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ABC转运蛋白调控植物根系分泌物外排的研究进展

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摘　要：根际微生态环境影响着植物的生长发育，良好的根际微生态环境有利于植株的生长。根系分泌物作为根际微生态环境的重要组成成分，是植物与根际环境交流的重要载体，植物可以通过调节根系分泌物的种类及含量，促进或抑制某些根际微生物的生长与繁殖，改变根际土壤微生物群落结构与功能，调控根际微生态环境，进而影响植株的生长发育。传统上根系分泌物被认为是通过被动途径运输到根际土壤中，随着研究的深入，现已证实根系能够依靠跨膜转运蛋白参与的主动运输途径，调控根系分泌物的种类及含量。ABC（ATP-binding cassette transporter）转运蛋白作为生物界最大的膜蛋白家族之一，能够通过利用水解ATP释放的能量，参与多种化合物的运输，如脂类、酚酸、激素等物质，在介导根系分泌物的跨膜运输、影响根际微生物的种类及丰度、调控根际微生态环境中发挥着重要作用。为了更深入明确根系分泌物的分泌机制及其对根际微生态的作用效应，总结根系分泌物的种类，描述根系分泌的基本过程，概述ABC转运蛋白的结构及种类，对近年来关于ABC转运蛋白调控根系分泌物外排进而影响根际微生态的研究成果进行详细综述，并对今后关于ABC转运蛋白基因在根系分泌物外排中的研究方向提出展望，以期为相关领域的研究提供参考与启示。

关键词：ABC转运蛋白；根系分泌物；分泌过程；根际微生态
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Research Progress of ABC Transporter in Regulating Plant Root Exudation Efflux

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Abstract: Rhizosphere microecological environment affects the growth and development of plants, and a good rhizosphere microecological environment is beneficial to plant growth. As an important component of rhizosphere microecological environment, root exudate was an important carrier for the communication between plants and rhizosphere environment. Plants can promote or inhibit the growth and reproduction of certain rhizosphere microorganisms by regulating the types and contents of root exudate, and change the structure and function of rhizosphere soil microbial community, further regulates rhizosphere microecological environment and influences plant growth and development. Traditionally, root exudates were considered to be transported to rhizosphere soil through passive pathways. With the deepening of research, it has been confirmed that roots can regulate the type and content of root exudates by active transport pathways involving transmembrane transporters. As the largest transporter family in the biological world, ABC (ATP-binding cassette transporter) transporters can participate in the transport of various compounds, such as lipids, phenolic acids, hormones and

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other substances, by utilizing the energy released by hydrolysis of ATP. ABC transporter plays an important role in mediating transmembrane transport of root exudates, influencing the species and abundance of rhizosphere microorganisms, and regulating rhizosphere microecological environment. In this paper, the types of root exudates were summarized, the basic process of root exudates was described, the structures and types of ABC transporters were outlined and the recent research findings on the efflux of root exudate regulated by ABC transporters and their influence on rhizosphere microecology were reviewed in detail. The future research direction of ABC transporter gene in root exudates was also proposed, aiming to offer insights and references for related research field.

Key words: ABC transporter; root exudate; secretory process; rhizosphere microecology

植物在生长过程中,根系在生长介质中摄取养分和水分的同时也不断向生长介质中分泌质子、无机离子以及大量的有机物质,这些物质和根组织脱落物统称为根系分泌物(root exudate)[1]。目前许多研究表明植物在面对环境胁迫时,如低温[2]、重金属镉胁迫[3]、高浓度二氧化碳[4]及病原菌胁迫[5]时,根系分泌物的成分和数量会发生变化,以适应不良的生长环境。YUAN等[6]发现,拟南芥受到丁香假单胞菌(*Pseudomonas syringaee* pv tomato)侵染时,其根系分泌物成分会发生变化来帮助植物募集有益根际微生物群落,进而提高对病原菌的抵抗能力。GU等[7]研究发现番茄在受到青枯雷尔氏菌(*Ralstonia. solanacearum*)侵染后,根系分泌物中的咖啡酸含量升高且抑制病原菌的生长。然而并非所有根系分泌物均能对根际微生态环境产生有益影响,刘一鸣等[8]证实蚕豆根系分泌物中一定浓度的对羟基苯甲酸含量可以增加土壤中尖孢镰刀菌(*Fusarium oxysporum*)的数量导致枯萎病加剧。LIU等[9]研究发现花生根系分泌物中苯甲酸可以促进花生根腐病病原菌(*Fusarium* sp.)菌丝生长、孢子萌发进而诱导土传病害。传统上根系分泌物被认为是通过被动途径运输到根际土壤中[10],随着研究的深入,人们发现植物能够通过调节根系细胞膜上的转运蛋白活性,主动调控根系分泌物质的外排过程,即根系能够依靠跨膜转运蛋白参与的主动运输途径,调控根系分泌物的种类及含量,进而影响根际微生态环境,在这个过程中ABC转运蛋白发挥着重要作用。为了更深入明确根系分泌物的分泌机制及其作用效应,本研究首先概述根系分泌物的种类和根系分泌物的分泌过程,然后重点阐述ABC转运蛋白在调控根系分泌物外排进而影响根际微生态环境中的作用,并对ABC转运蛋白今后的研究方向提出了展望,以期为ABC转运蛋白调控植物根系分泌相关研究提供理论指导。

1 根系分泌物

1.1 根系分泌物的组成

1979年,WAREMBOURG和BILLES[11]及ROVIRA等[12]将根系分泌物进行了分类,具体可划分为:分泌物、渗出物、裂解物质以及粘胶质。为便于研究,结合根系分泌物本身的属性,人们多将其划分为低分子有机化合物(糖类、氨基酸、脂肪酸等)、高分子黏性物质(多糖醛酸、生物酶等)和无机离子(Mg^{2+}、NO_3^-等),具体见表1。

根据根系分泌物的物种专一性,又可将其分为两大类,非专一性与专一性。非专一性根系分泌物是众多植物都会分泌的,包括但不限于单糖、寡糖、蛋白质、氨基酸和脂肪酸等。而专一性根系分泌物是某种植物特有的或者特殊的环境下[13]诱导分泌的化合物。例如,高粱可以释放一种高粱酮的分泌物,能够抑制其他植物的生长,高粱幼苗在水溶性苘麻根提取物中生长时会产生更多的高粱酮[14-15]。此外,有研究发现,缺锌处理下小麦耐缺锌基因型会比敏感基因型分泌更多的2’-脱氧麦根酸[16]。在铝胁迫环境下,小麦近等位基因系耐铝基因型分泌的苹果酸是铝敏感基因型的5~10倍[17]。

1.2 根系分泌的基本过程

植物根系合成的代谢物质至少需要穿过一层膜才能从根系细胞的细胞质进入根际,这个跨膜运输的过程涉及3种方式,包括被动运输、囊泡运输以及主动运输(图1)。传统的观点认为根系分泌是被动过程,如扩散和离子通道。扩散可以释放低分子量有机化合物[34],例如糖和氨基酸。当面临特定胁迫如营养胁迫或重金属铝胁迫时,植物会分泌特定羧酸盐(如柠檬酸盐、苹果酸盐和草酸盐),但它们不能通过根膜扩散,此时位于细胞膜上的离子通道开始发挥作用[35-36]。囊泡运输,主要参与高分子

表1　根系分泌物成分[18-33]

Table 1　Composition of root exudates

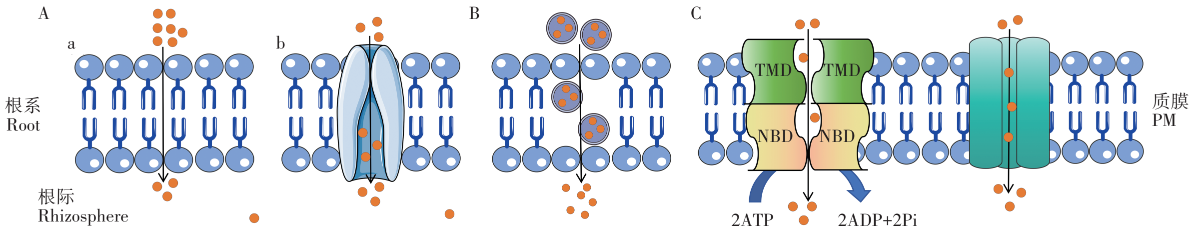
类别 Category		根系分泌物成分 Composition of the root exudates
低分子有机化合物 Low molecular weight organic compounds	氨基酸类 Amino acids	甘氨酸,丙氨酸,缬氨酸,亮氨酸,异亮氨酸,甲硫氨酸,脯氨酸,色氨酸,酪氨酸,半胱氨酸,苯丙氨酸,天冬酰胺,谷氨酰胺,苏氨酸,天门冬氨酸,精氨酸,组氨酸,乌氨酸,胱氨酸,赖氨酸、谷氨酸,γ-氨基丁酸,脱氧麦根酸,阿凡酸,麦根酸 Glycine, Alanine, Valine, Leucine, Isoleucine, Methionine, Proline, Tryptopha, Serine, Tyrosine, Cysteine, Phenylalanine, Asparagine, Glutamine, Threonine, Aspartic acid, Arginine, Histidine, Ornithine, Cystine, Lysine, Glutamic acid, Gamma-Aminobutyric acid, Deoxymugineic acid, Aminobutyric acid, Mugineic acid
	糖类 Carbohydrates	核糖,阿拉伯糖,葡萄糖,半乳糖,果糖,甘露糖,鼠李糖,麦芽糖,蔗糖,棉子糖,乙酰葡萄糖胺,乙酰半乳糖胺 Ribose, Arabinose, Glucose, Galactose, Fructose, Mannose, Rhamnose, Maltose, Sucrose, Raffinose, N-Acetylglucosamine, N-Acetylgalactosamine
	酚酸类 Phenolic acids	香豆酸,对香豆酸,阿魏酸,儿茶酸,原儿茶酸,咖啡酸,水杨酸,丁香酸,香草酸,异香兰酸,藜芦酸,龙胆酸,番石榴酸,东莨菪素,二羟基苯,对羟基苯甲酸,对羟基苯乙酸 Coumaric acid, ρ-Coumaric acid, Ferulic acid, Catechinic acid, Aminobutyric acid, Caffeic acid, Salicylic acid, Syringic acid, Vanillic acid, Isovanillic acid, Veratric acid, Gentisic acid, Psidiolic acid, Scopoletin, Dioxybenzene, ρ-Hydroxybenzoic acid, ρ-Hydroxyphenylacetic acid
	脂肪酸类 Fatty acids	亚油酸,亚麻酸,十八烯酸,软脂酸,硬脂酸,豆蔻酸 Linoleic acid, Linolenic acid, Oleic acid, Palmitic acid, Stearic acid, Myristic acid
	其他有机酸 Other organic acids	柠檬酸,苹果酸,琥珀酸,肉桂酸,酒石酸,乌头酸,马来酸,草酸,乳酸,甲酸,乙酸,丙酸,戊酸,丙二酸,乙醇酸,苯甲酸,苯乙酸 Citric acid, Malic acid, Succinic acid, Cinnamic acid, Tartaric acid, Aconitic acid, Maleic acid, Oxalic acid, Lactic acid, Formic acid, Acetic acid, Propionic acid, Valeric acid, Malonic acid, Glycolic acid, Benzoic acid, Phenylacetic acid
	类固醇 Steroids	豆固醇,菜油固醇,谷固醇 Stigmasterol, Campesterol, Sitosterol
	核苷酸类 Nucleotides	腺嘌呤,鸟嘌呤,尿嘧啶,次黄嘌呤核苷 Adenine, Guanine, Uracil, Inosine
	类黄酮 Flavonoids	柚皮素,儿茶素,花青素,山奈酚,甘草素 Naringenin, Catechin, Anthocyanin, Kaempferol, Glycyrrhizin
	维生素 Vitamins	维生素B1,B3,B5,B6,维生素H Thiamine, Niacin, Pantothenic acid, Pyridoxine, Biotin
	植物激素 Plant hormones	生长素,赤霉素,细胞分裂素 Auxin, Gibberellin, Cytokinin
	其他 Others	胆碱,肌醇,高粱醌,蜂花醇,稻壳酮B,香兰素,尿囊素 Choline, Inositol, Sorgoleone, Myricyl alcohol, Momilactone B, Vanillin, Allantoin
高分子粘性物质 High molecular weight viscous substances	多糖醛酸 Polysaccharide uronic acids	多聚半乳糖醛酸 Polygalacturonic acid
	生物酶类 Enzymes	脲酶,磷酸酶,硫酸酶,蛋白酶,淀粉酶,蔗糖酶,转化酶,磷酸酯酶,木聚糖酶,硝酸还原酶,吲哚乙酸氧化酶,多聚半乳糖醛酸酶 Urease, Phosphatase, Sulfatase, Protease, Amylase, Sucrase, Invertase, Phosphatase, Xylanase, Nitrate reductase, Indole-3-acetic acid oxidase, Polygalacturonase
无机离子 Inorganic ions	阳离子 Cations	H^+, K^+, Ca^{2+}, Na^+, Mg^{2+}, NH_4^+
	阴离子 Anions	SO_4^{2-}, Cl^-, NO_3^-,HPO_4^{2-}, CN^-

量物质的运输。除以上分泌途径外,研究发现定位在根系质膜上具有跨膜转运功能的膜转运蛋白可主动运输根系分泌物,在调控根系分泌物外排中发挥重要作用,其中ABC转运蛋白(ATP-binding cassette transporter)作为生物界最大的转运蛋白家族之一,其可以利用水解ATP释放的能量[37-38],对多种生物分子进行跨膜运输,如脂质、酚类物质、激素和化学药物等[39]。MATE转运蛋白,被认为次级活性转运体,需要依赖电化学梯度进行物质跨膜运输[40]。

2　ABC转运蛋白

2.1　ABC转运蛋白的结构及种类

ABC蛋白存在于各类细胞器中,其中多数定位于质膜和液泡膜,部分定位于线粒体、叶绿体、内质网等细胞器内[41]。依据结构域数量和排序方法的差异,ABC转运蛋白可分成2类,一类为全分子转运



A.被动运输(a.扩散,b.离子通道);B.囊泡运输;C.主动运输(ABC、MATE)
A.Passive transport (a. Diffusion, b. Ion channel); B.Vesicular transport; C.Active transport (ABC, MATE)

图1 根系分泌机制

Figure 1 Mechanism of root secretion

蛋白,即一条独立肽链含有2个“NBD(nucleotide domain)-TMD(transmembrane domain)”,排布为“TMD-NBD-TMD-NBD”,这种顺序定义为正向,反之“NBD-TMD-NBD-TMD”为反向;另一类为半分子转运蛋白,仅以1个“NBD-TMD”形式存在于独立肽链,排列成“TMD-NBD”或“NBD-TMD”[42]。NBD能够结合和水解ATP以驱动转运,TMD将其识别的底物进行跨膜转运。全分子ABC蛋白可以单独起作用,而半分子ABC蛋白必须形成同源或异源二聚体才能执行转运的功能[43]。ABC转运蛋白的结构如图2[44]。

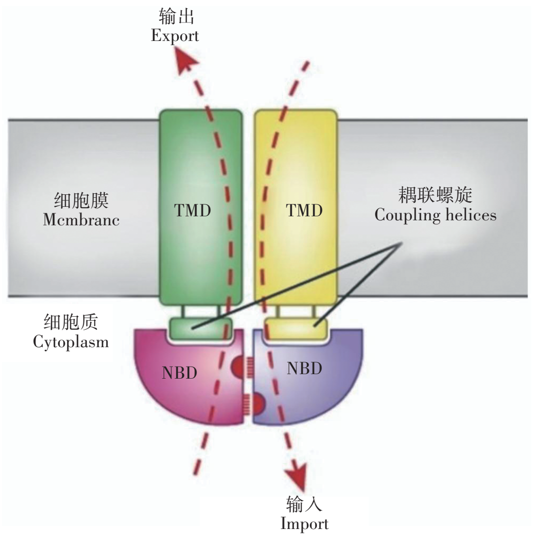


图2 ABC转运蛋白结构[44]

Figure 2 Architecture of ABC transporter

植物ABC蛋白家族体系庞大,成员众多。按照国际命名系统将植物ABC转运蛋白细分为8个亚族,分别为ABCA、ABCB、ABCC、ABCD、ABCE、ABCF、ABCG和ABCI[45],目前对ABCB、ABCC和ABCG亚家族研究较多,依据Sánchez-Fernández的命名法ABCG可分为半分子转运蛋白WBCs(White brown complex homolog)和全分子转运蛋白PDR(Pleiotropic drug resistance)。ABCB可分为全分子转运蛋白MDR(Multidrug resistance)及半分子转运蛋白ATM(ABC transporter of the mitochondria)和TAP(Transporter associated with antigen processing),ABCC主要是全分子转运蛋白MRP(Multidrug resistance associated protein)[45-46]。截至当前,ABCH亚族成员尚未在植物中发现。

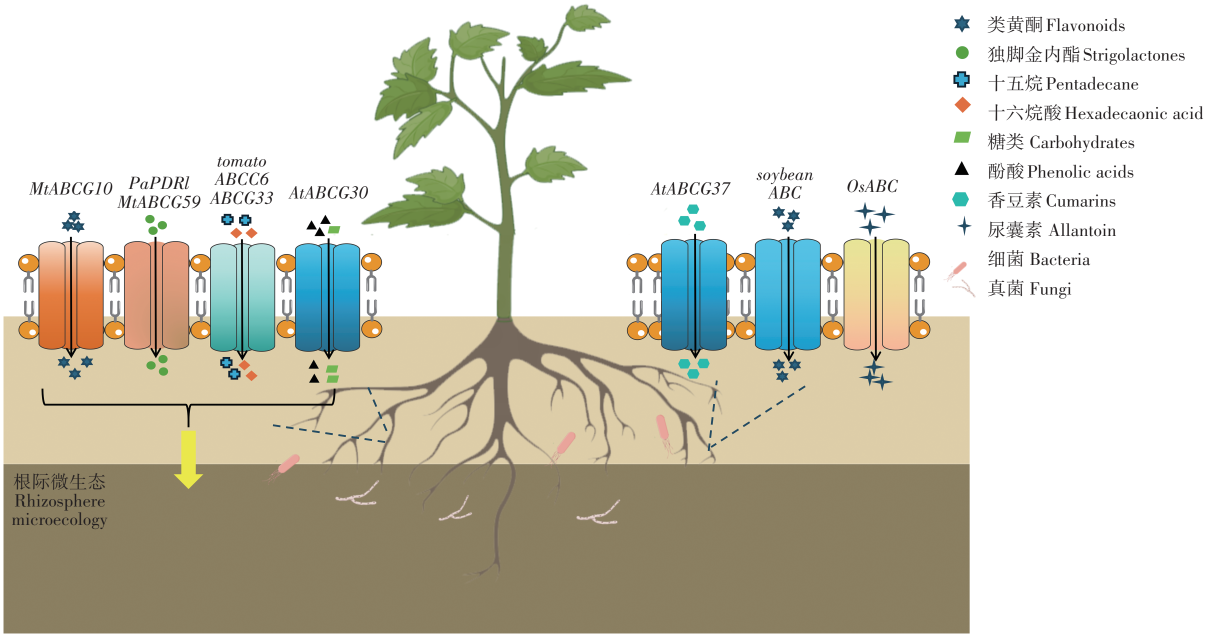
2.2 ABC转运蛋白在调控根系分泌物外排中的作用

在植物中,ABC转运蛋白参与多种化合物的运输[47],例如脂质转运,类固醇及植物激素的运输等[43,47-49]。根据现有的研究成果初步表明ABCA与脂质代谢有关[50-51];同时也有报道*SlABCA1*和*SlABCA2*两个基因在番茄根中优先表达,推测它们可能参与根系代谢物的分泌[52]。ABCB成员主要参与生长素及重金属的转运[53-57]。ABCC具有转运代谢产物花青素、植酸、叶酸等物质,缓解重金属毒害功能[58-62]。ABCD参与植物生长发育及β氧化反应[63]。ABCG功能广泛,具有转运代谢物质(4-香豆酸、甘草素、香紫苏醇和萜类物质等)[64-68]、运输激素物质(ABA、CTK等)[69-72]、参与器官形成[73-75]、逆境胁迫响应[76-78]等功能。ABCE亚族可能在核糖体生物合成、翻译控制和基因沉默调节的过程中发挥作用[79]。有文献报道ABCF可能参与根系生长发育,但具体功能有待验证[80]。有研究发现ABCI在果实发育期表达,表明在果实发育过程中可能扮演着特定的功能角色[81]。

除了上述功能,ABC转运蛋白在参与植株根系分泌物外排中具有重要作用。已有研究发现ABC转运蛋白是拟南芥、豆类等植物根系分泌的化学物质跨膜运输到根际的重要转运蛋白[82-84]。李佳琪[85]研究发现葱与葡萄间作后,葡萄根系分泌物可以显著抑制腐皮镰刀菌(*Fusarium solani*)的生长,进一步通过转录组学分析后发现葡萄*ABCC10*基因表达水平上调,推测ABC转运蛋白参与葡萄根系分泌

物成分外排。尿囊素是一种富含氮的根系分泌物成分，水稻中尿囊素的分泌可被典型的ABC转运蛋白抑制剂正钒酸钠抑制，表明尿囊素的分泌可能依赖于一种ABC转运蛋白[86]。SUGIYAMA等[87]研究发现，ABC转运蛋白抑制剂处理能够抑制大豆根系分泌物中的类黄酮转运，表明ABC转运蛋白很可能参与了大豆根部中类黄酮物质的分泌过程。刘倩文[88]证实在ABC转运蛋白抑制剂正钒酸钠处理下葡萄根系分泌物中很多代谢物的分泌随之受到抑制，说明ABC转运蛋白参与根系代谢物的分泌过程。BADRI等[89]研究发现拟南芥中7个ABC突变体的根系分泌特性存在差异。

ABC转运蛋白能够调控根系分泌物成分进而对根际微生态环境产生影响[89-90]。番茄中ABCC6和ABCG33转运蛋白基因的敲低会改变根系分泌物中的组成，其中十六烷酸（软脂酸）和十五烷发生显著变化，并对马铃薯白线虫（*Globodera pallida*）的孵化产生抑制作用[91]。拟南芥中有25个ABC转运蛋白基因在根中高度表达[82]，其突变体AtABCG30会导致根系分泌物中酚酸类物质含量上升，而糖类物质则相应减少，进一步影响了土壤微生物的菌群结构[89]，且拟南芥中ABCG37缺陷型植株会导致根系分泌的香豆素明显降低[92]。CROUZET[93]发现烟草ABCG转运蛋白基因*NtPDR1*在侧根高度表达，能够将细胞内萜类物质香紫苏醇转运到细胞外，表明该基因可能参与了代谢物的分泌，并发现茉莉酸甲酯处理烟草之后*NtPDR1*上调表达，认为ABC转运蛋白有可能参与植物防御。矮牵牛（*Petunia axillaris*）根系中PaPDR1参与独脚金内酯（SLs）的分泌[94]，苜蓿中与生物矮牵牛*PaPDR1*同源的基因*MtABCG59*也参与根系独脚金内酯的分泌，并影响丛枝菌根的定殖[95]。BANASIAK等[96]发现沉默*MtABCG10*基因，导致苜蓿对尖孢镰刀菌（*Fusarium oxysporum*）的抗性降低，表明该基因可能参与了抗性响应过程中与植物抗毒素合成相关的类黄酮水平的调节，揭示了转运蛋白基因在根系分泌物调控中的重要作用，以上研究结果为ABC转运蛋白影响根系分泌物成分进而影响根际微生物提供了有力证据。



*MtABCG10*和*soybean ABC*基因可能参与此物质的转运

MtABCG10 and *soybean ABC* genes may be involved in the substance transfer

图3　ABC转运蛋白在调控根系分泌物外排中的作用

Figure 3　The role of ABC transporters in regulating root exudates efflux

3　展望

土壤是农作物根系生长载体[97]，其中根际土壤是植物生长的重要区域，受根系分泌物的影响。目前已证实ABC转运蛋白可以调控根系分泌物的种类和含量，进而影响植物与根际微生物的相互作用，但具体哪种物质受到何种ABC转运蛋白的调控研究尚显匮乏，其在植物根系分泌物外排中的调控机制研究尚不明晰。针对ABC转运蛋白转运功能的研究，常用的手段是借助酵母异源表达系统在体外

来判定其转运能力。然而，随着技术的不断进步，利用发根农杆菌介导的转化技术已逐渐崭露头角，成为研究转基因植株的高效途径之一。目前，该方法已在多种植物中成功应用，如柑橘[98]、甘薯[99]、山桐子[100]、猕猴桃[101]等。这为ABC转运蛋白在调控根系分泌物方面的研究开辟了新的途径，为植物生物学研究提供了有力的工具和方法。

综上可见，未来关于ABC转运蛋白基因在根系分泌物外排中的研究可以从3方面深入开展：(1)鉴定与根系分泌物外排相关的ABC转运蛋白；(2)深入研究ABC转运蛋白在根系分泌物外排中的功能和分子机制，揭示其在植物生长发育和环境适应中的作用；(3)研究如何通过ABC转运蛋白来增强植物对特定根系分泌物的外排，提升对逆境环境的适应能力。通过这些研究方向的深入探索，不仅可以更好地理解ABC转运蛋白在植物根系分泌物外排中的功能，还能为调控土壤微生物群落提供新的思路和方法。

参考文献：

[1] 洪常青，聂艳丽. 根系分泌物及其在植物营养中的作用[J]. 生态环境，2003，12(4)：508-511.

[2] 姜丽娜，张黛静，林 琳，等. 低温对小麦幼苗干物质积累及根系分泌物的影响[J]. 麦类作物学报，2012，32(6)：1171-1176.

[3] GUO H P，FENG X，HONG C T，et al. Malate secretion from the root system is an important reason for higher resistance of *Miscanthus sacchariflorus* to cadmium[J]. Physiologia Plantarum，2017，159(3)：340-353.

[4] 陈改苹，朱建国，程 磊. 高CO_2浓度下根系分泌物的研究进展[J]. 土壤，2005，37(6)：602-606.

[5] 王桥美. 茶轮斑病与根际微生物群落关系的研究[D]. 广州：华南农业大学，2022.

[6] YUAN J，ZHAO J，WEN T，et al. Root exudates drive the soil-borne legacy of aboveground pathogen infection[J]. Microbiome，2018，6：156.

[7] GU Y A，WEI Z，WANG X Q，et al. Pathogen invasion indirectly changes the composition of soil microbiome via shifts in root exudation profile[J]. Biology and Fertility of Soils，2016，52(7)：997-1005.

[8] 刘一鸣，杨智仙，董 艳. 对羟基苯甲酸胁迫下间作对蚕豆枯萎病发生和根系抗氧化酶活性的影响[J]. 核农学报，2017，31(5)：987-995.

[9] LIU J G，LI X G，JIA Z J，et al. Effect of benzoic acid on soil microbial communities associated with soilborne peanut diseases[J]. Applied Soil Ecology，2017，110：34-42.

[10] VIVES-PERIS V，DE OLLAS C，GóMEZ-CADENAS A，et al. Root exudates：From plant to rhizosphere and beyond [J]. Plant Cell Reports，2020，39：3-17.

[11] WAREMBOURG F R，BILLES G. Estimating carbon transfers in the plant rhizosphere. In：Harley J. L. and Scott Russell R.(Eds.)，The soil-root interface[M]. Academic press，London and New York and San Francisco，1979：183-196.

[12] ROVIRA A D，FOSTER R C，MARTIN J K. Note on terminology：origin，nature and nomenclature of the organic material in the rhizosphere. In：Harley J. L. and Scott Russell R.(Eds.)，The soil-root interface[M]. Academic press，London and New York and San Francisco，1979：1-4.

[13] 张福锁. 根分泌物及其在植物营养中的作用(综述)[J]. 北京农业大学学报，1992，18(4)：353-356.

[14] DAYAN F E，HOWELL J，WEIDENHAMER J D. Dynamic root exudation of sorgoleone and its in planta mechanism of action[J]. Journal of Experimental Botany，2009，60(7)：2107-2117.

[15] DAYAN F E. Factors modulating the levels of the allelochemical sorgoleone in Sorghum bicolor[J]. Planta，2006，224(2)：339-346.

[16] RENGEL Z. Root exudation and microflora populations in rhizosphere of crop genotypes differing in tolerance to micronutrient deficiency[J]. Plant and Soil，1997，196：255-260.

[17] DELHAIZE E，RYAN P R，RANDALL P J. Aluminum tolerance in wheat(*Triticum aestivum* L.)(II. aluminum-stimulated excretion of malic acid from root apices)[J]. Plant Physiology，1993，103(3)：695-702.

[18] DAYAN F E，RIMANDO A M，PAN Z Q，et al. Sorgoleone[J]. Phytochemistry，2010，71(10)：1032-1039.

[19] 王晶莹. 缺铁胁迫下小金海棠根部铁高效相关蛋白的表达及其属性鉴定[D]. 北京：中国农业大学，2006.

[20] 刘 苹，赵海军，仲子文，等. 三种根系分泌脂肪酸对花生生长和土壤酶活性的影响[J]. 生态学报，2013，33(11)：3332-3339.

[21] 胡 飞，孔垂华. 花生对作物的化感作用[J]. 华南农业大学学报(自然科学版)，2002，23(1)：9-12.

[22] 黄维南,杨乃博,孙惠珍,等.无菌培养下植物离体根分泌物中的游离生长素[J].科学通报,1964(7):630-632.

[23] 吕卫光,张春兰,袁　飞,等.化感物质抑制连作黄瓜生长的作用机理[J].中国农业科学,2002,35(1):106-109.

[24] 杜英君,靳月华.连作大豆植株化感作用的模拟研究[J].应用生态学报,1999,10(2):209-212.

[25] 廖利平,邓仕坚,于小军,等.不同连栽代数杉木人工林细根生长、分布与营养物质分泌特征[J].生态学报,2001(4):569-573.

[26] 解文科,王小青,李　斌,等.植物根系分泌物研究综述[J].山东林业科技,2005(5):63-67.

[27] KATO-NOGUCHI H.Allelopathic substance in rice root exudates:Rediscovery of momilactone B as an allelochemical[J].Journal of Plant Physiology,2004,161(3):271-276.

[28] TANG C S,TAKENAKA T.Quantitation of a bioactive metabolite in undisturbed rhizosphere-benzyl isothiocyanate from *Carica papaya* L.[J].Journal of Chemical Ecology,1983,9(8):1247-1253.

[29] TANG C S,YOUNG C C.Collection and identification of allelopathic compounds from the undistured root system of bigalta limpograss (*Hemarthria altissima*)[J].Plant Physiology,1982,69(1):155-160.

[30] HORST W J,KLOTZ F,SZULKIEWICZ P.Mechanical impedance increases aluminium tolerance of soybean (Glycine max) roots[J].Plant and Soil,1990,124(2):227-231.

[31] MARSCHNER H.Mechanisms of adaptation of plants to acid soils[J].Plant and Soil,1991,134:1-20.

[32] MARSCHNER H.,RÖMHELD V,CAKMAK I.Root-induced changes of nutrient availability in the rhizosphere[J].Journal of Plant Nutrition,1987,10(9-16):1175-1184.

[33] YU J Q,MATSUI Y.Phytotoxic substances in root exudates of cucumber(*Cucumis sativus* L.)[J].Journal of Chemical Ecology,1994,20(1):21-31.

[34] BADRI D V,VIVANCO J M.Regulation and function of root exudates[J].Plant,Cell & Environment,2009,32(6):666-681.

[35] 顾嘉怡,吕欣平,周宇琨,等.水稻根系分泌物对氮素吸收利用的影响研究进展[J].杂交水稻,2024,39(4):9-15.

[36] BERTIN C,YANG X H,WESTON L A.The role of root exudates and allelochemicals in the rhizosphere[J].Plant and Soil,2003,256:67-83.

[37] ORELLE C,DURMORT C,MATHIEU K,et al.A multidrug ABC transporter with a taste for GTP[J].Scientific Reports,2018,8:2309.

[38] THEODOULOU F L,KERR I D.ABC transporter research:Going strong 40 years on[J].Biochemical Society Transactions,2015,43(5):1033-1040.

[39] HWANG J U,SONG W Y,HONG D,et al.Plant ABC transporters enable many unique aspects of a terrestrial plant's lifestyle[J].Molecular Plant,2016,9(3):338-355.

[40] WESTON L A,RYAN P R,WATT M.Mechanisms for cellular transport and release of allelochemicals from plant roots into the rhizosphere[J].Journal of Experimental Botany,2012,63(9):3445-3454.

[41] DAHUjA A,KUMAR R R,SAKHARE A,et al.Role of ATP-binding cassette transporters in maintaining plant homeostasis under abiotic and biotic stresses[J].Physiologia Plantarum,2021,171(4):785-801.

[42] REA P A.Plant ATP-binding cassette transporters[J].Annual Review of Plant Biology,2007,58:347-375.

[43] MCFARLANE H E,SHIN J J H,BIRD D A,et al.*Arabidopsis* ABCG transporters,which are required for export of diverse cuticular lipids,dimerize in different combinations[J].The Plant Cell,2010,22(9):3066-3075.

[44] LOCHER K P.Mechanistic diversity in ATP-binding cassette (ABC) transporters[J].Nature Structural & Molecular Biology,2016,23:487-493.

[45] LANE T S,REMPE C S,DAVITT J,et al.Diversity of ABC transporter genes across the plant kingdom and their potential utility in biotechnology[J].BMC Biotechnology,2016,16:47.

[46] 聂智毅,黎　瑜,曾日中.ABC转运蛋白与巴西橡胶树产胶代谢[J].热带农业科学,2013,33(12):25-34,40.

[47] KANG J,HWANG J U,LEE M,et al.PDR-type ABC transporter mediates cellular uptake of the phytohormone abscisic acid[J]Proceedings of the National Academy of Sciences of the United States of America,2010,107(5):2355-2360.

[48] YAZAKI K.ABC transporters involved in the transport of plant secondary metabolites[J].FEBS Letters,2006,580(4):1183-1191.

[49] YAZAKI K,SHITAN N,SUGIYAMA A,et al.Cell and molecular biology of ATP-binding cassette proteins in plants[J].International Review of Cell and Molecular Biology,2009,276:263-299.

[50] 赵　胡,李裕红.植物ABC转运蛋白研究综述[J].海峡科学,2012(2):13-16.

[51] SHIN S,CHAIRATTANAWAT C,YAMAOKA Y,et al.Early seed development requires the A-type ATP-binding cassette protein ABCA10[J].Plant Physiology,2022,189(1):360-374.

[52] OFORI P A,MIZUNO A,SUZUKI M,et al.Genome-wide analysis of ATP binding cassette (ABC) transporters in tomato[J].PloS One,2018,13(7):e0200854.

[53] MULTANI D S,BRIGGS S P,CHAMBERLIN M A,et al.Loss of an MDR transporter in compact stalks of maize br2 and sorghum dw3 mutants[J].Science,2003,302(5642):81-84.

[54] 徐艳霞.OsABCB14参与水稻生长素转运及铁平衡[D].杭州:浙江大学,2014.

[55] SIDLER M,HASSA P,HASAN S,et al.Involvement of an ABC transporter in a developmental pathway regulating hypocotyl cell elongation in the light[J].The Plant Cell,1998,10(10):1623-1636.

[56] GEISLER M,BLAKESLEE J J,BOUCHARD R,et al.Cellular efflux of auxin catalyzed by the Arabidopsis MDR/PGP transporter AtPGP1[J].The Plant Journal,2005,44(2):179-194.

[57] 李 洁.苦荞ABC转运蛋白基因的克隆与功能初步分析[D].杨凌:西北农林科技大学,2018.

[58] FRANCISCO R M,REGALADO A,AGEORGES A,et al.ABCC1,an ATP binding cassette protein from grape berry, transports anthocyanidin 3-O-Glucosides[J].The Plant Cell,2013,25(5):1840-1854.

[59] GOODMAN C D,CASATI P,WALBOT V.A multidrug resistance-associated protein involved in anthocyanin transport in *Zea mays*[J].The Plant Cell,2004,16(7):1812-1826.

[60] SONG W Y,PARK J,MENDOZA-CÓZATL D G,et al.Arsenic tolerance in *Arabidopsis* is mediated by two ABCC-type phytochelatin transporters[J].Proceedings of the National Academy of Sciences of the United States of America,2010,107(49):21187-21192.

[61] PARK J,SONG W Y,KO D,et al.The phytochelatin transporters AtABCC1 and AtABCC2 mediate tolerance to cadmium and mercury[J].The Plant Journal,2012,69(2):278-288.

[62] BRUNETTI P,ZANELLA L,DE PAOLIS A,et al.Cadmium-inducible expression of the ABC-type transporter *AtABCC3* increases phytochelatin-mediated cadmium tolerance in *Arabidopsis*[J].Journal of Experimental Botany, 2015,66(13):3815-3829.

[63] ZOLMAN B K,SILVA I D,BARTEL B.The *Arabidopsis* pxal mutant is defective in an ATP-binding cassette transporter-like protein required for peroxisomal fatty acid β-oxidation[J].Plant Physiology,2001,127(3):1266-1278.

[64] HAYASHI M,NITO K,TAKEI-HOSHI R,et al.Ped3p is a peroxisomal ATP-binding cassette transporter that might supply substrates for fatty acid β-oxidation[J].Plant &Cell Physiology,2002,43(1):1-11.

[65] 王晓珠,孙 杨,肖仁坚,等.甘蓝型油菜BnABCG8基因的克隆及表达分析[J].分子植物育种,2018,16(1):39-46.

[66] BIAŁA W,BANASIAK J,JARZYNIAK K,et al.*Medicago truncatula* ABCG10 is a transporter of 4-coumarate and liquiritigenin in the medicarpin biosynthetic pathway[J].Journal of Experimental Botany,2017,68(12):3231-3241.

[67] VAN DEN BRÛLE S,MÜLLER A,FLEMING A J,et al.The ABC transporter SpTUR2 confers resistance to the antifungal diterpene sclareol[J].The Plant Journal,2002,30(6):649-662.

[68] 将欣梅,曹 宁,程 瑶,等.辽东楤木三萜皂苷PDR转运蛋白筛选与表达模式分析[J].东北农业大学学报,2023,54(9):10-22,43.

[69] KANG J,YIM S,CHOI H,et al.Abscisic acid transporters cooperate to control seed germination[J].Nature Communications,2015,6:8113.

[70] KUROMORI T,MIYAJI T,YABUUCHI H,et al.ABC transporter AtABCG25 is involved in abscisic acid transport and responses[J].Proceedings of the National Academy of Sciences of the United States of America,2010,107(5):2361-2366.

[71] CAMPBELL E J,SCHENK P M,KAZAN K,et al.Pathogen-responsive expression of a putative ATP-binding cassette transporter gene conferring resistance to the diterpenoid sclareol is regulated by multiple defense signaling pathways in Arabidopsis[J].Plant Physiology,2003,133(3):1272-1284.

[72] KO D,KANG J,KIBA T,et al.*Arabidopsis* ABCG14 is essential for the root-to-shoot translocation of cytokinin[J].Proceedings of the National Academy of Sciences of the United States of America,2014,111(19):7150-7155.

[73] BESSIRE M,BOREL S,FABRE G,et al.A member of the pleiotropic drug resistance family of ATP binding cassette transporters is required for the formation of a functional cuticle in *Arabidopsis*[J].The Plant Cell,2011,23(5):1958-1970.

[74] FABRE G,GARROUM I,MAZUREK S,et al.The ABCG transporter PEC1/ABCG32 is required for the formation of the developing leaf cuticle in *Arabidopsis*[J].New Phytologist,2016,209(1):192-201.

[75] ALEJANDRO S,LEE Y,TOHGE T,et al.AtABCG29 is a monolignol transporter involved in lignin biosynthesis[J].Current Biology,2012,22(13):1207-1212.

[76] 李季肤,韩佳芮,贾怡丹,等.地毯草铝响应基因 AcABCG1 的克隆与表达分析[J].草地学报,2019,27(5):1147-1153.

[77] KIM D Y,BOVET L,MAESHIMA M,et al.The ABC transporter AtPDR8 is a cadmium extrusion pump conferring heavy metal resistance[J].The Plant Journal,2007,50(2):207-218.

[78] STRADER L C,BARTEL B.The *Arabidopsis* pleiotropic drug resisitance8/ABCG36 ATP binding cassette transporter modulates sensitivity to the auxin precursor indole-3-butyric acid[J].The Plant Cell,2009,21(7):1992-2007.

[79] 唐桃霞,孔维萍,任凯丽,等.植物 ABC 转运蛋白功能研究进展[J].西北农业学报,2023,32(1):1-10.

[80] KATO T,TABATA S,SATO S.Analyses of expression and phenotypes of knockout lines for *Arabidopsis* ABCF subfamily members[J].Plant Biotechnology,2009,26(4):409-414.

[81] OFORI P A,MIZUNO A,SUZUKI M,et al.Genome-wide analysis of ATP binding cassette(ABC)transporters in tomato[J].PLoS One,2018,13(7):e0200854.

[82] BADRI D V,LOYOLA-VARGAS V M,BROECKLING C D,et al.Altered profile of secondary metabolites in the root exudates of *Arabidopsis* ATP-binding cassette transporter mutants[J].Plant Physiology,2008,146(2):762-771.

[83] LOYOLA-VARGAS V M,BROECKLING C D,BADRI D,et al.Effect of transporters on the secretion of phytochemicals by the roots of *Arabidopsis thaliana*[J].Planta,2007,225(2):301-310.

[84] SUGIYAMA A,SHITAN N,SATO S,et al.Genome-wide analysis of ATP-binding cassette (ABC) proteins in a model legume plant,Lotus *japonicus*:comparison with *Arabidopsis* ABC protein family[J].DNA Research,2006,13(5):205-228.

[85] 李佳琪.葱间作对连作葡萄植株生长发育的影响[D].沈阳:沈阳农业大学,2021.

[86] YANG X F,LI L L,XU Y,et al.Kin recognition in rice (*Oryza sativa*) lines[J].New Phytologist,2018,220(2):567-578.

[87] SUGIYAMA A,SHITAN N,YAZAKI K.Signaling from soybean roots to rhizobium:An ATP-binding cassette-type transporter mediates genistein secretion[J].Plant Signaling & Behavior,2008,3(1):38-40.

[88] 刘倩文.对羟基苯甲酸介导葡萄根系分泌物成分影响根际微生物群落结构的机制研究[D].沈阳:沈阳农业大学,2022.

[89] BADRI D V,QUINTANA N,EL KASSIS E G,et al.An ABC transporter mutation alters root exudation of phytochemicals that provoke an overhaul of natural soil microbiota[J].Plant Physiology,2009,151(4):2006-2017.

[90] 姜琴芳,伏云珍,李　倩,等.间作作物种间相互作用对土壤细菌群落的影响[J].西北植物学报,2024,33(3):542-551.

[91] COX D E,DYER S,WEIR R,et al.ABC transporter genes *ABC-C6* and *ABC-G33* alter plant-microbe-parasite interactions in the rhizosphere[J].Scientific Reports,2019,9:19899.

[92] ZIEGLER J,SCHMIDT S,STREHMEL N,et al.*Arabidopsis* transporter ABCG37/PDR9 contributes primarily highly oxygenated coumarins to root exudation[J].Scientific Reports,2017,7:3704.

[93] CROUZET j,ROLAND j,PEETERS E,et al. NtPDRl,a plasma membrane ABC transporter from *Nicotiana tabacum*, is involved in diterpene transport[J].Plant Molecular Biology,2013,82:181-192.

[94] SASSE J,SIMON S,GüBELI C,et al.Asymmetric localizations of the ABC transporter PaPDR1 trace paths of directional strigolactone transport[J].Current Biology,2015,25(5):647-655.

[95] BANASIAK J,BORGHI L,STEC N,et al.The full-size ABCG transporter of *Medicago truncatula* is involved in strigolactone secretion,affecting arbuscular mycorrhiza[J].Frontiers in Plant Science,2020,11:18.

[96] BANASIAK J,BIAŁA W,STASZKóW A,et al.A *Medicago truncatula* ABC transporter belonging to subfamily G modulates the level of isoflavonoids[J].Journal of Experimental Botany,2013,64(4):1005-1015.

[97] 姜振峰,李珊珊,温明星,等.大豆苗期根系根际酶谱原位分析[J].东北农业大学学报,2022,53(11):1-9.

[98] RAMASAMY M,DOMINGUEZ M M,IRIGOYEN S,et al.*Rhizobium rhizogenes*-mediated hairy root induction and plant regeneration for bioengineering citrus[J].Plant Biotechnology Journal,2023,21(9):1728-1730.

[99] OTANI M,MII M,HANDA T,et al.Transformation of sweet potato (*Ipomoea batatas* (L.) Lam.) plants by Agrobacterium rhizogenes[J].Plant Science,1993,94(1-2):151-159.

[100] WANG H,CHENG K M,LI T j,et al.A highly efficient *Agrobacterium rhizogenes*-mediated hairy root transformation method of *Idesia polycarpa* and the generation of transgenic plants[J].Plants,2024,13(13):1791.

[101] LI P W,ZHANG Y L,LIANG J,et al.*Agrobacterium rhizogenes*-mediated marker-free transformation and gene editing system revealed that *AeCBL3* mediates the formation of calcium oxalate crystal in kiwifruit[J].Molecular Horticulture,2024,4:1.

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