato-Noguchi et al., 2002), inconsistent results have been reported with respect to their relative importance, which has led to the emergence of two different standpoints. The findings of some studies have indicated that rice utilizes terpenoids and flavonoids as allelochemicals (Lin et al., 2006). Kato-Noguchi et al. (2003) first isolated and identified momilactone B as an allelochemical from the Japanese rice variety ‘Koshihikari’ and its culture medium, which was demonstrated to exhibit inhibitory effects against cress (*Lepidium sativum*) and barnyard grass. Moreover, they established that concentrations of momilactone B in rice were significantly increased when grown under conditions of low nitrogen, UV-B radiation, a high density of barnyard grass, and exogenous jasmonic acid (JA) treatment. Under these conditions, there was a concomitant increase in the inhibition of barnyard grass growth, thereby tending to indicate that momilactone B might be an important allelopathic substance in allelopathic rice accessions (Kato-Noguchi and Ino, 2003; Kato-Noguchi, 2004, 2011). In China, Kong and colleagues have suggested that in addition to momilactone B, certain flavonoids and their sugar ligands can also be considered as allelochemicals. Among those identified are 5,7,4-trihydroxy-3,5-dimethoxyflavone and a flavone o-glycoside, detected in the rhizosphere soil of rice at each major growth stage, and which were shown to be regulated by JA and salicylic acid signaling molecules, as well as weed density (Kong et al., 2007, 2008; You et al., 2011). Furthermore, Sakamoto et al. (2004) have established that the biosynthesis of rice momilactone B is catalyzed by diterpene cyclases encoded by a cluster of genes and other related genes located on chromosome 4, and that their expression can be regulated by various signaling molecules or elicitors.

Among such potential elicitors, Li et al. (2020a) identified (-)-loliolide and JA in the root exudates of five types of barnyard grass, and observed that the concentrations of (-)-loliolide from two types of barnyard grass were significantly increased when this grass was co-cultured with rice, whereas concentrations of JA were significantly increased in the other three co-cultured barnyard grasses. Furthermore, the application of exogenous (-)-loliolide or JA to rice was found to promote an accumu-

lation of allelochemicals, which reached maximum levels within 6 h. Accordingly, these findings would tend to indicate that the (-)-loliolide and JA in barnyard grass exudates are important elicitors that are recognized by rice, thereby inducing an allelopathic response. Similar studies have identified neighbor detection and allelopathic responses between wheat (*Triticum aestivum*) and 100 other species of plants, and indicated that wheat can recognize homologous- and heterogeneous-specific neighboring plants and respond accordingly by increasing the production of certain allelochemicals, with (-)-loliolide and JA in the root exudates of different species being shown to trigger production of the wheat allelochemical 2-4-dihydroxy-7-methoxy-1, 4-benzoxazin-3-one (Kong et al., 2018).

It has also been shown that in both allelopathic and non-allelopathic rice accessions, the expression of genes encoding terpenoids, such as diterpenoid cyclase-related genes, can be regulated by the external environment, and that the up- or down-regulated expression patterns of these genes show similar tendencies in the two accession types when exposed to common stress factors (Wang et al., 2007). These findings thus indicate that the expression of these genes is not necessarily a specific inherited ecological characteristic of allelopathic rice. Moreover, it has been established that the degree of the up-regulated expression of these genes is not consistent with an increase of the rate of barnyard grass growth inhibition, thereby implying that terpenoids are not the sole allelochemicals involved in the allelopathic response (Lin et al., 2007; Sakamoto et al., 2004; Wang et al., 2007; Li et al., 2020d).

Kato-Noguchi (2011) has also reported that in addition to rice accessions, mosses (species of Bryophyta) also synthesize momilactone B under field conditions. These findings have therefore raised the question as to whether the terpene allelochemicals detected in paddy soils are indeed synthesized by allelopathic rice accessions, or instead they could be synthesized by mosses, and subsequently released into the rhizosphere soil. At present, however, there is insufficient experimental evidence to indicate whether terpenoids are indeed the allelochemicals of allelopathic rice that functions in the suppression of target weeds under natural conditions (Wang et al., 2013). In this regard, many scholars are of the

opinion that phenolic acids, rather than terpenoids, are the primary allelochemicals released by plants (Blum, 1996; Blum et al., 1999; Seal et al., 2004). Among these, Chou and Lin (1976), who was one of the first researchers to work on rice allelopathy in Asia, proposed that phenolic acids, produced by the decomposition of crop residues or secreted by crop roots into the soil, could be fixed by soil micelles or humic acids and consequently remain within the rhizosphere soil, thus having an important influence on the growth and development of both crops and weeds (Rice, 1984; Chou and Lin, 1976).

1.3 Gene regulation of allelopathic amensalism

Our earliest work on the beneficial allelochemicals produced by allelopathic rice ‘PI312777’ indicated that phenolic acids (*p*-hydroxybenzoic acid, cinnamic acid, and ferulic acid) are metabolites playing important functional roles in the allelopathic inhibition of weeds. The expression of genes encoding proteins involved in the synthesis of these phenolic compounds have determined in the ‘PI312777’ accession rice under a range of different conditions, and on the basis of our observations, we further examined the involvement of the key gene *PAL* (phenylalanine ammonia-lyase) in the regulation of rice allelopathic potential. We accordingly found that *PAL* plays a positive role in regulating rice phenolic acid concentrations and allelopathic capacity against weeds (Fang et al., 2008, 2010, 2011, 2016, 2020). Furthermore, we identified a MYB transcription factor, MYB57, that is associated with the regulation of rice allelopathy, and demonstrated that increasing the expression of *OsMYB57* in rice, using the transcriptional activator VP64, promoted an increase in the rate barnyard grass inhibition. We also found that expression levels of the phenylpropanoid pathway genes *OsPAL*, *OsC4H*, *OsOMT*, and *OsCAD* were also up-regulated, and that there was an increase in the content of L-phenylalanine. Moreover, on the basis of chromatin immunoprecipitation analysis, performed in conjunction with HiSeq, MYB57 was demonstrated to transcriptionally regulate a mitogen-activated protein kinase (MAPK11), which interacts with *PAL2;3*. The expression of *OsPAL2;3* was found to be higher in the allelopathic rice ‘PI312777’ than in the non-allelopathic rice ‘Lemont’, and was observed to be negatively regulated by Whirly transcription factors. Moreover, microbes with weed-suppression potential, including *Peni-*

cillium spp. and *Bacillus* spp., were found to accumulate in the rhizosphere of the rice accession ‘Kitaake’ with increased expression of *OsMYB57*, and shown to play a role in the induction of phenolic acid synthesis (Fang et al., 2020; Li et al., 2021).

Using allelopathic rice ‘PI312777’, derived *PAL* RNA interference (*PAL*-RNAi) or overexpression (*PAL*-OE) lines, and non-allelopathic rice ‘Lemont’ as donor plants, we went on to investigate the bio-interactions between rice allelochemicals and rhizosphere-specific microorganisms. We accordingly detected a higher level of phenolic acid exudation from the roots of ‘PI312777’ than from those of ‘Lemont’, which resulted in a significant increase in the population of *Myxococcus* in the rhizosphere soil. Overexpression of transgenic *PAL* was found to result in an increase in the exudation of phenolic acids, thereby promoting an increase in the population of *Myxococcus xanthus* in the rhizosphere soil of *PAL*-OE plants. Conversely, *PAL*-RNAi lines were characterized by lower phenolic acid exudation compared with the wild-type ‘PI312777’. Moreover, the exogenous application of phenolic acid was found induce *M. xanthus* growth, as well as an up-regulated expression of chemotaxis-related genes. In addition, quercetin was identified in the culture medium, bioassay determinations with which indicated that a quercetin concentrations of $0.53 \text{ mmol} \cdot \text{L}^{-1}$ inhibited the root length by 60.59%. Collectively, our findings thus indicate that *OsPAL* is among those genes that contribute to the effective regulation of rice allelopathy by controlling the synthesis of phenolic acid allelochemicals and phenolic acid (ferulic acid), which play functional roles in inducing the chemotactic aggregation of *M. xanthus*, thereby promoting the proliferation and accumulation of this microbe. It was subsequently established that production of the potential allelochemical quercetin detected in *M. xanthus* culture medium could be induced in response to ferulic acid (Li et al., 2020c). Moreover, we found that expression of miRNAs relevant to plant hormone signal transduction, nucleotide excision repair, and the peroxisome proliferator-activated receptor and p53 signaling pathways were enhanced in barnyard grass co-cultured with the allelopathic rice cultivar ‘PI312777’, with the expression levels of these miRNAs in barnyard grass plants being positively correlated with the allelopathic potential of

co-cultured rice. Treatment of barnyard grass plants with rice-synthesized phenolic acids was also found to enhance miRNA expression, whereas in contrast, treatment with rice-produced terpenoids had no obvious effect on miRNA expression. Furthermore, in investigations based on a hydroponic system, the largest numbers of *Myxococcus* spp. were detected in a culture solution containing the *PAL*-OE line, and increases in these microbes were similarly recorded in response to the addition of phenolic acids to the hydroponic medium. More interestingly, we also demonstrated that inoculation of barnyard grass with *M. xanthus* significantly increased miRNA expression in the treated plants, and that co-treatment with a mixture of ferulic acid and *M. xanthus* led to the strongest inhibition of barnyard grass growth. These findings thus provide evidence to indicate the involvement of *Myxococcus* spp. and the mediation of miRNA expression in rice allelopathy against barnyard grass (Fang et al., 2015). They also highlight the fact that the allelopathic activity of rice involves multiple interactions among rice, microorganisms, and target weeds mediated by phenolic acids in the root exudates released by donor plants of allelopathic rice accessions into the rhizosphere soil ecosystem. Nevertheless, given that other Chinese scientists have identified terpenoid compounds as promising allelochemicals in some rice accessions, based on observations that active dosages of terpenoids were considerably lower than those of phenolic acids (Kato-Noguchi, 2004; Kong et al., 2007, 2008; You et al., 2011), it would appear that different allelopathic accessions differ with respect to the underlying mechanisms of actions whereby they suppress the growth of target plants, which accordingly warrants further in-depth study.

1.4 Allelopathic amensalism of biological invasion

Biological invasion is a further process in which allelopathic amensalism has been implicated, and the allelopathic amensalism of invasive species is assumed to have contributed to significant depletions in the biodiversity of native species in invaded areas (Zheng et al., 2015). In China, the perennial creeping climber *Mikania micrantha* is regarded as one of the most serious invasive species. Although a species native to South and Central America, this plant has currently invaded more than 70 countries and regions in Asia, the South Pacific, and

other regions. In their studies of the allelopathy of *M. micrantha*, Huang et al. (2004, 2008) showed that extracts of this exotic plant collected in four different habitats all had a notable inhibitory effects on native species, even though differences were detected in the allelopathic potential of *M. micrantha* in these four habitats. Toxic compounds (allelochemicals) secreted from the roots of *M. micrantha* have been found to inhibit the seed germination and growth of neighboring plant, thereby enabling *M. micrantha* to form extensive single-species stands and diminish the biodiversity of invaded areas. Moreover, it has been established that the release of these allelochemicals into the soil results in an increase in the availability of nitrogen, as a consequence of an enrichment of the microbes involved in nitrogen cycling pathways. Higher concentrations of available nitrogen in the rhizosphere soil are also conducive to the rapid growth and invasive adaptation of *M. micrantha* (Liu et al., 2020).

A further plant species native to Central America, that has become a malignant invasive weed in many tropical and subtropical regions worldwide is *Chromolaena odorata*. Notably, in this regard, it has been found that the contents of odoratin (a chemical compound unique to *C. odorata*, that confers strong allelopathy and disease and insect resistance) in invasive populations are significantly higher than those in the native Central American populations, and that the inhibitory effect of odoratin on Chinese native species is also significantly higher than that on Mexican native species.

1.5 Intraspecific allelopathic amensalism

Allelopathic autotoxicity is among the intraspecific interactions that characteristically occur in consecutive cropping systems and is acknowledged to be one of the foremost problems associated consecutively grown monocultures. Autotoxicity arises when the same crop species or consanguinity crop is continuously monocultured in the same field for two or more years under normal cultivation management, and is typically manifested in worsening crop growth conditions and serious outbreaks of plant diseases and pest infections, consequently resulting in year-on-year reductions in yield and quality (Zhang et al., 2009, 2010). For example, it has been established that approximately 70% of medicinal plants, particularly those with tuberous roots and rhizomes, are seriously affected by the continuous mono-

cultural cropping or replanting-associated diseases (Jian et al., 2008), which are believed to be mainly attributable to the auto-toxic effects of allelochemicals released from the first cropped plants against those subsequently cropped in the same field. Moreover, it has been found that bio-interactions between allelochemicals and soil-borne pathogens contribute to aggravating the problems associated with monoculture cropping (Li et al., 2012a). The findings of previous studies have indicated that allelopathic autotoxicity arises as a consequence of intraspecific interactions among medicinal plants cultivated in continuous cropping systems, caused by exudation of allelochemicals from root systems into the rhizosphere soil, thereby resulting in detrimental effects on neighboring plants (Jian et al., 2008; Li et al., 2012b; Chen et al., 2007). On the basis of our recent studies on medicinal plant allelopathy, we identified ecological effects of the functional disorder of soil microorganisms mediated by medicinal plant root exudates as main reasons for the problems associated with consecutive monocultures (Wu et al., 2011b, 2013, 2014, 2015, 2016; Li et al., 2012a, b).

To gain further insights into the phenomenon of indirect allelopathic effects, our research group has used T-RFLP, high-throughput sequencing of 16S rRNA and ITS, metagenomic sequencing, and qPCR to systematically examine the problems associated with continuous monoculture of the congeneric species *Radix pseudostellariae* and *Radix glutinosa*. We accordingly established that the root exudates of *R. pseudostellariae* and *R. glutinosa*, functioning as rhizospheric intermediaries between plants and microbes, were responsible for increasing the population size of the pathogenic fungi *Fusarium oxysporum* and *Talaromyces helices*, whilst simultaneously reducing the abundance of potentially beneficial species of *Pseudomonas* and *Burkholderia*, thereby leading to a deterioration of the rhizosphere microbial community under consecutive monocultural cropping (Wu et al., 2016, 2017a, 2017b). In this regard, it has been suggested that soil microbial interactions (including quorum sensing and quorum sensing quenching in the microbial community) play an important role in causing an imbalance in the composition of microbial communities in replanted soil. To further characterize these interactions, we assessed the effects of artificially applied *R. pseudostellariae* root exudates on *R. pseudostellariae*, and in-

vestigated seedling growth, rhizosphere soil microbial communities, and soil physicochemical properties, and thereby established that different phenolic acids and other organic acids function as drivers that mediate the observed changes in the microbial community composition. Specifically, high-throughput sequencing and qRT-PCR analyses revealed that phenolic acids caused significant reductions in the relative abundances of *Trichoderma*, *Penicillium*, *Pseudomonadales*, *Xanthomonadales*, and *Streptomycetales*, whereas organic acids had significant negative effects on the relative abundances of *Pseudomonadales* and *Streptomycetales* and promoted significant increases in the abundances of *Fusarium*, *Xanthomonadales*, *Micrococcales*, and *Gemmatimonadales*. Furthermore, analysis based on the non-invasive micro-test technique indicated that root exudates contributed to increases in H^+ -efflux and plasma membrane H^+ -ATPase activity in pathogenic fungi, whilst tending to suppress these activities in beneficial fungi. These response further contributed to generating an acidic environment inimical to beneficial bacteria, but be conducive to the accumulation of specialized plant pathogens (Wu et al., 2011a, 2017a, 2019, 2020a, 2020c). Accordingly, the findings of this study enabled us to identify the mechanisms underlying the shift in microflora and structural disorder caused by root exudates in continuously monocultured *R. pseudostellariae* rhizosphere soil in response to stressful environmental conditions. Moreover, on the basis of these observations, we were able to establish that to effectively overcome the problems associated with monocultural cropping, it was necessary rectify the disease-conducive soil environment in order to appropriately remediate the disruption of microbial community structure, and thereby enhance ecosystem functions.

It is well accepted that during the entire growth process, plants release substantial amounts of root secretions, which are considered to serve as important carriers that contribute to mediating material exchange and energy flow, as well as facilitating interactions among plant and microbes in the soil ecosystem. Furthermore, the findings of an increasing number of studies have revealed that root exudates have a selective effect in shaping the structure of the rhizosphere microbial community, as is reflected in the often unique and representative rhizosphere microbial communities associated with

different plant species. Conversely, changes in the structure of rhizosphere microbial communities can have equally important effects on material cycling, energy flow, and signal transduction, thereby influencing plant growth and development. Consequently, in order to effectively rectify the problems linked to continuous monocropping, it will be essential to elucidate the mechanisms underlying rhizosphere interactions at the ecosystem level (Lin et al., 2015; Wu et al., 2020b).

Autotoxicity has also been detected in a range of medicinal plants, including *Panax notoginseng* and *Panax quinquefolium* (American ginseng). In the case of *P. notoginseng*, the accumulation of ginsenosides in rhizosphere soils, via the release of root exudates or root decomposition, has the effect of impeding seedling emergence and growth. The toxicity of these compounds is attributed to the accumulation of reactive oxygen species (ROS) in plants, leading to the root cell death. Within the soil, it has been demonstrated that ginsenosides promote changes in the composition of soil microbiota based on their differential carbon source utilization, whereby potentially pathogenic taxa, such as *Alternaria*, *Cylindrocarpum*, *Gibberella*, *Phoma*, and *Fusarium* are stimulated, and populations of beneficial taxa such as *Acremonium*, *Mucor*, and *Ochroconis* are inhibited, thus disrupting the balance of soil fungal microbiomes (Luo et al., 2020; Yang et al., 2015, 2018; Li et al., 2020b).

With respect to American ginseng, the phenolic compounds *p*-hydroxybenzoic acid, vanillin, syringic acid, vanillic acid, coumaric acid, ferulic acid, cinnamic acid, salicylic acid, and benzoic acid have been detected in rhizosphere soils and found display variable phytotoxicity against the cultivated plants of this species (Bi et al., 2010). In addition, allelopathic autotoxicity has also been documented in a number of commercially cultivated crop plants, including cucumber (*Cucumis sativus*), tobacco (*Nicotiana tabacum*), melon (*Cucumis melo*), and eggplant (*Solanum melongena*), for which numerous studies have sought to identify the causal toxic compounds, their impact on rhizospheric microbial communities, and problems associated with continuous monoculture. For example, by examining the adsorption of activated carbon in culture solutions to characterize the autotoxicity caused by root exudates of crops, such as cucumber and

watermelon (*Citrullus lanatus*), Yu et al. (1997, 2000) identified phenolic acids such as cinnamic acid in the exudates of cucumber and other plants, whereas Yao et al. (2006) found that replanting cucumber results in a reduction in the diversity of microbial communities in continuously cultivated soils. Furthermore, the application of *p*-coumaric acid to soil has been demonstrated to increase *F. oxysporum* population densities, thereby leading to an increase in soil dehydrogenase activity and reduction in cucumber leaf area (Zhou et al., 2012, 2018). Similarly, the direct phytotoxicity of phenolic acids has been shown to inhibit cucumber seedling growth via the promotion of detrimental plant-soil microbial interactions (Jin et al., 2020; Khashi et al., 2020).

In healthy soils, high levels of microbial diversity and activity are reflected in a larger number of competitors and antagonists, which contribute to restricting the activity of soil-borne pathogens, thereby enhancing natural disease suppression and reducing autotoxicity (Van Bruggen et al., 2006; Van Bruggen and Semenov, 2000). In this regard, supplementation with soil organic matter has been shown to promote increases in microbial biodiversity (Liu et al., 2018), and is accordingly a widely adopted farming practice.

1.6 Intraspecific allelopathic commensalism

Allelopathic commensalism, or facilitation, has also been observed in cropping system-associated intra- and interspecific interactions. Allelopathic auto-stimulation, also referred to as the self-promoting effect, describes the phenomenon whereby monocultured plants grow well with higher biomass yields and better quality with an increase in the number of years of consecutive monoculture in intraspecific interaction systems. In our case studies, we have examined the performance of *Achyranthes bidentata* as a typical medicinal plant characterized by self-promoting growth effects when continuously monocultured for several years (Wang et al., 2013; Li et al., 2010; Wang et al., 2017, 2019), the yield and medicinal qualities of which can be markedly enhanced under continuous cropping regimes (Wang et al., 2017, 2019). Using HPLC analysis to determine the contents of sterones and saponins, the main active medicinal constituents of *A. bidentata*, Li et al. (2010) demonstrated that the contents of sterones and saponins in the tuberous roots of

consecutively monocultured *A. bidentata* were comparatively higher than those in the tuberous roots of the newly planted *A. bidentata* in the same field, and Wang et al. (2017, 2019, 2021) have obtained similar results. These latter authors consistently identified three types of phytosterones in consecutively monocultured rhizosphere soil and culture medium of *A. bidentata* plants based on LC-MS/MS analysis, and established that these compounds are the main allelochemicals present in the root exudates of consecutively monocultured *A. bidentata* plants. Moreover, these phytosterones were found to have positive effects on dominant beneficial microbial species, including *Bacillus amyloliquefaciens* 4 and *Bacillus halodurans* 75, whereas in contrast, they were observed to have suppressive effects on the pathogenic fungi, *F. solani* and *F. oxysporum* in an *in vitro* interaction system. These findings accordingly indicate that in the context of intraspecific interactions, auto-stimulation might be a consequence of the positive interplay among beneficial microorganisms mediated by allelochemical phytosterones in consecutive monoculture systems. Moreover, this could provide an explanation as to why the consecutive monoculture of *A. bidentata* plants can differentially regulate the microbial flora, resulting in increases in beneficial microorganisms (biocontrol and plant growth-promoting bacteria), and reductions in pathogenic microorganisms. Thus, by positively enhancing properties of the rhizosphere soil environment, medicinal plants can increase yields and quality when cultivated in continuous cropping systems.

On the basis of these results, we can infer that it is essential to enhance the quality of the soil environment for crops. In this context, the rhizosphere environment can be considered to comprise three main compartments, namely, the endosphere (the area within the root), the rhizoplane (the soil adhering to the root surface), and the rhizosphere (the soil surrounding the root), which are considered distinct ecological niches colonized by different microbial populations that play differing soil ecosystem roles (Wang et al., 2021). Among these compartments, the endosphere, which serves as the strongest filter, is more directly under host genotype control, and the associated microbiota largely undergo re-establishment each time a plant resumes growth. This thus differs

somewhat from the gut microbiota of mammals, which is partially maternally inherited (Wang et al., 2017). The composition of the endosphere microbiota is, to a large extent, determined by the rhizoplane, which plays an important gating role that contributes to controlling microbial entry into the host tissue. This zone is characterized by more intimate host-microbe interactions, and a larger number of specialized communities are further enriched in the rhizoplane. The narrow zone rhizosphere is also envisaged as an area of intense competition among microorganisms for access to plant-derived nutrients. Our previous studies on rhizosphere interactions have revealed that crop species and genotypes, along with environmental and edaphic factors contribute to determining the distribution and diversity of the microbiota associated with the three constituent compartments. We found that the detected proportions of certain microbes (such as *Sphingomonas*, *Bacillus*, and *Pseudomonas*) across the three rhizocompartments of *A. bidentata* indicated that microbes typically colonized specific root niches. Moreover, abundances of the predominant genus *Bacillus* were observed to be higher in soils under multiple continuous monoculture than in those under less continuous monoculture. This selective property of plants could be attributable to the biofilm-forming capacity of these bacteria, which have antagonistic effects against pathogenic fungi. With respect to the endosphere, *Pseudomonas* was found to become the dominant bacterial genus in different continuous cropping samples, with a trend similar to that of *Bacillus*. This difference in the populations of rhizoplane and endosphere microbiota further clarify that the binding of *Bacillus* to the rhizoplane plays an important gating role. Moreover, compared with microbes colonizing the rhizosphere, *Pseudomonas* isolates detected in the endosphere were found to be engaged in metabolic pathways involved in the synthesis of plant signaling compounds associated with bacterial-plant interactions and root growth promotion (Wu et al., 2011b, 2020b). These observations would thus tend to emphasize the key importance of the metagenomic composition of the microbial community and core flora in rhizosphere soil with respect to the healthy growth of plants. In future studies, it will be necessary to further examine the composition of the second genome (microbiome) of

plants and successional mechanisms in soil ecosystems. Furthermore, the potential exists to utilize the principles and technologies of modern synthetic biology to artificially manipulate the regulation of rhizosphere biological processes, and thereby contribute to promoting the sustainable development of crop production.

1.7 Interspecific allelopathic commensalism

Although there is a diversity of interactions among different species in plant communities, traditionally, competitive interactions have been considered the fundamental driving forces of species evolution. Consequently, research has tended to focus primarily on the antagonistic types of interspecific interaction, such as competitive predation and abiotic stress. However, positive types of interspecific interactions, including commensalism, mutualism, and protocoeperation, have tended to receive comparatively little attention in the past, although in more recent times have become an intriguing area of research, both in China and other countries. In this regard, numerous scholars have reported on the mutually beneficial interspecific relationships (facilitation) in the rhizosphere soil of plant communities. In particular, positive plant-microbe interactions, mediated by root exudates released from intercropped crop plants, have been established to play important roles in enhancing nutrient utilization efficiency and grain yields in intercropping systems (Li et al., 2018; Chen et al., 2018), and can provide additional resources that enhance the soil microenvironment. Furthermore, plants can promote mutual survival via indirect positive interactions with microorganisms, mediated by allelochemicals released within root exudates. As a consequence of the increasing attention being focused on the positive interactions of intercropped plants in consecutive monoculture systems, researchers are gradually gaining a more comprehensive understanding of the respective types and roles of positive and negative interactions in the soil ecosystem. In recent years, the findings of a number of studies have provided evidence to indicate that interspecific rhizosphere facilitation is an important mechanism for increasing yields and enhancing the efficient utilization of nutrient resources in intercropping systems. Moreover, an increasing number of studies have revealed that plant facilitation under intercropping systems is, to a large extent, the outcome of

positive interactions among rhizosphere microorganisms mediated by root exudates, and on the basis of recent research developments in facilitation, there has emerged the theory of the realized ecological niche. The traditional concept of the niche is based on the assumption that there are negative interactions among neighboring species, and consequently different species are excluded from occupying the same niche. However, by reconsidering niche theory with the inclusion of positive interactions, such as those in intercropping systems, we find that the realized niche of a given species is potentially considerably wider than its functional niche. For example, intercropping of maize (*Zea mays*) with a legume crop can enhance its survival in phosphorus-deficient soils (Li et al., 2007) and the soil quality can be improved by the inter-root communication of intercropped plants. Another good example is that of macrophanerophytes, which at an early stage of succession, can have a positive effect on the succession process and provide better soil environments for the survival of those plant species appearing at later stages in the successional sequence.

In recent years, the practice of employing the principle of plant facilitation to enhance the realized niche of crops has become well established and exploited as a cultivation strategy in low-carbon circular agriculture. Previous studies in this regard have also pinpointed the importance of root exudates in driving interspecific facilitations via enhancing root nodulation and N₂ fixation under intercropping systems of maize and legume crops (Li et al., 2018; Chen et al., 2018). For example, Li et al. (2007) determined that intercropped maize promoted a two-fold increment in the exudation of flavonoids (signaling compounds for rhizobia) in these systems. Moreover, they observed a major up-regulation of flavonoid synthesis in faba bean (*Vicia faba*) roots 12 h after being treated with root exudates derived from maize, including an 11-fold increase in expression of the chalcone-flavanone isomerase gene, compared with that in the absence root exudates. Such a rapid response provides evidence indicating the pivotal signaling role played by flavonoids in inter-root communication between intercropped faba bean and maize (Li et al., 2007). Likewise, we have found that interspecific root interactions between maize and soybean (*Glycine max*)

have significant structural and functional effects. Notably, we demonstrated that the augmentation of interspecific root interactions under the treatment with interspecific root partition, in which root systems were completely separated by plastic film, shifted to no interspecific root partition in an intercropping system. In such intercropping systems, microbial diversity and evenness were found to be enhanced, thereby promoting increases in soil productivity and higher yields (Li et al., 2018).

In China, there has been a long history of intercropping, and a diverse range of intercropping patterns have developed, among which are the intercropping of maize and peanut (*Arachis hypogaea*) in North China; maize and soybean in Northeast China; wheat and soybean and soybean and maize in Northwest China; maize and peanut in Southwest China; wheat and pea (*Pisum sativum*), wheat and fava beans, barley (*Hordeum vulgare*) and soybean, and rape (*Brassica campestris*) and fava bean in the middle and downstream reaches of the Yangtze River; and multi-cropping systems in South China. Furthermore, in Yunnan Province, wheat/fava beans, barley/fava beans, rape/fava beans and maize/peanut are prevalent intercropping systems characterized by diverse planting techniques (Wang et al., 2013). As mentioned previously, it has been documented that maize root exudates promote the nodulation and nitrogen fixation in the roots of fava bean, and the important role of root exudates in this regard has been confirmed from both physiological and molecular aspects (Li et al., 2007). When these two crops are intercropped, significant increases in the concentration of the flavonoid genistein, a key signal substance promoting the dialogue between legumes and rhizobia, have been detected in the root exudates released by maize. In addition, intercropping has been established to alter soil microbial community composition and enhance the relative abundance of soil *Sordariales*, thereby further facilitating soil aggregation (Tian et al., 2019). Among gramineous crops, the intercropping of spring wheat and maize has also been found to promote the belowground interspecies interactions of these two crops, thus enhancing grain yields compared with the corresponding monocropping (Mu et al., 2013).

2 Prospects for allelopathic research

Recent advances in research on crop allelopathy

have resulted in a better understanding of allelopathic effects and development of associated practical strategies, and have also provided compelling evidence that both positive and negative allelopathic interactions are a consequence of changes in rhizosphere soil microbial composition and structure mediated by allelopathic root secretions. Accordingly, there is an imperative for further in-depth studies of rhizosphere soil microbial structure and function. Moreover, from the perspective of the sustainable production of high-yielding good quality crops, there is a need to develop strategies that will facilitate the appropriate regulation of rhizosphere ecology.

Given the widely recognized predominant role of interactions between allelochemical compounds and specific microorganisms underlying the allelopathy phenomenon, more attention should also be focused on the behavioral responses of microorganisms to allelochemicals, and in this regard, it would be of particular interest to identify potential quorum sensing and related mechanisms. From a practical standpoint, a further important field in theoretical research on allelopathy is the isolation of beneficial bacteria and verifying the utility of bacterial biological fertilizers. Moreover, in view of the characteristics of allelopathy, a priority area for future research is the identification of dominant genes regulating allelopathic mechanisms, thereby contributing to enhancing the genetic characterization and breeding of allelopathic varieties, which will in turn enable us to develop our own crop germplasm intellectual property.

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