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·专题论坛·

豆科植物早期共生信号转导的研究进展

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摘要 豆科植物与根瘤菌建立特异的共生关系, 在寄主根部产生固氮根瘤。此过程包含了共生信号识别与传递、根瘤菌侵染、根瘤形成以及固氮功能实现等生物学事件。研究人员已经从2种豆科模式植物蒺藜苜蓿(*Medicago truncatula*)和百脉根(*Lotus japonicus*)的共生固氮体系中, 筛选到许多与根瘤菌共生相关的突变体及其相对应的功能基因, 建立起包含结瘤因子识别、共生信号传递和转录响应在内的早期共生信号途径。该文对豆科植物早期共生信号途径的新进展进行了综述。

关键词 豆科植物, 根瘤菌, 共生, 根瘤, 信号转导

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生物固氮占全球植物所需氮素的75%, 是生命科学的重大课题。生物固氮体系中, 限于豆科植物的共生固氮体系效率最高。豆科植物-根瘤菌固氮系统每年固定约5 000万吨的氮营养, 这相当于全球农业系统中化肥的年使用总量(Smil, 1999a, 1999b)。根瘤菌利用ATP能量将空气中的分子态氮气转化成离子态氨, 以环境友好的方式交换给宿主, 直接被豆科植物吸收利用(Smil, 1999a, 1999b), 避免了工业氮肥在生产和施用过程中所产生的种种弊端。因此, 开展豆科植物-根瘤菌共生关系的相关研究对于我国农林生产以及生态环境维护与改善有重大意义。

另一方面, 豆科植物可以与丛植菌根真菌(arbuscular mycorrhiza fungi, AMF)建立共生关系, 以提高自身对磷元素的吸收和利用(Parniske, 2008)。与根瘤菌固氮系统相比, AMF共生更为古老和广泛, 70%–90%的陆地植物能够与AMF建立共生关系(Remy et al., 1994)。鉴于其具有重要的生态意义, 科学家开始研究AMF共生系统的分子机制, 并取得了一系列重要进展。如AMF共生关键信号分子Myc因子的分离和鉴定(Maillet et al., 2011); 独脚金内酯调控AMF的分枝和共生信号传递(Akiyama et al., 2005; Kretzschmar et al., 2012)。研究发现, 豆科植物中的2个共生系统共享一段信号识别和转导途径(Catoira et al., 2000; Op den Camp et al., 2011)。研究者普遍认为起源较晚的根瘤菌共生信号转导途径是从AMF共生进化而来的(Parniske, 2008), 人们对其共生机制的了解也更为清楚。本文主要论述有关根瘤菌共生信号转导的研究进展。

豆科植物与根瘤菌建立特异的共生关系, 两者相互作用产生共生固氮发生的器官——根瘤, 它是一系列发育程序的结果。根瘤固氮体系的建立开始于豆科植物和根瘤菌间复杂的分子信号交换: 宿主根系分泌的类黄酮类物质首先被特异的根瘤菌感知, 诱导根瘤菌产生并分泌特定的信号分子(结瘤因子、蛋白质或多糖分子等)进行分子对话, 调节宿主植物根瘤发育的相关反应, 从而奠定了共生固氮体系形成的基础。其中, 结瘤因子(Nod因子)是共生互作中的关键信号分子, 其结构决定了根瘤菌宿主特异性。豆科植物感知Nod因子后, 启动2个响应程序。其一, Nod因子诱导根毛细胞膜去极性化、碱性化和钙振荡等, 导致根毛生长异化、弯曲变形(图1), 并在根毛内部形成侵染线, 根瘤菌沿侵染线向豆科植物根系内部移动; 其二, 与此同时, 豆科植物感知Nod因子后, 在根的内皮层诱导发育程序的开始, 导致根瘤原基的形成和生长。当根瘤菌从侵染线被释放到发育的根瘤原基中时, 这2个程序便汇聚在一起, 形成根瘤。氮的固定就发生在这个豆科植物特有的器官中。

豆科植物与根瘤菌共生关系的建立极为复杂但

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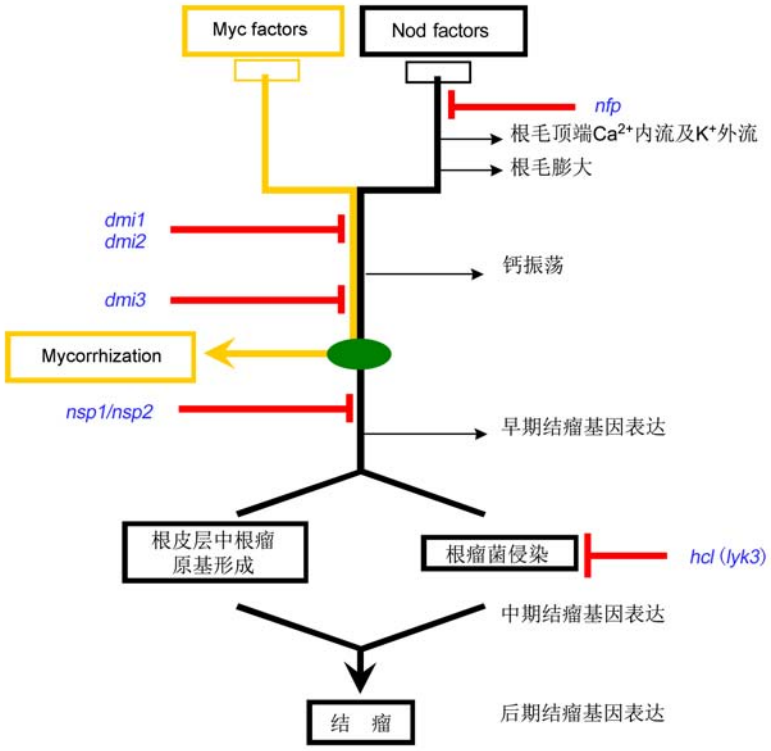

图1 蒺藜苜蓿共生信号转导通路模型(Riely et al., 2004; Jones et al., 2007; Oldroyd and Downie, 2008)

Figure 1 Model of symbiotic signal transduction pathway in *Medicago truncatula* (Riely et al., 2004; Jones et al., 2007; Oldroyd and Downie, 2008)

有序，涉及植物细胞与细菌间的识别、植物根系不同细胞层间的信号传递、单细胞根毛极性生长的异化、多细胞器官根瘤的形态建成、分子态氮向离子态氨的转化等。因此豆科植物-根瘤菌共生关系成为生物学领域的研究热点和前沿。蒺藜苜蓿(*Medicago truncatula*)和百脉根(*Lotus japonicus*)作为豆科植物遗传学模式系统的确立及蒺藜苜蓿基因组测序的完成(Young et al., 2011)极大地促进了该共生关系的研究进程(Cook 1999; Young et al., 2003; Udvardi et al., 2005)。而且它们还是许多重要豆科农林作物的近缘种，有利于研究成果从模式植物向豆科作物的转化。近年来，以结瘤因子为探针，从2个豆科模式植物的共生固氮体系中筛选到许多与根瘤菌共生相关的突变株及其相对应的功能基因，这些突变体被阻断在宿主-根瘤菌互作的不同阶段，为结瘤因子受体的发现及其信号转导途径的建立提供了基础材料。限于篇幅，本文仅论述根瘤菌共生早期的信号转导，主要包括结瘤因子的信号识别、共生信号转导和早期转录响应3个方面。

1 结瘤因子信号识别

在2种豆科模式植物中，Nod因子的假定受体都已被克隆出来。蒺藜苜蓿中的受体为MtNFP和MtLYK3 (Limpens et al., 2003; Arrighi et al., 2006);百脉根的假定受体为LjNFR1和LjNFR5(Madsen et al., 2003; Radutoiu et al., 2003)。它们所编码的蛋白均由胞外LysM域、跨膜域和激酶域组成，属LysM受体类似激酶。

蒺藜苜蓿的*nfp*突变体没有根毛变形和钙振荡等所有最早期的Nod因子响应(Amor et al., 2003; Radutoiu et al., 2003)(图1)。这些突变表型表明，其相应的蛋白位于Nod因子信号转导途径的顶端，因此它被认为是蒺藜苜蓿中编码Nod因子受体的候选者。

百脉根的*nfr1*和*nfr5*均不表现早期Nod因子响应，以受体复合体的形式传递共生信号(Madsen et al., 2011)。*LjNFR5*是*MtNFP*在百脉根中的直系同源物，它们所编码的受体胞内域缺少激酶活性(Arrighi et al., 2006; Madsen et al., 2011)。实验证明，另外一个受体LjNFR1具有激酶活性，能够激活下游共生信号途径(Madsen et al., 2011; Nakagawa et al., 2011)。*MtLYK3*是*LjNFR1*在蒺藜苜蓿中的直系同源物，但是其蒺藜苜蓿的突变体仍然保留了钙振荡和根毛变形等早期共生响应(Wais et al., 2000; Catoira et al., 2001; Smit et al., 2007)。因此，MtLYK3和LjNFR1在2种豆科植物的共生信号途径中分别处于不同的位置。与百脉根NFR1和NFR5在共生信号途径的顶端以受体复合体的形式存在不同，蒺藜苜蓿中MtNFP被认为是“信号传递受体”(signaling receptor)，而MtLYK3为“入口受体”(entry receptor)(Ardourel et al., 1994; Smit et al., 2007)(图1)。它们对NF因子的结构要求、在侵染线形成中的作用以及在根瘤形态建成中的功能均有所区别。

将百脉根的Nod因子受体(*NFR1*和*NFR5*)转基因到蒺藜苜蓿中，能够使蒺藜苜蓿的转基因植株在百脉根共生细菌*Mesorhizobium loti*的诱导下结瘤(Radutoiu et al., 2007)，扩大了蒺藜苜蓿的共生根瘤菌范围。而且，百脉根属2个不同种的共生细菌特异性是由NFR5 LysM域中的单个氨基酸决定的(Radutoiu et al., 2007)。特异性被限定在这些受体类似蛋白的LysM域，有力地支持了它们是绑定Nod因子的受体。

上述位于细胞膜上的受体(Madsen et al., 2011; Haney et al., 2011)只有将共生信号传递到胞质信号元件，才能进一步引发共生响应和根瘤的形成。最早期的共生响应之一是根毛的变形，这一过程需要细胞骨架的重排。植物Rop蛋白能够通过调控肌动蛋白控制根毛的极性生长和形态(Gu et al., 2005; Yang and Fu, 2007)。最近的研究表明，百脉根LjRop6能够与Nod因子受体LjNFR5直接进行蛋白互作(Ke et al., 2012)，其基因干扰导致侵染线形成和根瘤数目下降，表明它参与百脉根的共生过程(Ke et al., 2012)。LjNFR5在蒺藜苜蓿中的直系同源物MtNFP，在体外似乎也能够与几个MtRops进行蛋白互作(未发表资料)，表明它们可能也具有参与调控蒺藜苜蓿共生过程的潜力。

蒺藜苜蓿*hcl*(*LYK3*)突变体虽然表现出根瘤菌侵染缺失，但其仅表现出部分的共生转录响应缺失(Mitra et al., 2004b)。相比于NFP对共生信号转导的调控机制，LYK3如何影响根瘤菌侵染还不清楚。侵染所需的基因是LYK3信号途径上的潜在元件。E3泛素连接酶PUB1与LYK3蛋白互作，负调控根瘤菌的侵染过程(Mbengue et al., 2010)。LYK3可以活化PUB1并使之泛素化，进而促进侵染信号转导元件降解；或者PUB1直接标靶LYK3使之降解(Mbengue et al., 2010)。MtRPG、MtRIT1和MtFLOT4等均参与调控侵染线的形成，是正常根瘤菌侵染所必需的(Arrighi et al., 2008; Miyahara et al., 2010; Haney and Long, 2010; Lefebvre et al., 2010; Haney et al., 2011)；但是它们在依赖LYK3的信号途径中如何协作调控侵染过程仍不清楚。

Nod因子受体MtNFP/LjNFR5和MtLYK3/LjNFR1特异调控根瘤菌共生，其相应突变体中丛植菌根真菌共生不受影响，说明在这2种豆科植物中存在着其它的受体特异调控菌根真菌共生。但是，在能够与根瘤菌建立共生关系的唯一非豆科植物榆科*Parasponia*属中，一个类似MtNFP/LjNFR5的LysM受体PaNFP能够同时调控根瘤菌和菌根真菌共生，表明2个共生系统共享同一个宿主受体(Op den Camp et al., 2011)。这意味着根瘤菌的Nod因子和菌根真菌的Myc因子(mycorrhizal factor)拥有非常类似的分子结构。Maillet等(2011)对Myc因子的分离鉴定结果证实了这个推测。宿主植物在下游信号转导中如何区分Nod因子和Myc因子，从而形成根瘤菌共生特有的根瘤器官，将是值得深入研究的课题。*Parasponia*属作为唯一能够建立根瘤菌共生的非豆科植物，比较其根瘤菌共生和丛植菌根共生的信号途径和进化关系，将对固氮共生系统向非豆科植物的转移研究提供极大的帮助。

2 结瘤因子识别后的信号转导

部分鉴定出的不结瘤突变体能够表现部分的Nod因子响应，表明它们在信号途径中位于Nod因子受体的下游。这些突变体同时表现出丛植菌根真菌共生的缺失，暗示了其相应的基因同时调控根瘤菌和丛植菌根真菌共生过程。因此，这些蛋白调控的信号转导途径被称为共同共生途径(common symbiosis pathway,

CSP)。在蒺藜苜蓿中主要包括MtDMI1、MtDMI2和MtDMI3; 在百脉根中主要包含LjCASTOR、LjPOLLUX、LjSYMRK和LjCCaMK。

蒺藜苜蓿的*dmi1*突变体和百脉根*castor*和*pollux*突变体能够表现出根毛变形, 但是没有钙振荡和皮层的细胞分裂, 因此判定它们相应的蛋白在Nod因子信号转导途径中位于上述Nod因子受体激酶的下游发挥功能(Catoira et al., 2000)(图1)。它们编码细胞核的离子通道, 是共生互作早期观察到的钙振荡所必需的(Ané et al., 2002, 2004; Imaizumi-Anraku et al., 2005; Peiter et al., 2007; Riely et al., 2007; Charpentier et al., 2008; Kosuta et al., 2008; Capoen et al., 2011)。*MtDMI1*是*LjPOLLUX*的直系同源基因及*LjCASTOR*的旁系同源基因(Zhu et al., 2006; Edwards et al., 2007)。LjCASTOR和LjPOLLUX是偏好阳离子的非选择性离子通道(Charpentier et al., 2008)。竞争实验表明, 相比于其它阳离子(如Na^+和Ca^{2+}), LjCASTOR更偏好于K^+。酵母K^+运输突变体的互补实验表明, LjPOLLUX也能够运输K^+(Charpentier et al., 2008)。百脉根的共生信号转导同时需要CASTOR和POLLUX两个离子通道; 但是蒺藜苜蓿似乎只有离子通道DMI1在信号转导途径中发挥作用。虽然在百脉根中至少已鉴定出30个*castor*突变体等位基因, 但是到目前为止并没有发现蒺藜苜蓿的*castor*突变体(Perry et al., 2009)。最新研究表明, 豆科植物野豌豆族和车轴草族的DMI1发生了进化, 替代了POLLUX和CASTOR两个蛋白的功能, 从而大大降低了CASTOR在这2个族群中的功能重要性(Venkateshwaran et al., 2012)。点突变实验表明, 该离子通道“滤器”结构域中的单个氨基酸取代(Ser to Ala)赋予DMI1新的功能(Venkateshwaran et al., 2012)。

研究表明, 蒺藜苜蓿*MtDMI2*与其同源体百脉根*LjSymRK*是共生结瘤过程中所必需的(Endre et al., 2002; Stracke et al., 2002), 其突变体在不同的共生互作阶段产生多效性的影响。在感知Nod因子后, *dmi2*突变体产生根毛变形, 但是没有钙振荡、皮层细胞分裂和细菌侵染(Catoira et al., 2000; Stracke et al., 2002; Miwa et al., 2006)(图1)。蒺藜苜蓿*dmi2*突变体的根毛还表现出非共生的接触响应——根毛为响应机械刺激停止生长但不重启生长(Esseling et al., 2004)。MtDMI2及其同源体不但调控根瘤菌和丛植菌根真菌共生, 而且调控木麻黄科植物粗枝木麻黄(*Casuarina glauca*)和野麻科植物北美假大麻(*Datisca glomerata*)的放线菌内共生过程(Gherbi et al., 2008; Holsters, 2008; Markmann et al., 2008)。

MtDMI2和LjSymRK编码富含LRR重复的受体类似激酶(Endre et al., 2002; Stracke et al., 2002), 其胞外的3个LRR域被认为参与配体蛋白互作, 进而导致磷酸化, 从而活化受体激酶(Yoshida and Parniske, 2005)。MtDMI2和LjSymRK作为受体激酶几乎参与调控整个共生过程(Kouchi et al., 2010)。因此, 准确揭示MtDMI2和LjSymRK的生化功能和调控机制极为重要。蛋白互作筛选表明, MtDMI2/LjSymRK的激酶域能够与甲羟戊酸合酶MtHMGR1(Kevei et al., 2007)、ARID型DNA绑定蛋白LjSIP1(Zhu et al., 2008)、E3连接酶LjSINA4和LjSIE3(Den Herder et al., 2012; Yuan et al., 2012)以及MAP激酶激酶LjSIP2(Chen et al., 2012)蛋白互作。HMGR1催化甲羟戊酸的形成, 甲羟戊酸是细胞分裂素、植物类固醇类激素等特定类异戊二烯类物质的重要前体。HMGR1的基因干扰分析说明, 它参与根瘤菌的侵染和根瘤的形成过程(Kevei et al., 2007)。SIP1是富含AT的DNA绑定蛋白, 能够特异绑定*LjNIN*的启动子, 而LjNIN是根瘤菌侵染、侵染线形成和根瘤原基形成所必需的(Schauser et al., 1999)。E3泛素连接酶LjSINA4与LjSymRK共定位, 并使LjSymRK从质膜上消失。LjSINA4的异位表达降低了LjSymRK的蛋白水平, 破坏了侵染线的正常发育, 表明LjSINA4负调控百脉根的根瘤菌共生(Den Herder et al., 2012)。有趣的是, 另外一个E3泛素连接酶LjSIE3在植物体内也能够直接绑定LjSymRK, 并将LjSymRK作为底物使之泛素化。LjSIE3的过量表达和RNAi分析表明, 它正调控根瘤菌侵染和结瘤过程(Yuan et al., 2012)。来自2个不同家族的E3连接酶均能与LjSymRK蛋白互作, 但是对根瘤菌共生却表现出相反的调控作用, 这可能与不同E3连接酶对受体激酶的作用机制不同有关。E3可以通过泛素化直接调控受体激酶的降解; 而受体激酶可以通过磷酸化调控E3连接酶活性, 进而调控下游原件的蛋白稳定性(Yuan et al., 2012)。Den Herder(2012)和Yuan (2012)的实验结果表明, 这两个机制可能同时存在于E3连接酶和LjSymRK的蛋白互作中。MAP激酶激酶LjSIP2在植物体内与LjSymRK

的激酶域直接互作, 其激酶活性被LjSymRK负调控。基因干扰分析证明, SIP2在百脉根早期共生信号转导、根瘤形态建成和根发育过程中具有重要功能(Chen et al., 2012)。Chen等(2012)发现了LjSymRK激酶域的第1个磷酸化靶蛋白, SIP2作为MAP激酶激酶说明MAP激酶信号传递网络参与建立根瘤菌-豆科植物共生系统。该研究为MAP激酶信号传递和生物固氮领域的研究提供了新的视角。上述的研究结果说明, LjSymRK/MtDMI2可能与下游共生响应的多个关键调控蛋白形成蛋白复合体。MtSYMREM1也能够与MtDMI2受体激酶蛋白互作(Lefebvre et al., 2010), 它作为脚手架蛋白可能参与根瘤菌侵染过程中信号传递复合体的装配; 而且MtDMI2受体的质膜定位需要MtSYMREM1的作用(Lefebvre et al., 2010)。但是MtDMI2/LjSymRK胞外LRR域的配体以及作用机制仍不甚清楚。

蒺藜苜蓿*dmi1*和*dmi2*突变体在Nod因子响应中不能引发钙振荡, 而*Mtdmi3*/*Ljccamk*的功能缺失突变体却保持了这种能力, 但是仍然表现出根瘤菌和丛植菌根真菌共生的缺失(Wais et al., 2000)。由此得出*MtDMI3*/*CCaMK*在*DMI1*和*DMI2*的下游发挥功能(图1)。*MtDMI3*/*LjCCaMK*编码含有钙和钙调素绑定域的蛋白激酶, 表明MtDMI3/LjCCaMK可能感知Nod因子诱导的钙振荡, 并通过使下游蛋白磷酸化将信号翻译成生理响应(Lévy et al., 2004; Mitra et al., 2004a; Tirichine et al., 2006)。在*Mtdmi3*/*Ljccamk*功能获得突变体中, 当自抑制域被去除掉后, 导致结瘤信号途径自动激活, 在没有根瘤菌或Nod因子的情况下, 转基因植株就可以诱导结瘤基因的表达、产生根瘤(Gleason et al., 2006; Tirichine et al., 2006)。上述的研究结果与最近的突变体遗传学研究(Hayashi et al., 2010; Madsen et al., 2010)表明, 共同共生通路足以激活皮层细胞分裂和后续的根瘤形成, 因此, 钙波信号在根瘤发育的信号转导中应处于核心位置(Oldroyd and Downie, 2006)。CCaMK蛋白包含1个激酶域、1个钙调素绑定域以及EF域(Patil et al., 1995; Takezawa et al., 1996), CCaMK绑定Ca^{2+}导致蛋白构象改变并解除激酶活性, 继而借助底物磷酸化激活下游信号转导(Sathyanarayanan et al., 2000)。LjCCaMK的钙调素绑定域和EF域被认为是上游共生信号产生的钙离子浓度变化的感应器。功能缺失突变体(突变位于EF域)研究表明, 第3个EF域是LjCCaMK活化的关键域, 它能促进内共生体的侵染, 但是其功能获得突变体(激酶域的$CCaMK^{T265D}$突变)却能够弥补这些EF域突变对共生表型的影响(Shimoda et al., 2012)。而钙调素绑定域的突变阻止了钙调素的绑定, 从而抑制了$CCaMK^{T265D}$在根瘤菌侵染中的活性, 但是丛植菌根真菌共生却不受影响。表明根瘤菌共生和丛植菌根真菌共生对LjCCaMK的钙调素绑定需求是不同的(Shimoda et al., 2012)。功能获得突变体能同时激活根瘤菌共生和丛植菌根真菌共生信号转导, 但是这种激活需要$CCaMK^{T265D}$的核定位(Takeda et al., 2012)。这些研究表明, 更为古老的丛植菌根真菌共生主要由CCaMK的激酶活性调控, 而更为进化的根瘤菌共生需要CCaMK调控域的复杂调控(Takeda et al., 2012)。CCaMK在2种共生关系中不同活化状态的生化属性仍需进一步研究。

上述研究证明, CCaMK同时调控根瘤的器官形成和根瘤菌侵染2个不同的过程。CCaMK如何分别激活这2个过程呢? 研究表明, CYCLOPS/IPD3分别在百脉根和蒺藜苜蓿中与CCaMK蛋白互作(Messinese et al., 2007; Yano et al., 2008)。CCaMK与CYCLOPS蛋白互作需要CaM绑定域和EF域的参与, CCaMK能够直接磷酸化CYCLOPS; *cyclops*突变体阻断了根瘤菌和丛植菌根真菌的侵染过程, 却能开启根瘤的器官形成(Yano et al., 2008)。因此CYCLOPS被定义为“共同共生通路”的新元件, 是CCaMK下游特异调控根瘤菌侵染的信号转导分支(Yano et al., 2008)。而LjCIP73则在CCaMK下游调控根瘤的器官形成(Kang et al., 2011)。与CYCLOPS不同, CIP73只能与CCaMK的激酶域互作, CaM绑定域和EF域抑制CCaMK与CIP73的互作; 与CYCLOPS类似, CIP3也能够被CCaMK磷酸化。CIP73的基因干扰使根瘤数目减少, 但这与根瘤菌侵染无关(Kang et al., 2011)。由此可知, CCaMK能够通过不同的互作蛋白分别调控根瘤的器官形成和根瘤菌侵染2个过程, 但是豆科植物通过何种机制协调这2个过程还需要深入研究。

3 结瘤因子早期转录响应

蒺藜苜蓿*nsp1*和*nsp2*突变体均表现钙振荡, 但是缺少皮层细胞分裂, 且表现异常的结瘤基因表达(Catoira et

al., 2000; Oldroyd and Long, 2003)(图1)。这表明在Nod因子信号转导途径中NSP1和NSP2在DMI3下游发挥功能。*NSP1*和*NSP2*编码假定的GRAS家族的转录调控因子，表明这些蛋白可能调控Nod因子初始的转录响应(Kaló et al., 2005; Smit et al., 2005; Heckmann et al., 2006; Murakami et al., 2006)。这2个转录因子几乎参与调控所有的根瘤菌共生响应，包括Nod因子诱导的早期结瘤基因表达、根瘤形成和根瘤功能等(Catoira et al., 2000; Oldroyd and Long, 2003; Mitra et al., 2004b; Heckmann et al., 2006)。

在接种了*S. meliloti*的根部，NSP1和NSP2与DMI3都定位于细胞核，这为DMI3调控NSP1和NSP2活性的假设提供了有力的旁证。鉴于DMI3是菌根真菌共生所必需的，但是NSP1和NSP2则不是，说明Myc因子信号激活一组不同的转录因子。这2个信号如何被区分开目前还不清楚。生化研究表明，NSP2与NSP1在细胞核中能够进行蛋白互作形成复合体；NSP2的LHRI域(GRAS类蛋白的保守域之一)是其与NSP1蛋白互作的充要条件，能够与NSP1的多个结构域直接互作(Hirsch et al., 2009)；当用缺少了LHRI域的NSP2转化*nsp2-2*不结瘤突变体时，不能恢复突变体的结瘤能力，说明NSP1-NSP2蛋白互作是根瘤器官形成所必需的(Hirsch et al., 2009)；且NSP1蛋白通过其LHRI和LHRII结构域直接绑定*NIN*、*ENOD11*、*ERN*等早期结瘤基因的启动子，诱导这些早期共生响应基因的表达(Hirsch et al., 2009)。NSP1和NSP2并不是丛植菌根真菌共生过程所必需的。最新的研究结果表明，一个依赖NSP2的信号转导途径促进了丛植菌根真菌在根部的定植(Maillet et al., 2011)。这说明NSP2的功能并不仅限于Nod因子的信号传递，非豆科植物中存在*NSP*基因的直系同源体似乎也暗示了这一点。Liu等(2011)发现NSP1和NSP2是蒺藜苜蓿和水稻(*Oryza sativa*)合成独角金内酯激素所必需的，其突变体大大降低了独角金内酯关键合酶DWARF27的表达。这表明NSP1和NSP2除了调控根瘤菌共生的转录响应，还能在非共生条件下调控独角金内酯的生物合成。

4 结语

共生互作的分子基础研究在过去10年中发生了革命性的突破，这与技术的进步和模式豆科植物的发展紧密相关。通过对突变体进行筛选已经鉴定出很多个共生的关键调控蛋白，但更多蛋白还需要鉴定。研究者面对的新挑战是如何将这些蛋白从生化上彼此联系起来，进而与不同的共生响应联系起来，从而建立共生信号识别与传递、根瘤菌侵染、根瘤形成以及固氮功能实现等完整共生过程的基本调控网络。分子生物学与遗传学、细胞学、生物化学、生理学等技术手段的综合运用，对于在上述领域获得新突破将极为重要。转录组、蛋白质组和代谢组学研究正揭示大量的下游候选基因，这些基因的差异表达暗示它们可能参与共生过程的不同方面。大量的反向遗传学平台在豆科植物中已经或正在被构建，利用这些平台降低或者敲除一些下游基因在豆科植物体内的表达，从而揭示这些基因的功能(Van den Bosch and Stacey, 2003; Tadege et al., 2005)。比较基因组学的研究将有助于更好地了解豆科植物如何与根瘤菌建立精密而复杂的共生系统。随着技术的不断创新和新资源平台的出现，人类对植物与它们的共生搭档互相作用机制的揭示也会不断深入。

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Research Progress in Early Symbiotic Signal Transduction in Legumes

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Abstract Legumes have a symbiotic relationship with soil bacteria known as rhizobia, which induce the formation of a nitrogen-fixing nodules in the host. This symbiotic process includes Nod factor recognition and signaling, rhizobial infection, nodule formation, and establishment of functional (nitrogen-fixing) symbiosis. Genetic screens in model legumes *Medicago truncatula* and *Lotus japonicus* have identified symbiotic mutants that are blocked at different stages in the legume-rhizobium interaction. An early symbiotic signal transduction pathway is established that contains Nod factor recognition, signal transduction, and transcriptional response. In this review, we survey recent progress in understanding these aspects of the interaction.

Key words legume, Rhizobium, symbiosis, nodule, signal transduction

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