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豆科禾本科作物间作的根际生物过程研究进展

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摘　要:间作作为一种可持续发展的种植模式不仅具有产量和养分获取的优势，而且能够保证粮食安全、降低作物减产风险。在众多间作组合中，豆科禾本科作物间作由于种间促进及生态位互补作用，而在世界范围内被广泛应用。根际是作物-土壤-微生物相互作用的界面，是养分、水分及有害物质从土壤进入作物系统参与食物链物质循环的必经门户，在根际中所发生的生物过程不仅决定着养分的供应量和有效性，而且也影响着作物的生产力和养分利用效率。因此，本文从豆科禾本科间作的根际生物过程角度出发，综述了豆科禾本科间作对根系形态、根际微生物、根系分泌物及其生态效应的研究进展，为豆科禾本科间作体系在修复重金属污染土壤、提高土壤中养分有效性以及植物遗传改良等方面的应用提供理论依据。

关键词:根际；根系分泌物；豆科；禾本科；间作；根际过程

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Rhizosphere Biological Processes of Legume//Cereal Intercropping Systems: A Review

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Abstract: Intercropping, a sustainable planting pattern, was widely used in the wordwide. It not only has the advantages of yield and nutrient acquisition, but also can ensure food security and reduce the risk of crop failures. The majority of intercropping systems involve legume//cereal combinations because of interspecific facilitation or complementarity. The rhizosphere is the interface between plants and soil where there are interactions among a myriad of microorganisms and affect the uptake of nutrients, water and harmful substances. The rhizosphere biological processes not only determine the amount of nutrients and the availability of nutrients , but also affect crop productivity and nutrient use efficiency. Hence, this paper summarized the progress made on root morphology, rhizosphere microorganisms, root exudates and ecological effect in the perspective of the rhizosphere biological process, which would provide theoretical basis for improving nutrient availability, removing heavy metals, and plant genetic improvements.

Keywords : rhizosphere; root exudates; legume; cereal; intercropping; rhizosphere process

间作是指两种或两种以上作物分行或分带相间种植在同一田块上的种植模式[1]。间作在世界范围内分布广泛，中国间作种植模式年播种面积超过2 800万 hm^2[2]，而在世界其他地区如印度、印度尼西亚、马里、尼日尔、中美和西欧等地都通过间作这一种植模式提高作物生产力[3]。间作与单作相比不仅具有产量和养分获取的优势，维持大多数土壤肥力特性的特点[4-5]，而且具有保证粮食安全、降低作物减产风险的作用[6]。在众多间作系统中，豆科禾本科间作历史悠久，在中国当前所应用的100多种间作组合中，70%

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的组合都有豆科作物的参与[7]。豆科禾本科间作体系被广泛应用的原因在于豆科作物由于自身的固氮作用，能够有效固定空气中的氮，在与禾本科作物间作时，其所固定氮素的一部分可以通过各种途径转移并被禾本科作物所利用，从而提高氮素的利用效率[8-10]。另一方面，豆科与禾本科作物间作使得地上部以及地下部的时间、空间生态位分离[11]，从而能够更好地利用自然界中的光、热、水分等资源，同时挖掘土壤中不同层次的养分资源，达到显著提高产量的优势。

根际作为作物-土壤-微生物相互作用的界面，担负着水分、养分及有害物质从土壤流入作物系统的门户作用，而根际过程能够影响作物水分、养分资源的高效利用、土壤中养分有效性的提高、农作物的化感作用、植物对环境胁迫的适应性、土传病害的防治以及环境的生态效应等。但是当前对于豆科禾本科间作的研究主要集中在地上部产量优势、养分获取等方面，而对于地下部相互作用的研究较少。因此，通过对豆科禾本科间作作物根际过程特别是生物过程的进一步研究，以期能够对修复重金属污染土壤、提高土壤中养分有效性以及植物遗传改良等方面提供理论依据。

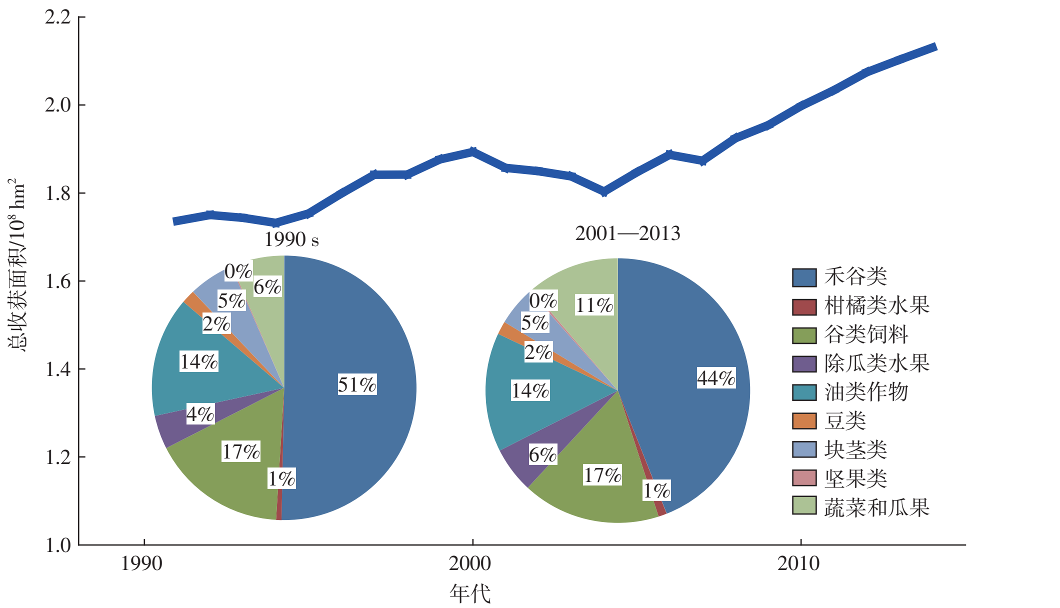
1 豆科禾本科间作的类型及优势

豆科禾本科间作体系作为一种可持续发展的种植模式不仅引起了许多国家的关注[12-13]，而且豆科禾本科作为世界上重要的粮食作物对于保障全球粮食安全具有重要意义。根据联合国粮农组织公布的最新数据显示，中国禾本科作物的收获面积高达 9 大类作物总收获面积的 50%（图 1），由此可见，禾本科作物对于保障中国粮食安全所起到的重要作用。豆科禾本科间作种植体系不仅在中国具有悠久的历史，而且由于其所产生的优势作用而在世界范围内被广泛应用，具体间作的类型及其产生的间作优势如表 1 所示。而从中国间作种植分布状况来看，中国西北灌溉区主要以小麦//大豆、玉米//蚕豆、小麦//蚕豆的体系为主，而中国北部以花生//玉米体系最为典型[14]，小麦//蚕豆由于能够显著提高小麦产量、促进养分利用，有效控制病害，而使其在中国南部（特别是云南地区）得以广泛应用[15-19]。除此之外，豆科禾本科间作体系也被广泛应用于除南极洲以外的各大洲，并且对于许多温带和热带地区当地的粮食安全都作出了重大贡献[20]。

2 豆科禾本科间作对根际生物过程的影响

2.1 豆科禾本科间作对根系形态的影响

根构型是指根系在土壤中的空间造型及分布，是决定植物获取土壤中养分资源的关键因素[40-42]。根构型是由基因型及环境因素共同影响的，不考虑基因型的差异，根构型最终受到各种各样的环境因素影响，如土壤中养分含量及其分布、机械阻抗及水分含量



The categories follow FAOSTAT except that legumes here include groundnuts and soybeans, which were originally categorized as oilcrops in FAOSTAT

图 1 中国 9 大类作物收获面积及各类作物在近 20 年所占比例（数据来源：FAOSTAT）

Figure 1 Annual China total area harvested for nine crop categories, and the proportions of every category in two decades (1990—2013)

表 1 豆科禾本科作物间作类型及其优势

Table 1 The advantages and types of legume//cereal intercropping systems

间作作物类型	土壤类型	间作对作物的影响	参考文献
小麦//蚕豆	红壤、水稻土	间作具有产量优势,提高土壤中养分的有效性,降低小麦、蚕豆发病率和病情指数	[16,18,21-23]
玉米//蚕豆	旱成土	间作具有产量优势,提高缺磷土壤磷的有效性,且能缓解氮肥施用对蚕豆结瘤和共生固氮的抑制效应	[24-26]
玉米//花生	砂土、粘壤土	间作显著促进了花生对铁的吸收,同时也能促进植物 Zn、K、P 养分的吸收	[27]
水稻//花生	高沙土	间作刺激花生的生物固氮作用,提高花生的固氮率和生物固氮量	[28]
燕麦//箭筈豌豆	沙壤土	间作提高了土壤细菌的多样性指数和丰度	
玉米//豇豆	79% 沙土,11% 壤土, 10% 粘土	提高土壤中磷的有效性及玉米产量	[29]
玉米//大麦	旱成土	间作与单作相比有产量优势及更高的土地潜在利用率,但产量优势与土壤肥力及氮肥施用率相关	[30]
小麦//菜豆	深色始成土	间作提高了小麦地上部及地下部的生物量	[31]
甘蔗//大豆	赤红壤	甘蔗//大豆可以提高土地当量比,能够提高土地单位面积的生产力,具有一定的产量优势	[32-34]
甜玉米//大豆	赤红壤	甜玉米//大豆具有一定的产量优势, 有利于提高土地的利用率,更能充分利用养分资源。减量施氮下的甜玉米//大豆不仅能保证作物产量, 提高土地利用率,而且能降低土壤 N_2O 的排放	[35-36]
豌豆//大麦	丹麦(12%粘土、25%粉砂土、63%沙土)、英国(8.5%粘土、18.5%粉砂土、73.5%沙土)、法国(15%粘土、47.5%粉砂土、37.5%沙土)、德国(17%粘土、80%粉砂土、3%沙土)、意大利(25%粘土、48%粉砂土、27%沙土)	间作提高了植物对光、热、水等资源的利用率,促进了豌豆的共生固氮作用、且能够显著抑制杂草生长	[37-39]

等。在养分胁迫条件下,植物根系可以通过形态构型、生理及与微生物互作的适应性变化改变根际过程,提高对土壤磷的吸收利用[42-44]。另一方面,根构型也受到邻近植物的竞争作用大小的影响 [45]。研究表明在玉米//蚕豆体系中,间作玉米与单作玉米相比,总根长、根表面积及根生物量都显著增加[46]。Zhang 等[47]的研究也表明玉米//蚕豆体系中玉米的根长随着供磷水平的增加而显著增加。而 Li 等[48]在对玉米//蚕豆体系的研究中提出,由于蚕豆根系分布较浅,间作的玉米根系分布在蚕豆根系下方并与上层土壤剖面的蚕豆根系交错在一起,两个物种根系分布的兼容性可能是玉米//蚕豆间作种间促进效应的机制之一。

2.2 豆科禾本科间作对根际微生物的影响

自德国植物病理学家 Lorenz Hiltner 于 1904 年将根际定义为植物根系周围、受根系活动影响的微域土壤(图 2),对根际的研究也就越来越受到人们的关注,伴随着现代仪器分析方法以及分子生物学的巨大进步,对根际微生物的研究也逐渐加强。根际微生物

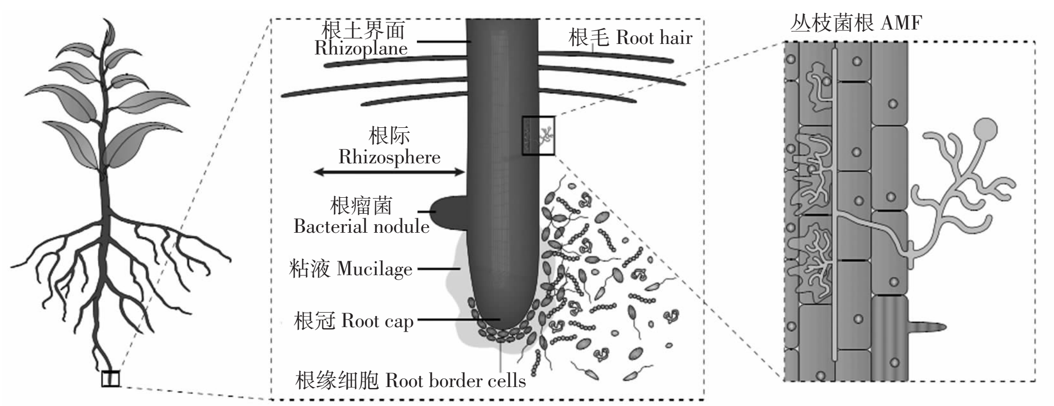


图 2 根际放大图,包括腐生和共生的细菌真菌(包括丛枝菌根)[49]

Figure 2 The magnified pictures of the rhizosphere, containing saprophytic and symbiotic bacteria and fungi, including arbuscular mycorrhizal fungi(AMF)[49]

主要包括细菌、真菌(包括丛枝菌根真菌)、卵菌、病毒和古生细菌等,这些微生物一般以根淀积物(如根分泌物、黏胶物质、边缘细胞等)为食。土壤作为一个巨大的微生物种子库,植物生长的地方就已经决定了根系所能接触到的本土微生物种类,而不同的植物品种通过影响根系形态、根淀积物的类型与数量又能改变根际微生物的组成和活性[49]。

豆科禾本科间作作为不同作物种类组合而成的复合群体,对根际微生物数量、生物量及种群改变必然会有很大影响。沈雪峰等[50]在对甘蔗//花生系统研究中得出,间作与单作相比能够显著提高花生和甘蔗根际土壤细菌及真菌的数量,唐秀梅等[51]在研究木薯//花生对土壤微生态的影响时,也得到了相同的结论。而章家恩等[52]的研究表明,间作能显著提高玉米和花生根区的土壤细菌数量,但土壤真菌及放线菌数量只在间作玉米根区得到显著提高。董艳等[53]在对小麦//蚕豆体系的研究中也发现,间作能增加小麦蚕豆根际微生物的数量。另一方面,根际微生物生物量也受到间作体系的影响,Tang 等[54]的研究表明,小麦在与鹰嘴豆、扁豆间作时,豆科作物根际的微生物生物碳及微生物生物磷含量都显著增加。而 Song 等[55]的研究表明,小麦//蚕豆与单作相比显著提高了小麦根际微生物量碳,但却显著降低小麦根际微生物量氮,同时在小麦//蚕豆、玉米//蚕豆体系中,单作蚕豆根际生物量碳显著高于间作蚕豆。

豆科禾本科间作不仅能够改变根际微生物的数量和生物量,而且对根际微生物种群的组成也有一定的影响,宋亚娜等[56]在对小麦//蚕豆体系的研究中发现,根际细菌群落多样性在小麦蚕豆生长进入花期时得到显著提高。李冬梅[57]的研究也表明,小麦//苜蓿显著提高了根际微生物群落多样性。同时,Qiao 等[29]发现燕麦//箭筈豌豆也能够提高土壤细菌的多样性指数和丰度。

2.3 豆科禾本科间作的根分泌物变化及其生态效应

2.3.1 豆科禾本科植物根分泌物的化感作用

经过多年的研究,存在于豆科禾本科作物中的一部分自毒物质已经被识别(表 2),并且这些自毒物质的化感作用是通过影响细胞分裂、水分和离子的吸收、暗呼吸作用、ATP 的合成、氧化还原平衡、基因表达和防御反应等进行的[58]。韩丽梅等[59]通过对大豆根分泌物的研究发现,经过两周培养的根分泌物抑制了胚根的生长,由此表明化感物质存在于大豆根分泌物中。Tang 等[60]的试验也表明禾本科牧草的根分泌物能使豆科植物的生长受到抑制,使其根系生长减慢,根瘤数量也显著降低,而且还发现番木瓜的根分泌物具有很强的毒性,这可能是因为根分泌物中含有大量的酚类物质。然而豆科以及禾本科作物根分泌物也会产生化感促进作用,研究表明,导致红壤地区连作花生青枯害发生严重的原因很可能与花生根系分泌物中苯乙酮的积累对花生青枯病原菌产生的化感促进作用有关[61]。除此之外,刘苹等[62]也发现,花生根分泌物对根腐镰刀菌菌丝的生长也有一定的化感促进作用。

2.3.2 豆科禾本科植物根分泌物对养分有效性的影响

研究表明根系分泌物可以调控植物根际的养分有效性,根系分泌物不但可以直接提高根际中难溶性养分的活化和利用效率,而且可以通过影响根际微生物的种群分布进而影响根际养分的生物有效性[72]。在豆科禾本科间作体系中,由于豆科作物的生物固氮作用或根际有机酸的分泌导致的根际 pH 值的降低,对于活化土壤中难利用态的磷都具有重要作用[31,73],陈佰岩等[74]和王宇蕴等[21,75]的研究结果也验证了这一结论。Li 等[24]和 Song 等[55]的研究也都表明间作能够提高土壤中磷的有效性。Li 等[76]的研究结果表明:玉米//蚕豆的种间相互作用促进了蚕豆的生物固氮,同时也提高了玉米和蚕豆获取氮的能力。肖靖秀等[18]研究发现小麦//蚕豆可以提高小麦钾吸收量 32%~69%。除此之外,间作对于微量元素的吸收也有重要影响,试验表明,花生与小麦或玉米间作后,花生叶片和籽粒 Fe 含量均会提高,从而改善单作花生缺 Fe 新叶黄化的现象,实现花生籽粒 Fe 的富集[27,77-80]。另外有盆栽研究表明,将花生与不同品种玉米(丹玉13 和中单 2 号)、高粱、燕麦、小麦和大麦等不同的禾本科植物间

表 2 豆科禾本科作物中已识别的自毒物质

Table 2 List of known autotoxins

植物	自毒物质媒介	自毒物质	参考文献
苜蓿	根系	紫苜蓿素、4-甲氧基紫苜蓿素、香豆素、肉桂酸、水杨酸、邻羟基香豆、绿原酸和亲水肉桂酸	[63-66]
蚕豆	根系分泌物	乳酸、脂肪酸、琥珀酸、苹果酸、苯甲酸、香草酸、对羟基苯甲酸、甘醇酸、对羟苯乙酸	[67-68]
豌豆	根系分泌物	苯甲酸、肉桂酸、香草酸、对羟基苯甲酸、3,4-二羟基苯甲酸、香豆酸和芥子酸	[69]
小麦	秸秆残留物	阿魏酸、香豆酸、对羟基苯甲酸、丁香酸和香荚兰酸	[70-71]

作时，都能显著改善花生 Fe、Zn 甚至 Cu 的营养状况,尤其是与燕麦、小麦、大麦间作的花生新叶叶绿素和活性 Fe 含量提高幅度更大[81]。但 Xia[82]的研究表明,玉米与蚕豆、大豆及鹰嘴豆间作促进了玉米对微量元素 Fe、Mn、Cu、Zn 的吸收,但是降低了玉米籽粒中 Fe、Mn、Cu、Zn 的浓度。

2.3.3 豆科禾本科植物根分泌物对重金属活性的影响

根系分泌物不仅可以改善根际养分的有效性,而且对土壤中重金属的活性也有一定的影响,产生这种影响的原因可能是:(1)根系分泌物通过改变根际酸碱反应、氧化还原状况等条件而影响土壤中重金属活性。徐卫红等[83]的研究表明,根分泌的有机酸、氨基酸等有机物被根际微生物利用,使根际土壤的氧化还原低于非根际土，从而改变根际土壤中变价重金属如 Cr、Cu 等的形态及有效性;(2)根系分泌的大分子量黏胶物质通过与重金属离子(如 Pb^{2+}、Cu^{2+}和 Cd^{2+})的络合而形成稳定的螯合体,从而将重金属离子固定在土壤中。黄国勇等[84]的研究表明,根系分泌的粘胶物质与根际土壤中的 Cu^{2+}络合，形成稳定的螯合体,将其固定在污染土壤中;(3)根系分泌物中的低分子量的有机酸、多肽以及氨基酸对土壤中富余的重金属离子也具有较强的络合能力,从而减轻有害金属离子对作物的影响。陈秀玲等[85]的研究表明,小麦与花生间作缺铁条件下,小麦的根系分泌物与土壤中 Cd^{2+}的螯合产物不容易被作物吸收。而有些植物如小麦、黑麦、大麦和豌豆等在遭受铝毒害时，根系分泌较多的 OH^-,将铝沉淀在根表[86]。在铝胁迫条件下植物根系会产生许多种有机酸,耐铝型小麦作物品种根系分泌苹果酸;菜豆和玉米能大量分泌柠檬酸,铝与有机酸形成螯合物达到解铝毒的目的[87];(4)根际微生物种群、微生物分泌物以及根系与微生物的相互作用的改变对土壤中重金属的生物有效性产生重要影响。根系分泌物可以加强土壤中微生物的活性[88],而微生物在将大分子化合物转化为小分子化合物过程中生成的产物对根际重金属有显著的活化作用。另一方面微生物也可以分泌出质子、有机质,增加对植物根际重金属元素的活化能力[89]。因此,通过筛选具有不同特性的豆科禾本科作物组合对于改善土壤中重金属活性具有重要意义。

2.3.4 豆科禾本科植物根分泌物中的黏胶物质对土壤结构的影响

植物根系释放的分泌物与土壤颗粒能够形成根壳,玉米根系能够释放大量粘液,从而形成明显的根壳[90]。根壳在养分和水分的吸收、缓解环境胁迫中具有重要作用[90-96]。这是由于粘液的吸湿性导致根壳的含水量高于土体,从而促进了养分水分的活化与吸收[92,95-96]。Sprent[91]的研究表明,土壤颗粒与根系的粘结主要是由于粘液的粘合作用而形成的。粘液与土壤的粘结作用对于土壤颗粒的团聚来说是十分重要的,尤其是在干旱条件下能保证根系与土壤的紧密接触[72]。

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间作种植体系不但具有充分挖掘光、热、水等自然资源的潜力,而且能够充分利用时间和空间,提高作物生产力,因此,间作在未来的农业体系中具有很强的发展空间。然而当前对于间作体系的研究多集中于地上部，对于植物地下部的交互作用还不清楚,特别是间作体系中根分泌物的释放及其作用机制、养分高效利用的根际动态过程等方面的研究亟需加强,另一方面，间作体系对根际微生物的研究还需逐步加强,可以结合分子生物学等方面的知识和技术将其明朗化，也有助于我们对地下部的作用机理更为了解,从而通过根际调控充分发挥作物的自身生物学潜力,提高养分资源利用效率和作物生产力。

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