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化感水稻抑草作用的根际生物学特性与研究展望

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摘 要: 当前水稻化感作用研究主要集中在其遗传生理与分子生态特性和水稻化感物质的分离鉴定及其抑草作用的根际生物学过程与机制两方面。水稻化感作用是个可遗传的数量性状, 控制该性状的 QTL 主要定位在第 2、第 3、第 8、第 9 和第 10 染色体上, 并存在显著的 QTL 上位性作用及其与环境的互作效应, 但未见控制化感作用性状的 QTL 遗传信息与何种化感物质的产生紧密相关的研究报道。从现有水稻化感物质的分离鉴定结果看, 水稻化感物质可分为三大类, 即酚酸类、萜类和黄酮类物质。这三类物质对靶标植物(稗草)均有抑制作用, 但酚酸类物质起化感抑草作用的有效浓度较另两类物质的高, 且从土壤中检测到的浓度比室内测定的化感抑草作用有效浓度低得多。因此, 酚酸类物质是否是一类化感物质经常遭到一些学者的质疑。然而, 也有研究结果表明, 逆境引起的水稻化感作用潜力增强与其合成酚酸类物质的基因表达增强以及所合成的该类物质分泌释放到根际土壤中的量增多有关。当抑制化感水稻的 *PAL-2-1* 基因表达后, 其酚酸类物质含量降低, 根际微生物数量也随之减少, 其中黏细菌属的细菌丰度明显降低, 化感抑草效果下降, 因而认为在田间条件下化感水稻 *PAL-2-1* 基因调控其酚酸类物质合成, 经根系分泌进入根际土壤后引起根际特异微生物的趋化性聚集, 在这一过程中, 释放的根系分泌物可能被土壤中存在的多样性微生物所降解, 从而降低其在土壤中的浓度, 但正是通过土壤微生物的降解与转化作用, 引发了化感物质与根际微生物的藕合效应, 并由此产生了水稻化感抑草现象。因此, 深入研究这一根际生物学过程对于最终揭示水稻化感作用机制有着极其重要的理论与实际意义。

关键词: 化感作用; 根际生物学特性; 水稻; 特异微生物

Rhizobiological Properties of Allelopathic Rice in Suppression of Weeds and Its Research Prospect

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Abstract: Two reviewed areas of the research include the genetic physiological and molecular ecological characteristics, and the allelochemical identification, rhizospheric biological process and mechanism of rice allelopathy. As a quantitative trait, the allelopathy is mediated by both genetic and environmental factors. QTLs for allelopathy are found mainly on chromosomes 2, 3, 8, 9, and 10 significantly interacting with the additive×additive epistatic effects and the environment. However, no relevant study has been reported concerning the correlation between the QTL genetics and allelochemical synthesis. Phenolic acids, terpenoids and flavonoids have been identified in laboratory to be the metabolites showing allelopathic potentials on the target weed (barnyardgrass). Since a concentration higher than what is normally required to exhibit the allelopathic effect in rice rhizospheric soils for phenolic acids, some researchers questioned its association with the allelopathy. On the other hand, our studies indicated that the rice allelopathic potential was enhanced under stress from the increased phenolic acids in soil. Furthermore, the gene expression of phenylalanine ammonia-lyase (*PAL-2-1*) in the allelopathic rice, PI312777, was inhibited by the RNA interference (RNAi). The transgenic rice showed decreases in the phenolic acid concentration and the rhizospheric bacterial diversity as com-

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pared with its wild type (WT), especially for myxobacterium, whose population was significantly lowered. The results suggested that the phenolic acids might be regulated by *PAL-2-1* gene, and then be released into the soil resulting in the chemotactic aggregation of the rhizosphere characteristic microbes. Some species of microorganisms with vast diversity existing in soil could conceivably degrade plant root exudates leaving little allelochemicals to be detected. The degradation and transformation by the rhizosphere microorganisms might have a coupling effect with the allelochemicals to result in the crop's allelopathic effect on weeds as observed. Consequently, studying the rhizospheric biological process could eventually reveal the detailed mechanism of the rice allelopathy.

Keywords: Allelopathy; Rhizobiological properties; Rice; Special microorganism

利用作物化感作用(Allelopathy)来控制田间杂草被认为是一项环境友好型的可持续农业技术,已成为当代农业生态学的研究热点^[1-2]。植物化感作用指的是植物通过挥发、分泌、淋溶和降解等方式释放其次生化合物并进入环境(特别是土壤环境)中,从而影响临近生物(如田间微生物和杂草等)生长发育的化学生态学现象^[1-2]。对伴生杂草具有抑制作用的水稻称为化感水稻。水稻化感作用研究始于20世纪80年代,美国遗传育种学家Dilday在田间试验中首次发现对水生杂草 ducksalad [*Heteranthera Limosa* (Sw.) Wild]具有明显化感抑制作用的水稻品种^[3]。其后,他对来自多个国家的12 000份水稻品种进行抑草潜力评价,获得约5000份水稻品种对杂草 redstem (*Ammannia coccinea* Rottb.)存在化感作用。之后,世界各国研究人员开始广泛开展水稻化感作用的相关研究,并取得了重要进展^[3-17]。室内的部分研究成果已进入田间试验评价阶段,也取得了一定的成效。王海斌等^[18]连续3年的田间试验结果表明,不同化感水稻田间抑草效果达85%~92%,化感水稻在不除草与化学除草两种处理条件下,前者与后者相比,产量虽有所下降,但由于不用化学除草剂,其生产成本明显降低,产品质量显著提高。对非化感水稻而言,不除草条件下,田间杂草侵染严重,产量比经过化学除草处理的减少50%左右,显示了利用水稻化感作用控制田间杂草的可行性。然而,实践表明水稻化感作用是个复杂的化学生态学现象,其遗传表现受环境条件的强烈调控,特别是栽培管理得当与否,可导致水稻化感抑草能力相差高达20%~30%,产量高低相差30%~40%,严重影响其推广应用速度。因此,深入研究水稻化感抑草作用的遗传生态特性与分子生态学机制,分离鉴定水稻化感物质并揭示其抑草作用的根际生物学过程与机制,对于有效进行遗传改良与栽培调控,促进化感水稻尽快应用于生产实际具有极其重要的理论

与实际意义^[1,19],因而成为当前水稻化感作用研究主要内容。这也是近几届国际化感作用大会的议题之一。本文综述了近年来国内外该领域的研究进展,并结合我们多年的工作和研究结果,进一步分析了水稻化感作用研究存在的问题和主攻方向,以期阐明水稻化感作用机制,促进其尽快应用于生产实际提供理论依据。

1 水稻化感作用的遗传生态特性及其化感物质的分离鉴定

美国遗传生态学家Dilday及其研究小组对化感水稻种质资源与遗传评价研究作出了重大贡献,他们借助美国农业部农业系统实验室(USDA-ARS)从包括我国云南和台湾省在内的110个国家和地区收集的17 279份水稻种质资源的优势,运用田间抑制圈和室内化学指纹检测法开展长达12年化感作用水稻的筛选与评价工作,获得了对水田主要杂草 Ducksalad [*H. Limosa* (Sw.) Wild]、Redstem (*A. coccinea* Rottb.)和稗草(*Echinochloa crusgalli* L.)具抑制作用的品种材料,并率先进行水稻化感作用的数量遗传、QTL定位以及品种选育工作,检测到7个与化感作用相关的QTL,其中对化感作用效应最大的QTL,解释了16.1%遗传变异。他们通过常规系统育种方法,利用Taichung65/Taichung Native1的杂交后代再与非化感作用的品种Rexmont杂交,通过系统选择获得了对上述靶标杂草具较强抑制作用的高产品种PI312777;同时又从IR8//85894A4-18-1/TN-1多元配组中获得了靶标杂草具抑制作用的品系PI338046,再用PI338046与高产品种Katy(产量7869 kg hm⁻²)杂交,通过系统选择在F₆群体中获得一个株系后定名为stg94L42-130。经检测该品系是对上述伴生杂草具显著抑制作用的高产品种(产量高达9882 kg hm⁻²),证实了选育高产抗草品种的可行性^[20-23]。丹麦学者Olofsdotter在菲律宾国际水稻研究所(IRRI)期间也相继开展了水稻化感作用种质

资源筛选与遗传评价研究, 并取得重要进展^[9]。这些材料通过交流, 已成为各国同行专家开展水稻化感作用基础研究的重要种质资源。Jensen 等^[24-25]运用强化感作用水稻 IAC165 与弱化感作用水稻 CO39 杂交后代的重组自交群体(RILs), 构建一个含 140 个 DNA 标记, 涵盖水稻 12 条染色体的连锁图谱, 并进行化感抑草作用性状的 QTL 定位研究, 结果检测到与水稻化感作用密切相关的主效应 QTL 位点, 分别定位于第 2、第 3 和第 8 染色体上, 解释了 6.19%~12.00%的所有表型变异。之后, Ebaba 等^[26]、徐正浩等^[27]、Zeng 等^[28]、Lee 等^[29]分别应用不同的化感水稻遗传群体, 进行了化感作用性状的 QTL 定位研究, 一共得到了 23 个与化感作用相关的 QTL, 分别定位在 12 条不同的染色体上, 解释了 9.4%~36.5%的表型变异。熊君等应用强化感作用水稻 Dular 与弱化感作用水稻 Lemont 杂交, 构建了含有 123 个株系的重组自交群体(RILs)的连锁遗传图谱, 并进行了化感作用性状的 QTL 上位性及其与环境的互作效应研究, 结果发现 3 对控制化感作用 QTL 存在显著的加加上位性及其与环境的互作关系, 因此, 在化感品种选育实践中, 应强调最佳 QTL 位点的合理组配而不是简单叠加, 同时强调应重视环境对化感作用遗传表现的调控作用^[30-32]。然而, 控制化感作用性状的 QTL 遗传信息与何种化感物质的产生紧密相关的研究还未见报道^[33]。已有研究结果表明水稻化感抑草作用是自身合成的化感物质通过根系分泌或残体降解, 进入根际土壤从而影响邻近杂草生长发育的现象。显然, 该现象包括作物合成化感物质的基因表达与调控和化感物质释放并进入根际土壤生态系统的两个既有联系又有区别的生物学过程, 因此水稻化感作用的遗传表现及其抑草作用是一种复杂的根际化学生态学现象。

在水稻化感物质及其生物合成方面, 前人已做了大量的研究, 但结果不尽相同。一种观点认为萜类和黄酮类是水稻化感物质。日本学者 Kato-Noguchi 等^[34-35]最早在日本水稻品种 Koshihikari 的植株及其培养液中分离鉴定到二萜类物质稻壳酮(momilactone B), 并发现其对靶标植物水芹 *Cress (Lepidium sativum L.)* 产生生长抑制作用的起始浓度为 $3 \mu\text{mol L}^{-1}$, 对水芹根系和下胚轴抑制率达 50%的浓度分别为 $36 \mu\text{mol L}^{-1}$ 和 $41 \mu\text{mol L}^{-1}$ 。研究还表明, momilactone B 对稗草的起始作用浓度要大于 $1 \mu\text{mol L}^{-1}$,

对稗草根系和地上部植株的生长抑制率达 50%的浓度, 分别为 $28.70 \mu\text{mol L}^{-1}$ 和 $46.41 \mu\text{mol L}^{-1}$ 。之后, 他们又在另外 8 个日本水稻品种中检测到这种物质, 品种间浓度相差最高达 4.5 倍。同时发现, 供试水稻在低氮、UV-B 辐射、高稗草密度和外源茉莉酸(JA)处理下, 其 momilactone B 浓度显著增加, 对稗草生长的抑制率也提高^[36-37], 因而认为 momilactone B 是一类重要的水稻化感物质。我国学者孔垂华及其团队也支持其部分观点, 并认为除 momilactone B 外, 一些黄酮类及其糖配基类物质如 5,7,4'-trihydroxy-3',5'-dimethoxyflavone 和 flavone O-glycoside 也是化感物质^[38-39], 并在水稻各主要生育期的根际土壤中检测到这类物质^[40]。同时认为, 这类物质的生物合成受 JA 和水杨酸(SA)信号分子以及杂草密度的调控^[41]。Sakamoto 等^[42]研究发现水稻 momilactone B 的生物合成是由一组位于第 4 染色体上的编码二萜类环化酶(diterpene cyclases)等相关基因的基因簇完成的, 其功能表达能被各种信号分子或诱导物质(elicitors)调控。然而, 也有研究结果表明, 无论是化感水稻还是非化感水稻, 编码萜类, 特别是二萜类环化酶相关基因的功能表达, 均能被外界环境条件调节, 而且上下调的程度和性质表现趋势一致, 因此这种基因的表达模式并不是化感水稻特有的遗传生态特性, 且其上调表达的强度并不与稗草生长抑制率提高相一致, 暗示着萜类化合物不一定是化感物质^[43]。近年来, Kato-Noguchi^[44]研究还发现并不是只有水稻才能合成 momilactone B, 如苔藓(*Bryophyta* spp.)也可合成这类物质。所以, 在农田条件下, 检测到的这类物质, 并不一定就是水稻自身合成并由根系分泌释放到根际土壤中的。因此, 萜类尽管是一类作用浓度较低的化感物质, 但认为萜类就是化感水稻在自然条件下对杂草呈抑制作用的化合物, 还缺乏充分的实验证据^[45]。因此, 迄今仍有很多学者持第 2 种观点, 即认为植物酚酸类物质是化感作用物质。持这种观点的化感作用奠基人 Rice^[46]和亚洲较早研究水稻等作物化感作用的台湾学者 Chou^[47]研究认为, 由作物残体分解产生的或通过作物根系分泌而进入土壤的酚酸类物质, 能够被土壤团粒结构物质(micelles)或腐植酸所固定, 并停留在根际土壤中, 从而对作物和杂草生长发育产生重要影响; 之后, 一些学者也相继提供试验证据支持酚酸类物质是一类化感物质的观点^[48-50]。Einhellig 等^[51-52]和何华勤等^[53]的研究表明, 水稻酚酸类化感

物质的产生与释放均受外部环境条件的影响,且逆境胁迫能调节基因表达,加快化感物质的合成,促进化感物质从作物内部释放到外部土壤环境中,从而提高化感作用效果。Shin等^[54]和Kim等^[55]研究表明,化感水稻经UV-B胁迫处理后,与未经处理的相比,其合成酚类化感物质的关键酶苯丙氨酸解氨酶(PAL)和肉桂酸-4-羟化酶(CA4H)基因启动早,酶活性峰值高,且到达时间明显提前。同时他们研究还发现,当化感水稻与不同密度的伴生杂草(稗草)共培养时,其化感作用潜力随着稗草密度的加大而明显增强。针对这一遗传生态现象,熊君等设计了化感—竞争分离生测法研究强、弱化感水稻在不同氮素条件下的化感作用与资源竞争能力的变化,结果发现化感水稻随供氮水平降低化感作用增强,非化感水稻则减弱,证实了水稻化感作用存在的真实性,很好地回答了“究竟是化感作用还是资源竞争”这个国际上一直争论的焦点问题^[56-59]。在该稻—稗共生系统中,随供氮、磷水平下降,伴生杂草密度加大,化感水稻叶片、根系中合成酚类化合物的一些关键酶蛋白表达丰度增强,而合成萜烯类化合物的关键酶蛋白表达丰度减弱(植株体内C、N交叉竞争的结果),因而认为逆境引起的化感作用潜力增强与酚酸类物质合成代谢增强有关^[53,60-62],且SA及其衍生物在此过程中起着重要的化学识别、信号传导和基因表达调控的作用^[63-65]。

2 水稻化感作用的根际生物学特性

据统计,自20世纪80年代以来,研究化感作用的论文明显增加。从1981年到1990年10年期间,共发表SCI收录论文112篇,1991—2000年为627篇,而2001—2010年为1615篇。进一步分析发现,在对应的年限中,检索到属于化感互作(allelopathy interactions)的SCI收录论文分别为6、8和212篇,可见研究植物与植物(杂草)、植物与土壤微生物以及植物-微生物-土壤环境间的化感互作关系正日益受到重视^[66]。特别是近年来,随着研究的不断深入,许多研究结果表明,在田间条件下水稻化感抑草作用是由化感水稻释放的物质与根际土壤微生物相互作用的结果。因为无论是植物分泌的作用浓度较低的萜类和黄酮类物质,还是作用浓度较高的酚酸类物质,都不可能一成不变地存留在根际土壤中,因而认为在田间条件下,植物化感作用能力并不与土壤中实际化感物质浓度呈正相关^[67]。提出“新武器假

说”(Novel Weapon Hypothesis)的美国学者 Vivanco 及其研究团队的研究结果表明,在室内条件下,入侵植物矢车菊(*Centaurea maculosa*)能够分泌一种多酚化合物,即消旋儿茶素(racemic catechin),是重要的化感物质。他们运用活体细胞荧光染色法检测该物质的作用方式及其分子机理,发现该化感物质在一定浓度下,能激发邻近的本地植物根系分生组织产生大量活性氧(ROS)及其化学波,并由此导致钙信号传递的级联反应,从而引起全基因组水平基因表达的改变,最后引起受体细胞的程序性死亡(PCD),该结果发表在 *Science* 上后引起极大的反响^[68-69]。但许多学者认为儿茶素这种化合物在自然生境中的化感作用浓度不可能达到室内所测试的有效浓度那样高^[70],更何况还存在土壤微生物的降解作用^[67]、土壤有机质的吸附作用^[70]和化感物质之间的结合与转化^[71],因此对儿茶素是否是化感物质提出了质疑。Bias等^[72]因为无法证明这种化感物质在土壤中的真实浓度,撤回了发表在 *Plant Physiology* 上的那篇论文,但仍保留发表在 *Science* 上的那篇大作,并提出尽管暂时还无法证明土壤中的真实浓度,但儿茶素的化感作用机制具有重现性,因而坚持认为儿茶素是一类化感物质,但其作用方式与作用机制还需深入揭示^[73]。Hoagland等^[74]研究指出芸苔属植物(*Brassica* spp.)的菜籽饼(brassicaceous seed meal, BSM)活性成分芥子油甙是一类介导性化感物质,他们发现应用该菜籽饼作为连作苹果园的有机肥,能有效抑制果园杂草,防止连作障碍,究其原因,主要与施用含有活性成分芥子油甙的菜籽饼后能诱发一种土著根际土壤微生物,即腐霉菌(*Pythium* spp.)种群的大量增殖有关;Mazzola等^[75]也研究发现类似的现象,即施用油菜菜籽饼作为有机肥不仅能改良土壤肥力,同时还具有控制土传病害和有效抑制果园杂草发生的功效;并指出这种油菜菜籽饼的主要活性成分是芥子油甙(glucosinolate)。在室内条件下,该类化感物质对多种杂草均具有抑制作用,但其有效作用浓度远比施用该菜籽饼所含的芥子油甙有效浓度高得多。进一步分析表明,改用不含芥子油甙的芥菜菜籽饼作有机肥则没有这种除草功效,而发现真正引起除草作用的是含有较低浓度芥子油甙的菜籽饼施入土壤后诱发大量具有除草作用的专一性真菌 *Pythium*。此外,高粱的化感物质 sorgoleone 在所有的土壤中均被矿化,其中来自美国的土壤矿化速率最快^[76];葱芥

(*Alliaria petiolata*)的类黄酮类化感物质在非灭菌的土壤中半衰期少于 12 h, 在灭菌土壤中也仅存在 45.5 h^[77]; 张重义和林瑞余等的研究也发现添加一定浓度且具有作用效果的萜类和酚酸类化感物质在土壤中 3~7 d 就被降解了 50%~90%, 认为这与土壤存在降解该类物质的微生物有关^[78-79]。这些研究均说明在自然环境或农田生态系统中, 不管是何种化感物质, 尽管其起始浓度有高有低, 均能被环境微生物所降解、固定或转化。正是由于这些根际微生物对根系分泌物(化感物质)的降解与转化作用, 产生了与土壤微生物的藕合效应, 并由此介导了根际生物生态学过程, 进而取得较好的化感抑草作用。因此, 包括现任国际化感作用协会主席 Weston 在内的许多学者均研究认为作物化感作用是其化感物质与其根际土壤微生物综合作用的结果, 这种观点也是第六届世界化感作用大会的主流思想^[67,80-82]。

然而, 植物化感互作的根际生物学过程与机制还有待深入揭示。Blum 等^[83]初步研究了酚酸类物质通过植物根系分泌或人工添加进入根际土壤生态系统的不同土壤部位, 即根表土壤(rhizoplane)、根际土壤(rhizosphere)和根外土壤(bulk soil)环境后, 相继发生了化感互作效应的根际微生物生态学过程与机制, 提出了土壤中存在大量利用酚酸类物质作为碳源的微生物, 因此绝大多数植物释放或人工添加的酚酸类物质均能被微生物所利用和转化, 从而促进自身的繁衍与增殖。在这一过程中, 有些酚酸类化感物质由于被土壤微生物降解与转化, 其化感作用降低, 但有些化感物质则通过微生物的利用、转化或合成新的物质而增强其化感作用效果^[48,84]。Inderjit 总结了自然界避免土壤微生物对化感物质的生物降解与转化作用, 从而延长化感物质在土壤的存留时间, 提高化感作用的 4 种策略。其一是常绿多年生, 或通过再生栽培而实现连续和周期性的化感物质分泌与补偿(replenishment)。其二是有些植物会分泌一些较难降解的化合物, 如在一种植物 *Pluchea lanceolata* 体内能检测到槲皮甙(quercitrin)和槲皮黄酮(quercetin)两种黄酮类物质, 但是在该植物生长的土壤中只能检测到槲皮甙, 说明槲皮甙比槲皮黄酮更不容易被土壤微生物所降解, 因此存留在土壤的时间更长, 浓度较高, 化感作用强。其三是化感物质供体植物通过接近靶标植物的根系-土壤界面而分泌化感物质, 从而提高化感作用。其四是一些土壤微生物能优先利用根际分泌物, 并把分泌

物中的碳水化合物作为主要碳源, 合成和释放酚酸类物质或其他微生物化感毒素(toxin), 从而影响化感作用^[85-86]。Kaur 等^[67, 87]甚至认为植物根系分泌物与化感作用并没有直接的生物学相关, 因为多数植物根系分泌物或叶片淋溶物(leachate)中均含有中性物质(neutral substances)、促进作用物质(promoters)和抑制作用物质(inhibitors), 一些微生物能优先利用中性物质如葡萄糖作为主要碳源, 合成释放香豆酸(p-coumaric acid), 从而使土壤酚酸类物质浓度增加, 化感作用增强。也有一些微生物能优先利用蛋氨酸(methionine), 从而促进合成酚酸类微生物的增殖, 提高酚酸类物质的化感作用。而分泌物中的一些组分如硝酸盐, 能抑制土壤中合成酚酸类微生物的生长而降低化感作用, 因而提出土壤理化性状及其生物学特性也会影响化感作用, 暗示通过栽培促控技术可以有效提高化感作用。王海斌、何海斌和熊君等研究发现低氮、干旱或高密度伴生稗草胁迫能使水稻化感作用明显增强。他们进一步应用系统生物学的原理与方法, 系统研究逆境诱发水稻化感作用增强的分子生态过程与机制, 发现化感水稻能够通过其分泌的化感物质介导其根际微生物活性。在这一根际生态学过程中, 化感水稻 *PAL* 是起关键作用的功能基因, 荧光定量 PCR (qRT-PCR)分析表明, 化感水稻比非化感作用水稻的 *PAL* 响应逆境胁迫而增强表达的灵敏度高出 5.6 倍, 而化感与非化感水稻合成萜类物质的相关基因响应逆境胁迫而表达增强的程度却差异不明显^[43,56,88]。Song 等^[56]和方长句等^[89]研究结果表明, 水稻 *PAL* 是一个基因家族, 至少包含 11 个基因成员, 同一家族的不同基因成员调控不同的防御机制, 他们应用 qRT-PCR 分析了低氮及高密度稗草胁迫下, 强化感水稻 PI312777 及非化感水稻 Lemont 根系 *PAL* 各基因成员的表达变化模式, 结果发现, 不同化感潜力水稻 *PAL* 基因的表达有所不同, 化感水稻 PI312777 根系 *PAL* 基因家族的各成员, 在低氮及稗草胁迫下多数增强表达, 其中位于化感水稻第 2 染色体上的第 1 个 *PAL* 基因(*PAL-2-1*)上调表达最明显; 但在相同处理下, 非化感水稻 Lemont 的 *PAL* 基因家族的各成员, 特别是 *PAL-2-1* 基因表达差异不明显。进一步分析结果表明, *PAL-2-1* 功能基因被抑制后, 其转基因水稻的酚酸类化感物质合成能力明显降低, 化感抑草潜力下降, 暗示 *PAL-2-1* 可能与胁迫条件下增强化感水稻杂草抑制能力有关^[90]。

3 研究展望

以上介绍的关于水稻化感抑草作用及其根际生态学特性,多数是在室内条件下获得的。尽管 Dilday 及其研究团队最早在田间条件下观察到化感水稻抑制伴生杂草 ducksalad 等的生长而形成的田间杂草抑制圈现象^[20-23];王海斌等^[18]的田间试验中也发现从国外引进的水稻 PI312777 在田间条件下的确具有明显的抑制杂草现象,并证明这种抑草现象是由水稻化感作用引起的^[56-58]。然而,已如上述,包括作者在内的许多研究结果均表明,在土壤中所检测到的酚酸类化感物质浓度要比室内所测试的有效作用浓度低得多。尽管如此,仍然可以观察到田间条件下水稻的化感抑草作用现象。究其原因,我们认为可能与上述化感水稻与土壤微生物存在互作效应有关。熊君等研究结果表明在田间适度旱育胁迫条件下,与非化感水稻相比,化感水稻对伴生杂草的抑制作用能力明显增强;应用限制性片段长度多态性(T-RFLP)技术,进一步分析化感与非化感水稻苗期根际土壤微生物多样性及其功能差异发现,与非化感水稻相比,化感水稻的根际土壤存在明显的特异微生物种群,其中 7 种被鉴定为黏细菌(Myxobacteria),从而提出在田间水分适度胁迫条件下,化感水稻对伴生杂草的抑制作用较强主要与其根际特异微生物种数量显著增多有关^[91];之后,他们又分析了抑制 PAL 表达的转基因化感水稻和野生型化感水稻的根际土壤微生物多样性差异,结果发现化感水稻 PI312777 的 PAL-2-1 基因抑制表达后,其根际微生物数量随之减少,其中黏细菌属种群明显减少,甚至未能被检测到,其结果验证了在田间条件下水稻对伴生杂草的化感抑制能力的高低可能与其 PAL-2-1 基因表达介导的根际土壤特异微生物种群多少有关。王海斌等利用宏蛋白组学方法分析化感与非化感水稻根际土壤的差异蛋白也证实了上述结论,即在逆境胁迫下,化感水稻根际土壤特异微生物黏细菌种群确实明显增多,且其根际土壤中存在显著上调表达的黏细菌特异蛋白,如趋化性蛋白(chemotaxis proteins)和 ABC 转运蛋白(ATP-binding cassette transporter protein)^[92-93]。然而,这些土壤特异微生物,究竟是如何在化感水稻 PAL-2-1 基因表达调控的介导下,对土壤种子库(soil seed bank)的杂草种子萌发产生抑制作用还未见报道。因此,深入揭示这一根际微生物生态学过程与分子生态学机制

具有十分重要的理论与实践意义。

前人研究发现土壤黏细菌等由于缺乏 PAL 基因,必须从土壤中吸取苯丙氨酸(Phenylalanine)和肉桂酸(cinamic acid)等氨基酸和酚酸类物质,并以此为底物合成具有抗病原真菌的化感物质(Soraphen A, B)等众多次生化合物,对于促进土壤微生物多样性有着极其重要的生态作用,因而被称为是土壤生态系统中生产自然产物的化工厂,近年来受到世界各国同行的重视^[94-95]。已有研究结果表明,黏细菌属于腐生和半腐生菌,它们能够分泌蛋白酶和几丁质酶,降解植物残体并从中获得所需的 C、N 物质,特别是在 A-signal 和 C-signal 介导下,通过特定基因编码包括趋化(药)性蛋白(chemotaxis protein)在内的许多功能蛋白,用于自动感应根际环境中丰富与否的营养信息,控制细胞运动和形态发生,产生游动爬行(gliding)和群聚集结(swarming or aggregating)等行为,实现细胞与细胞间的通讯,识别菌群密度,引发群体效应(quorum sensing),并形成子实体(fruiting bodies)或生物被膜(biofilm)等^[96-99]。微生物的群体效应是近来日益受到广泛关注的特定微生物种群的群体行为调控机制,很多细菌和真菌均有这种能力,具有 quorum sensing 的微生物种群能分泌一种或多种自诱导剂(autoinducer),如一些细菌的菌群数达到一定的阈值(quorum, 菌落或集落数)时,能自发合成并分泌高丝氨酸内酯(AHL)信号分子,并通过感应这些自诱导剂来判断菌群密度和周围环境变化,从而启动一系列相应基因的调节表达,以调节菌体的群体行为。已有研究结果发现酚类物质能够作为农杆菌和根瘤菌等群体效应的信号分子^[100]。那么,化感水稻根系分泌物中的酚酸类等物质究竟对特异微生物起何种作用,并通过何种途径提高水稻在田间的化感抑草能力,值得深入研究。探明这一科学问题,对于最终揭示水稻化感作用的根际生物学过程与分子生态学机制,具有十分重要的理论与实践意义。

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