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饲草自交不亲和性与近交衰退

赵洪[1]*, 宋丽珍[2], 张玉娥[1], 程佑发[2], 薛勇彪[1]*

[1]中国科学院遗传与发育生物学研究所, 北京 100101; [2]中国科学院植物研究所, 北京 100093

摘要 显花植物自交不亲和性(Self-Incompatibility, SI)是一种广泛分布的种内生殖障碍, 在防止植物近交衰退并促进其异交中发挥了重要作用。然而, 该性状也严重限制了自交制种与杂交育种进程, 而包含绝大多数饲草种类的豆科、菊科与禾本科植物的自交不亲和机制尚不明确, 因此饲草自交不亲和性成为制约我国乃至世界饲草产业发展的主要原因之一。现有研究已经发现五类自交不亲和性的分子机制, 并对其生化与演化机制有了比较深入的了解, 为解析豆科、菊科与禾本科饲草自交不亲和性的分子机制奠定了基础。本文简要综述五类自交不亲和机制, 豆科、菊科与禾本科饲草自交不亲和性及其近交衰退的研究进展。

关键词 自交不亲和性, 饲草, 近交衰退

被子植物约有 20 多万种, 是植物界种类最多、分布最广和适应性最强的类群。因具有独特的花器官, 被子植物又称为显花植物。其中, 约 85%的显花植物为雌雄同花, 而该构造显著增加了自交授粉的概率, 进而导致有害基因纯合以致于近交衰退。为此, 显花植物演化出多种异交促进机制, 其中约 60%的显花植物进化出了自交不亲和性(Self-Incompatibility, SI), 即正常可育的雌雄同花植物自花授粉不能产生合子的现象(de Nettancourt, 2001)。作为一种种内生殖隔离机制, SI 可有效避免自交、促进异交, 从而增加后代的遗传多样性并增强其生存能力。SI 在显花植物中分布非常广泛, 涉及大约 320 多个科。其中, 绝大多数自交不亲和植物的 SI 由一个多态且复等位的 *S* 位点/基因座控制。该位点一般包含两类基因: 决定花柱识别特异性的花柱 *S* 基因和决定花粉识别特异性的花粉 *S* 基因。二者紧密连锁, 构成一个独立的遗传单元, 称为 *S*-单倍体型(Takayama and Isogai, 2005)。来自同一 *S* 单倍体型的花柱和花粉 *S* 因子之间的识别称为自己识别, 而来自不同 *S* 单倍体型的花柱和花粉 *S* 因子间的识别称为异己识别。在自交不亲和植物中, 自己的花粉不能在柱头上萌发或能够萌发但是花粉管不能伸长到达胚珠, 从而发生自交不亲和反应(Self-Pollen Incompatibility, SPI); 而异己的花粉则能完成传粉受精, 最终发生异交亲和反应(Cross-Pollen Compatibility, CPC)。

根据花的形态是否存在差异, SI 可以分为同型 SI (Homomorphic SI) 和异型 SI

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* 通讯作者。zhhong@genetics.ac.cn; ybxue@genetics.ac.cn

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(Heteromorphic SI)。基于花粉自交不亲和表型在遗传控制上的差异，同型SI又分为配子体自交不亲和性(Gametophytic SI, GSI)和孢子体自交不亲和性(Sporophytic SI, SSI)。GSI的花粉表型由单倍体花粉(即配子体)携带的*S*基因型决定，而SSI中花粉亲和与否则由产生花粉的二倍体亲本(即孢子体)的*S*基因型决定。异型SI主要指花柱异型(Heterostyly)，其不亲和表型与雌蕊和雄蕊形态有关。根据其形态差异，异型SI又分为二型花柱(Distyly)和三型花柱(Tristyly) (de Nettancourt, 2001; Takayama and Isogai, 2005; Franklin-Tong, 2008; Zhang et al., 2009; Fujii et al., 2016)。现有的研究发现五类不同分子机制的SI，且均分布于真双子叶植物，其中包括常见于车前科(Plantaginaceae)、茄科(Solanaceae)、蔷薇科(Rosaceae)和芸香科(Rutaceae)的配子体Type 1 (1类) SI，十字花科(Brassicaceae)的孢子体Type 2 (2类) SI，罂粟科(Papaveraceae)的配子体Type 3 (3类) SI以及分别发现于报春花科(Primulaceae)和时钟花科(Turneraceae)的异型花柱Type 4 (4类)和Type 5 (5类) SI (Shore et al., 2019; Matzke et al., 2020, 2021; Zhao et al., 2022)。近年来，对这些SI的分子、生化及演化机制研究取得了显著的进展。

饲草产业是我国畜牧业发展及大粮食安全的重要保障，而我国目前仍面临饲草育种水平低和育成品种少等困境，这与 SI 在饲草中广泛分布密切相关。SI 使得植株自交结实率极低，只能通过杂交固定优良表型，效率远远低于自交亲和品种。由于杂种优势的应用，美国 2002 年的玉米单位面积产量达到 1961 年的 2.1 倍(Duvick, 2005)。然而，即使是在饲草育种水平较高的美国，由于对紫花苜蓿 SI 和自交衰退的分子机制缺乏认识，导致无法获得纯自交系从而有效利用杂种优势，其紫花苜蓿单位面积产量自 1990 年以来的 30 年间几乎没有明显提高(Parajuli et al., 2021)。已知饲草常见于豆科、禾本科和十字花科，菊科和藜科中也有所分布。然而，目前对豆科、禾本科、菊科和藜科自交不亲和的分子机制仍知之甚少。一般情况下，属于同一科属的植物自交不亲和机制相同。因此，解析豆科与禾本科 SI 分子机制对于提高饲草育种水平和效率以及饲草改良具有重大意义。本文将简要阐述近年来已报道的各类型自交不亲和机制，豆科、菊科与禾本科饲草自交不亲和性及其近交衰退的研究进展。

1 自交不亲和性的分子机制

1.1 Type 1自交不亲和性

Type 1 SI植物的花柱和花粉*S*决定因子分别为花柱特异表达的S-核酸酶和花粉特异表达的N端为F-box且C端为FBA/FBK (F-Box Associated/F-Box associated Kelch repeat)结构域的SLF (*S*-locus F-box)蛋白(Anderson et al., 1986; McClure et al., 1989; Sassa et al., 1996, 2007; Xue et al., 1996; Lai et al., 2002; Ushijima et al., 2003; Qiao et al., 2004a; Sijacic et al., 2004; Liang et al., 2020)。当花柱道传输组织细胞合成进而分泌至细胞外基质的S-核酸酶通过花粉管细胞膜进入其细胞质后，可通过静电势基于“同性相斥，异性相吸”的原理与SLF进行自己和异己识别(Li et al., 2017)。异己S-核酸酶因与SLF的互作区带有相

反的静电势而相互吸引，促使SLF招募SSK1 (SLF-interacting SKP1-like 1)、Cullin1和Rbx1形成SCF复合体并行使E3泛素连接酶的功能，从而多聚泛素化异己S-核酸酶使之分步进入26S蛋白酶体进行降解(Qiao et al., 2004b; Huang et al., 2006; Zhang et al., 2009; Zhao et al., 2010, 2021; Xu et al., 2013; Entani et al., 2014)；而自己S-核酸酶因与SLF的互作区带有相同的静电势而相互排斥，使得SLF无法形成SCF复合体对其泛素化，因此自己S-核酸酶可以在细胞质中发挥细胞毒性，主要表现为降解核糖体RNA、调节花粉管尖端钙离子流和破坏细胞骨架动态平衡(McClure et al., 1990; Gu et al., 2015; Qu et al., 2017; Chen et al., 2018; Yang et al., 2018)，最终使得花粉管生长停滞在花柱道中约三分之一处(图1)。

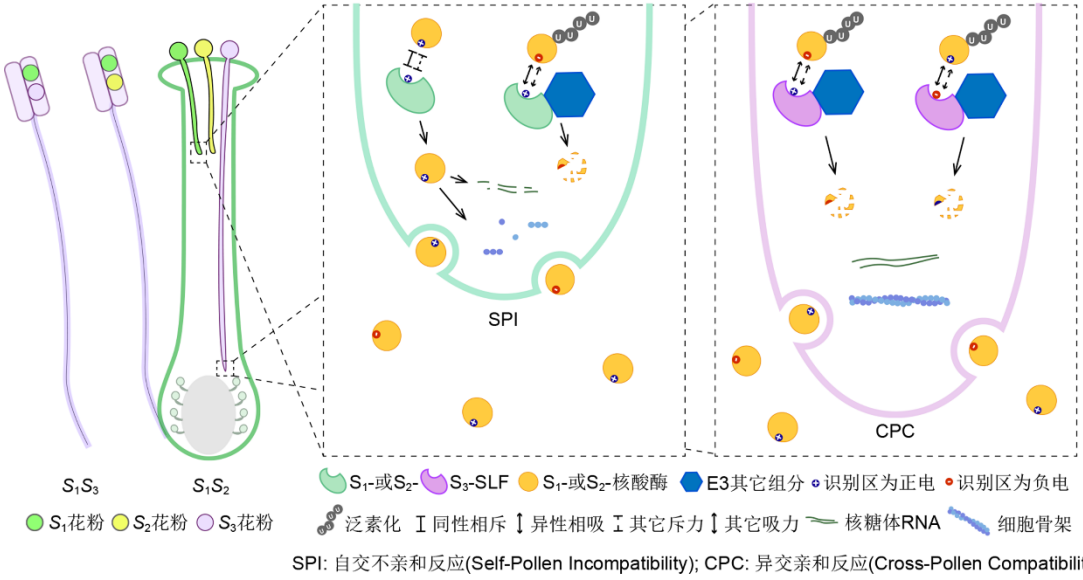

图1 Type 1自交不亲和性的分子机制

车前科、茄科、蔷薇科和芸香科 Type 1 (1 类)自交不亲和性的分子与生化机制示意图。*S* 表示 *S* 基因。图片左侧表示花药、花粉及授粉花柱，右侧虚线框中分别表示花粉管中发生的自交不亲和反应(Self-Pollen Incompatibility, SPI)和异交亲和反应(Cross-Pollen Compatibility, CPC)。

Figure 1 Molecular mechanisms of Type 1 SI

Schematic diagram of the Type 1 SI in Plantaginaceae, Solanaceae, Rosaceae and Rutaceae. *S* indicates the *S* gene. The anther, pollen and pollinated pistils are shown on the left, with SPI (Self-Pollen Incompatibility) and CPC (Cross-Pollen Compatibility) reactions occurring in pollen tubes on the right dashed boxes.

1.2 Type 2自交不亲和性

Type 2 SI的花柱和花粉*S*决定因子分别为花柱乳突细胞特异表达的跨膜受体激酶SRK

(*S*-locus receptor kinase)和花药绒毡层细胞特异表达进而分泌于花粉表面的小的配体SCR (*S*-locus cysteine-rich protein) (Schopfer et al., 1999; Suzuki et al., 2000; Takasaki et al., 2000)。当自交授粉后，SCR可与自己SRK的胞外结构域特异互作，促使SRK同源二聚化及自磷酸化(Cabrillac et al., 2001; Takayama et al., 2001)。随后，定位于乳突细胞膜上的MLPK (*M*-locus protein kinase)可被SRK磷酸化，进一步磷酸化并激活ARC1使其作为E3泛素连接酶泛素化泡外复合体亚基Exo70A1、乙二醛酶GLO1 (Glyoxalase 1)和磷脂酶PLD1 (Phospholipase D alpha 1)等亲和因子并将其导向降解途径(Gu et al., 1998; Stone et al., 2003; Kakita et al., 2007; Samuel et al., 2008, 2009; Sankaranarayanan et al., 2015, 2017; Scandola and Samuel, 2019)。其中，Exo70A1介导的囊泡转运可将水和花粉管渗透生长所需的酶运输至花粉与花柱乳突细胞的互作面，从而促进花粉的吸水萌发及花粉管的渗透生长；GLO1为乙二醛酶途径的一个限速酶，可在亲和反应的细胞质中解毒甲基乙二醛MG (Methylglyoxal)使其不能修饰并破坏GLO1和Exo70A1等蛋白，对于细胞生命活动的正常运行至关重要；PLD1则能在亲和反应中催化磷脂酸PA (Phosphatidic acid)的产生进而增强乳突细胞的胞吐作用以促进花粉萌发。然而，自交授粉后，由于这些亲和因子的降解使得自己花粉不能萌发并长出花粉管，因此产生SPI。此外，不亲和授粉还可促进乳突细胞中活性氧ROS (Reactive Oxygen Species)的产生(Zhang et al., 2021)以及谷氨酸盐受体样通道蛋白GLR (Glutamate receptor-like channel)所介导的钙离子内流(Iwano et al., 2015)，从而抑制并拒绝自交花粉(图2)。

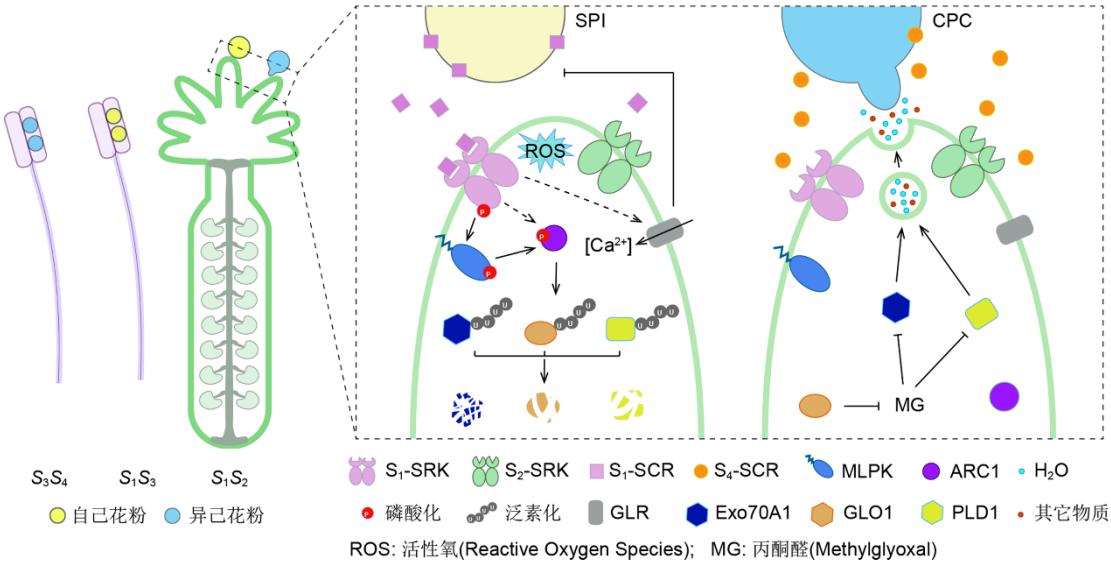

图2 Type 2自交不亲和性的分子机制

十字花科 Type 2 (2 类)自交不亲和性的分子与生化机制示意图。图片右侧虚线框中表示柱头乳突细胞中分别发生的 SPI 和 CPC 反应。*S*、SPI 和 CPC 等标注含义参考图 1。

Figure 2 Molecular mechanisms of Type 2 SI

Schematic diagram of Type 2 SI in Brassicaceae with SPI and CPC reactions occurring in stigma papillae cells shown on the right dashed box. The meanings of *S*, SPI and CPC are identical to that described in Figure 1.

1.3 Type 3自交不亲和性

Type 3 SI的花柱*S*基因*PrsS* (*Papaver rhoeas stigma S*)编码的小的分泌蛋白可以作为配体与花粉*S*基因*PrpS* (*P. rhoeas pollen S*)编码的定位于花粉细胞膜上的受体进行自己识别，并最终引发自己花粉的细胞程序性死亡(Programmed Cell Death, PCD) (Foote et al., 1994; Thomas and Franklin-Tong, 2004; Wheeler et al., 2009)。在此过程中，Ca^{2+}和K^+的快速内流为最早发生的细胞事件之一。由于细胞质中游离Ca^{2+}浓度瞬时增加，进而导致无机焦磷酸酶(Inorganic pyrophosphotases, sPPases) Pr-26.1a/b磷酸化并失活、MAPK (Mitogen-activated protein kinase)蛋白p56磷酸化并激活、微丝解聚以及ROS和NO含量爆发(Thomas et al., 2006; Li et al., 2007; Wilkins et al., 2011)。其中，自己花粉中失活的无机焦磷酸酶Pr-26.1a/b由于无法通过水解无机焦磷酸(Inorganic Pyrophosphate, PPi)促进生物合成与细胞的快速生长，因而抑制了自交花粉管尖端的生长(de Graaf et al., 2006)。激活的MAPK则可促进NO产生并介导可逆不亲和反应向不可逆PCD转变。此外，不亲和授粉还可诱导花粉中ROS的爆发，该信号分子的显著增多与微丝解聚均可诱导下游PCD的产生(Wilkins et al., 2011)，从而导致自己花粉管生长受阻(图3)。

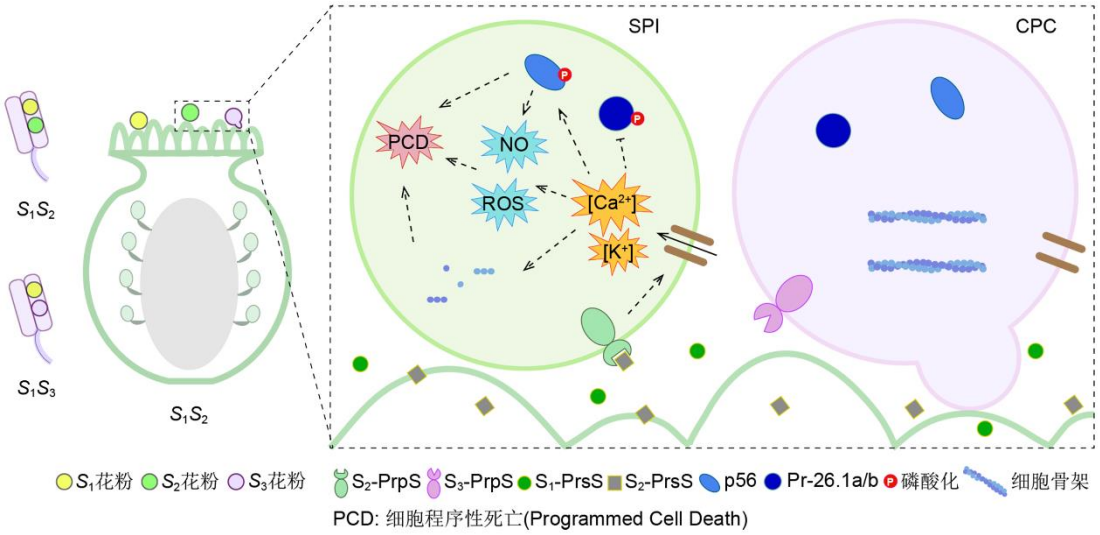

图3 Type 3自交不亲和性的分子机制

罂粟科 Type 3 (3 类)自交不亲和性的分子与生化机制示意图。图片右侧虚线框表示自己和异己花粉中分别发生的 SPI 和 CPC 反应。其它标注含义参考图 1 和 2。

Figure 3 Molecular mechanisms of Type 3 SI

Schematic diagram of Type 3 SI in Papaveraceae with SPI and CPC reactions occurring in self and cross pollen cells shown on the right dashed box. The meanings of other annotations are identical to that described in Figure 1 and 2.

1.4 Type 4和5自交不亲和性

Type 4 SI由一个半合子*S*超基因位点控制，其中包括紧密连锁的控制花柱长度和雌性SI的*G*位点基因*CYP* (*Cytochrome P450*)，控制花药位置的*A*位点基因*GLO2* (*GLOBOSA2*)，以及未知功能的*KFB* (*Kelch repeat F-box*)、*CCM* (*Conserved cysteine motif*)和*PUM* (*Pumilio-like RNA-binding protein*) (Huu et al., 2016, 2020; Li et al., 2016)。当*S*位点基因型为*S*/*s*时，表现为短花柱(S-morph/Thrum)；当其为*s*/*s*时，则为长花柱(L-morph/Pin) (Lewis and Jones, 1992)。这两种不同形态的花杂交时表现为完全亲和，而自交时则为不亲和或结实率极低。研究表明，*CYP*基因在短型花柱中特异表达，其编码产物CYP734A50通过失活油菜素甾醇(Brassinosteroids, BRs)抑制花柱伸长，这与BR在长型花柱中十分丰富，而在短型花柱中几乎检测不到相一致。长型花柱中丰富的BR进一步促进短花柱花的花粉受精而抑制长花柱花的花粉受精，使得短花柱和长花柱花的花粉给长花柱授粉后分别表现为亲和与不亲和；而在短花柱中由于CYP734A50对BR造成抑制，使其无法促进短花柱花的花粉并抑制长花柱花的花粉，因此两种花粉给短花柱授粉后分别表现为不亲和与亲和(Huu et al., 2022) (图4)。与Type 4 SI不同的是，Type 5 SI的*S*位点由三个基因构成(Shore et al., 2019)。其中，*TsSPH1* (*Turnera subulata SPH1*)在花药和花丝中表达，*TsYUC6*只在花药中表达，*TsBAHD*则在花柱中表达并包含保守的BAHD酰基转移酶活性域(Shore et al., 2019; Matzke et al., 2020)。与CYP734A50功能相似，TsBAHD可通过酰化作用抑制BR进而调控自交和异交花粉管的生长(Matzke et al., 2021)。

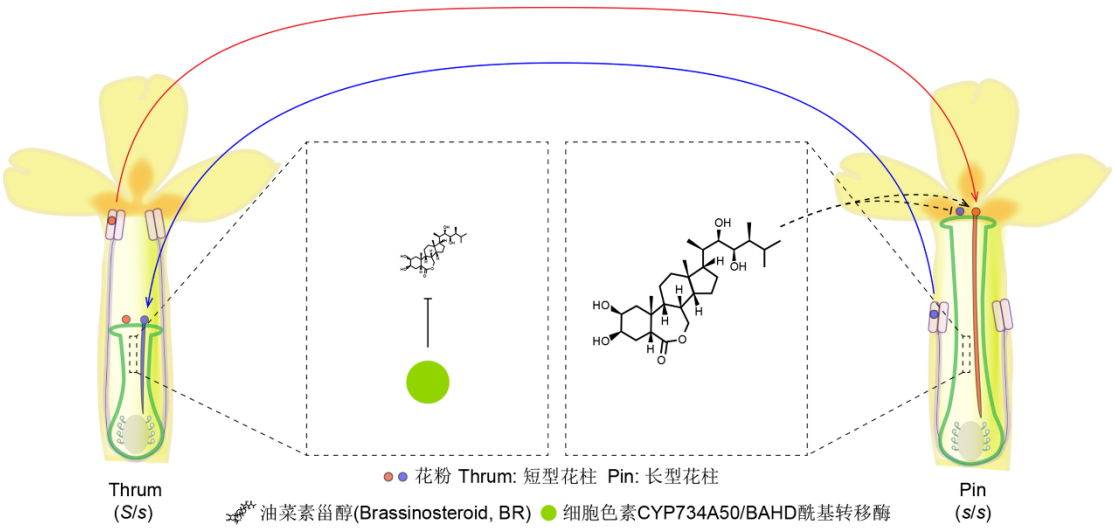

图4 Type 4和5自交不亲和性的分子机制

报春花科和时钟花科 Type 4 和 5 (4 和 5 类)自交不亲和性的分子机制示意图。图片左右两侧分别表示短型花柱(短花柱和长花药)与长型花柱(长花柱和短花药)。红色和蓝色箭头指示授粉方向。黑色虚线箭头及其平末端形式分别表示 BR 对异交和自交花粉的促进和抑制作用。

Figure 4 Molecular mechanisms of Type 4 and 5 SI

Schematic diagram of Type 4 and 5 SI in Primulaceae and Turneraceae. Short style with long anther and long style with short anther are seperately shown on the left and right sides. Red and blue arrows indicate the pollination direction. The black dotted arrow and its flat terminal form represent the promotion and inhibition effects of BR on the cross and self pollen, respectively.

2 SI的起源与演化

被子植物在进化过程中, 由于受到来自自交和异交的选择压力, 其SI也会频繁地丢失和重获(de Nettancourt, 2001; Franklin-Tong, 2008)。然而, 关于SI是如何起源和演化的以及五类SI机制的演化关系是什么一直以来都为未解之谜。最近, 研究人员通过系统基因组演化分析、分子遗传学验证和生物学功能研究发现, 起源于真双子叶植物的最近共同祖先的1类SI最为古老, 而2-5类SI则为丢失了1类SI后分别在十字花科、罂粟科、报春花科和时钟花科中进化产生的新的SI机制。此外, 能够编码雌性自交不亲和决定因子T2类核酸酶和雄性自交不亲和决定因子FBK或FBA结构域蛋白的1类*S*-like位点结构在被子植物起源之初即已产生, 表明该类*S*位点极其古老, 可能为1类自交不亲和*S*位点的初始形式且与被子植物的起源和早期扩张有关(Zhao et al., 2022) (图5)。

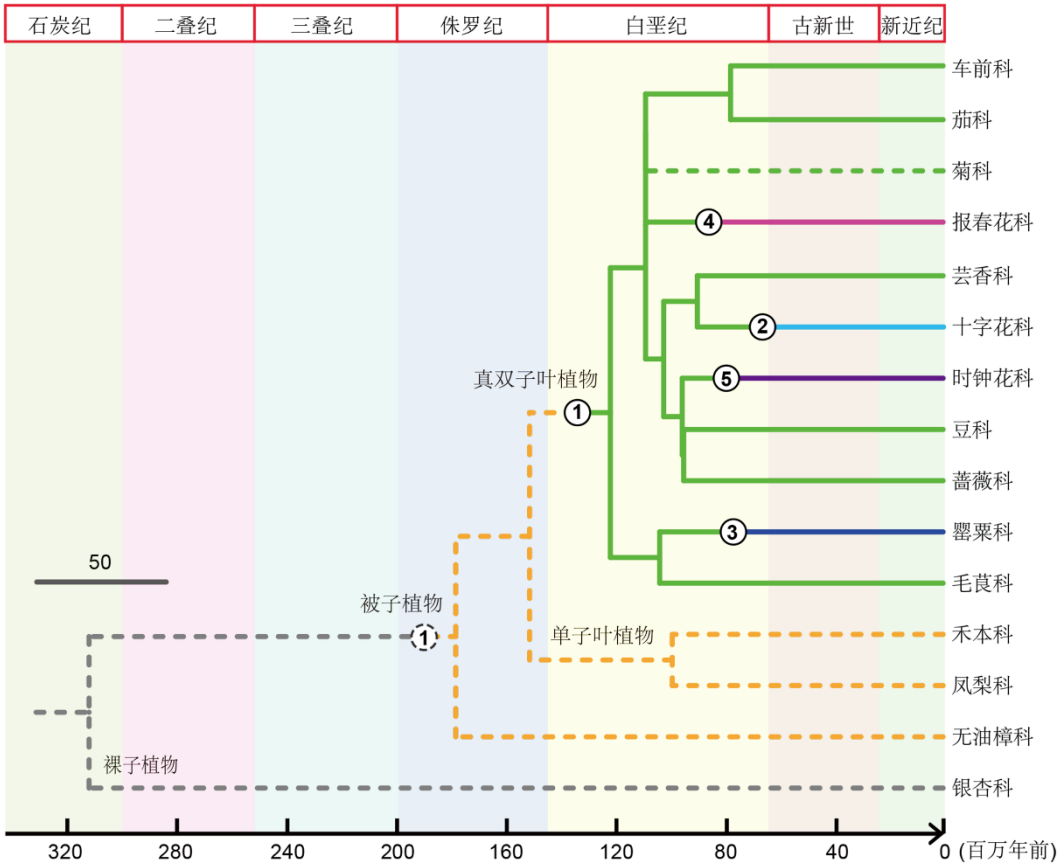

图5 Type 1-5 SI的起源与演化机制

Type 1-5 (1-5 类)自交不亲和代表物种的科水平物种进化树。进化树由 TimeTree (http://www.timetree.org/)网站生成，下方数轴为演化时间轴。圆圈中的序号分别表示五类SI。绿色、浅蓝色、深蓝色、玫红色和深紫色实线分别指示 Type 1、Type 2、Type 3、Type 4 和 Type 5 *S* 位点。灰色虚线表示不具有 *T2 RNase* 与 *FBA*/*FBK* 连锁位点，橙色虚线表示具有能够编码 Class I/II T2 RNase 和 FBA/FBK 结构域蛋白的 Type 1 *S*-like 结构，绿色虚线代表不具有 Class III *T2 RNase*/*S-RNase* 与 *FBA*/*FBK* 紧密连锁形成的 Type 1 *S* 位点。

Figure 5 Origin and evolution of Type 1-5 SI

Phylogenetic tree constructed by TimeTree (http://www.timetree.org/) showing several representative families/species seperately possessing Type 1-5 SI. The axis under the tree indicates the evolutionary time. The serial number in circles represents the five SI types. Green, light blue, dark blue, rose, and dark purple lines indicate Type 1-5 *S*-locus, respectively. The gray dotted line represents no *T2 RNase* linked to *FBA*/*FBK*, the orange Type 1 *S*-like structure encoding Class I/II T2 RNase and FBA/FBK proteins and the green no Type 1 *S* containing Class III *T2 RNase*/*S-RNase* tightly linked to *FBA*/*FBK*.

3 饲草自交不亲和性研究进展

3.1 豆科饲草自交不亲和性

豆科(Fabaceae)约有650个属18000个物种，是被子植物中仅次于菊科和兰科的第三大科。其中，紫花苜蓿、白三叶和红三叶草等均为优质饲草的代表，在我国畜牧业中占据十分重要的地位。SI在豆科植物中分布非常广泛，其中云实亚科中约62.3%的物种具有自交不亲和现象，含羞草亚科中约66.7%，蝶形花亚科约22.1% (Arroyo et al., 1981)。尽管一些栽培种已丢失SI，但是由于野生种仍保留该特性，进而对杂交育种及野生种质资源保存造成严重限制。因此，对豆科特别是其饲草自交不亲和机制的研究对于有效促进畜牧业发展具有重要意义。豆科SI通常表现为配子体型(Atwood, 1940; Brewbaker, 1954, 1957)，即当花粉*S*单倍体型与母本*S*基因型中的一个相同时，则为不亲和。豆科植物的花柱通常为湿柱头(Heslop-Harrison and Shivanna, 1977)，与茄科、车前科、蔷薇科和芸香科等Type 1 SI植物的柱头类似。不同于具有Type 2 SI的十字花科的干柱头，自己和异己花粉落在湿柱头后，都可以吸水萌发并长出花粉管，而对自己花粉管生长的抑制作用则一般发生在花柱中。然而，据相关研究记载，豆科植物对自交花粉管的拒绝既可以发生在柱头，常见于岩黄耆属(*Hedysarum*)、银合欢属(*Leucaena*)、百脉根属(*Lotus*)物种；也可发生于花柱中，如羊蹄甲属(*Bauhinia*)、染料木属(*Genista*)、苜蓿属(*Medicago*)、酸豆属(*Tamarindus*)和车轴草属(*Trifolium*)物种；还有一些物种的花粉无法在胚珠完成受精或者受精后败育即发生合子后生殖障碍，如菜豆属(*Phaseolus*)、牧豆树属(*Prosopis*)、紫檀属(*Pterocarpus*)、金合欢属(*Acacia*)、云实属(*Caesalpinia*)、朱缨花属(*Calliandra*)、黄檀属(*Dalbergia*)、刺桐属(*Erythrina*)和孪叶豆属(*Hymenaea*)物种(Delaney and Igić, 2022)。此外，称为“牧草之王”的紫花苜蓿还具有部分自交不亲和性，其自交结荚率在不同品种或个体间差异较大，平均约为27.6% (Brink and Cooper, 1938；何咏松和吴仁润, 1987)。

关于豆科自交不亲和的详细分子机制，目前尚无报道。由于Type 1 SI起源于真双子叶植物的最近共同祖先且最为古老，加之豆科植物绝大多数具有湿柱头且一些物种如白三叶(*T. repens*)自交授粉后花柱对自己花粉管的抑制作用与Type 1 SI相似(Casey et al., 2010)，因此研究人员普遍认为Type 1 *S*可能控制了该类物种的SI。Casey等(2010)虽然定位到了控制白三叶SI的单一*S*位点，且该位点大体上与蒺藜苜蓿(*M. truncatula*)的1号染色体共线，但是并未明确其中是否包含*S-RNase*和*SLF*。Aguiar等(2015)在蒺藜苜蓿和鹰嘴豆(*Cicer arietinum*)中确实鉴定到了Type 1 *S*的类似结构。然而，虽然系统发育分析表明所鉴定到的T2核酸酶和F-box蛋白分别能够与S-RNase和SLF聚为一枝，但其均能在除雌蕊和雄蕊以外的其它组织中表达。另外，鹰嘴豆S-RNase候选基因的序列多态性也不符合*S*基因特征。因此，研究人员推测该物种以至于豆科可能不具备Type1 SI。尽管如此，由于豆科SI在属内及属间均表现出显著差异(Delaney and Igić, 2022)，因而无法排除部分属或物种仍保留Type 1 SI，而另一些属或物种则在丢失了Type 1 SI后又进化产生了新的自交不亲和机制(Zhao et al., 2022)。

3.2 菊科饲草自交不亲和性

菊科(Asteraceae)约有 1000 属 30000 个物种，是被子植物的第一大科，其中串叶松香草(*Silphium perfoliatum*)、苦荬菜(*Lactuca indica*)和菊苣(*Cichorium intybus*)等均为产量高、营养丰富且适应性强的优质饲草。据估计，菊科中超过 60%的物种为自交不亲和(Ferrer and Good-Avila, 2007)，例如松香草属的全叶松香草(*Silphium integrifolium*)、向日葵属的向日葵(*Helianthus annuus*)、莴苣属的生菜(*Lactuca sativa*)和菊苣属的菊苣(*Cichorium intybus*)。然而，关于菊科 SI 的详细分子机制目前仍知之甚少。与十字花科 SI 类似，菊科植物花粉亲和与否也由孢子体基因型决定(Hiscock, 2000; Hiscock et al., 2003; Allen et al., 2011)，但其 SSI 的分子机制与十字花科的 Type 2 SI 并不相同。在糙叶千里光(*Senecio squalidus*)中，Tabah 等(2004)尽管克隆到了花柱表达的 *SRK-like* 基因，但后续研究表明，糙叶千里光和菊苣的 SRK-like 并非 *S* 决定因子。McInnis 等(2005)发现一个 *S* 相关的花柱特异的过氧化物酶基因 *SSP* (*S-associated stigma-specific peroxidase*)，但其并不直接参与控制糙叶千里光的 SSI。Gonthier 等(2013)在菊苣中将 *S* 位点定位至一个 1.8 cM 的 QTL 区域，但是并未报道控制其 SSI 的详细基因。Price 等(2022)在全叶松香草中将 *S* 位点定位于 6 号连锁群一个 LOD 峰值为 18.9 cM 的 QTL 区间内，进一步通过与自交不亲和的向日葵和生菜进行候选 *S* 位点的共线性分析，鉴定到 43 个 *S* 类似基因。其中，柱头特异蛋白 STIG1-like (Stigma Specific Protein 1-like)是一类小的富含半胱氨酸的蛋白，类似十字花科的 SCR 和罂粟科的 PrsS，在番茄(*Solanum lycoperscium*)中最初发现于柱头分泌物中，可以结合花粉特异表达的激酶来促进花粉管生长(Huang et al., 2014)。更有趣的是，在该基因下游 109 kbp 处存在一个丝/苏氨酸蛋白激酶编码基因，而这两类紧密连锁的基因是否通过类似 Type 2 的 SRK-SCR 模块调控菊科的 SSI 还需进一步研究。但是，值得一提的是由于在该位点及其与菊科其它物种的共线区域中，并未发现 SRK 类似基因，因此菊科 SSI 应该采取的是不同于十字花科的分子机制(Price et al., 2022)。此外，研究人员还在向日葵 17 号染色体与全叶松香草的假定 *S* 位点共线的区域中，发现 12 个紧密连锁的 *F-box* 基因，但其附近并未注释到 *S-RNase* (Price et al., 2022)，该结果与最近报道的 SI 的起源、丢失与重获的动态分析结果相一致(Zhao et al., 2022)，提示菊科在丢失了起源最早的 Type 1 SI 后，又进化产生了新的自交不亲和机制，而这些不与 *S-RNase* 连锁的 *F-box* 是否通过招募新的 *S* 基因参与控制菊科 SSI 则有待进一步探究。

3.3 禾本科饲草自交不亲和性

禾本科是被子植物中的第四大科，单子叶植物的第二大科，约有660个属11000个物种，包含重要的谷物、饲草和能源作物。SI在禾本科中广泛分布，其中至少16个属表现为自交不亲和，例如黑麦草属的多年生黑麦草(*Lolium perenne*)、赖草属的羊草(*Leymus chinensis*)、大麦属的球茎大麦(*Hordeun hulhosum*)和稻属的长雄蕊野生稻(*Oryza longistaminata*)等。

禾本科SI属于配子体型，但与双子叶植物不同的是，其通常受两个非连锁且复等位的*S*和*Z*位点控制(Lundqvist, 1954; Hayman, 1956)。当花粉的*S*和*Z*单倍体型与雌蕊的*S*和*Z*基因型均匹配时，则不能在柱头表面正常萌发，进而产生SPI。此外，双位点控制的特性使得禾本科植物不同来源的花粉授粉后可出现0、50%、75%和100%四种不同程度的亲和现象(Yang et al., 2008)。

尽管早在上世纪中期即已发现 *S* 和 *Z* 双位点与禾本科 SI 之间的关系，但其详细基因尚未被成功克隆。在多年生黑麦草和黑麦中(*Secale cereale*)，研究人员发现磷酸葡萄糖异构酶(Phosphoglycoisomerase, PGI-2)和 Prx7 过氧化物酶编码基因分别与其 *S* 位点共分离(Cornish et al., 1980; Wricke and Wehling, 1985)，β-葡糖苷酶(Beta-glucosidase)和酯酶编码基因与黑麦的 *Z* 位点共分离(Gertz and Wricke, 1989)。与此同时，在天蓝鹳草(*Phalaris coerulescens*)中，一个编码硫氧还蛋白(Thioredoxin, Trx)的 *Bm2* 基因起初被认为与 *S* 基因型共分离，但随后通过定位分析证明该基因其实并不在 *S* 位点内(Li et al., 1994, 1995; Baumann et al., 2000)。Kakeda(2009)在球茎大麦(*Hordeum bulbosum*)中发现两个花药表达的 *F-box* 基因与 *S* 位点紧密连锁，但其生物学功能尚无报道。Shinozuka 等(2010)基于 SNP 分子标记和 BAC 测序，定位到了 *Z* 位点的 9 个编码基因，进一步通过表达模式和序列多态性分析，发现其中的 *LpTC116908* 和 *LpDUF247* 可能与其自交不亲和相关。Manzanares 等(2016)通过对多年生黑麦草 7 个定位群体 10177 个个体进行定位并结合 BAC 测序和转录组分析，发现一个编码 DUF247 (Domain of unknown function 247, DUF247)结构域蛋白的基因能够与 *S* 位点共分离。此外，该基因在花粉中高表达且具有序列多态性，提示其可能作为一个花粉 *S* 基因发挥功能，并将其命名为 *LpS-DUF247*。Lian 等(2021)通过序列相似性分析在长雄蕊野生稻的 5 号染色体上发现多个 *S* 位点候选基因，其中包括两个花粉基因 *OlSS1* 和 *OlSS2* 和一个花柱基因 *OlSP*，但其作用机制并不清楚。在羊草中，Chen 等(2019)基于自交和异交授粉花柱的转录组分析，提出自交授粉可能会激活钙离子和植物激素为主的信号级联反应并最终导致 PCD。

在最新报道的 SI 起源、丢失与重获的高度动态进化机制中，研究人员发现能够编码 Class I/II T2 RNase 和 FBA/FBK 结构域蛋白的 1 类 *S*-like 位点结构在被子植物起源之初即已产生且广泛分布于禾本科，暗示其可能与禾本科 SI 有关(Zhao et al., 2022)。进一步对其功能与演化机制的深入研究有望为禾本科 SI 提供新的理解和认识。

4 自交不亲和性的应用与展望

SI不仅是一个非常重要的生物学问题，而且在生产实践上也有非常重要的应用价值。一方面，SI作为一种严格的种内生殖障碍，不仅可以通过限制自交从而省去人工去雄及雄性不育系选育等耗时耗力的工作，还能有效防止近交衰退并促进杂种优势利用。尽管如此，另一方面，SI则严重限制了自交育种和纯系培育，虽然可以通过杂交获得种子，但后代性状均一

性差，并且难以固定亲本优良表型。因此，有效克服SI对于种质繁殖及杂交育种同样至关重要。研究表明，通过改变生理和环境条件，如利用乙醚、二氧化碳、氯化钠盐溶液或高温处理能够打破十字花科植物SI，其中二氧化碳处理法最为有效并已广泛应用于十字花科蔬菜作物的种子繁育(Lao et al., 2014)。与之类似，使用钙离子通道拮抗剂氯化镧和戊脉安(Verapamil)以及蛋白激酶抑制剂薰草菌素A (Lavendustin A)也可促进黑麦和多年生黑麦草的自交花粉管生长至子房(Wehling et al., 1994; Klaas et al., 2011)。此外，育种家还尝试通过给自交不亲和植物转入SI抑制基因、敲除或敲低*S*基因或其他不亲和相关基因从而获得稳定遗传的自交亲和植株。例如，从二倍体马铃薯(*Solanum chacoense*)的一个自交亲和突变体中所鉴定到的*Sli* (*S-locus inhibitor*)基因已有效应用于马铃薯的纯系培育和二倍体杂交育种(Hosaka and Hanneman, 1998a, 1998b; Phumichai et al., 2005)。此外，禾本科草类植物中也存在一些自交亲和控制位点，如多年生黑麦草的*T*和*SF*位点(Thorogood et al., 2005; Do Canto et al., 2018)，通过渐渗引入这些位点也有望打破禾本科饲草SI。但是，渐渗系构建往往耗时较长且容易引入附加性状，而通过基因编辑敲除引发SPI反应的某些基因如花柱*S*基因*S-RNase*进而获得自交亲和株系的方法相比之下则更加简单有效(Ye et al., 2018; Enciso-Rodriguez et al., 2019)。此外，在饲草中，杂种优势尚未得到有效利用。SI造成群体中的个体中基因组高度杂合，从而掩盖并累积了大量隐性有害基因。通过克服SI创制饲草纯自交系，并进一步利用杂种优势，还需要鉴定不同饲草资源材料中造成自交衰退的有害基因，并设法清除或通过组合使其在杂交种中保持杂合状态。因此，未来对豆科与禾本科等饲草自交不亲和性详细分子机制的揭示有望为其遗传育种提供新的机遇。

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Self-Incompatibility and Inbreeding Depression of Forage Crops

Hong Zhao[1]*, Lizhen Song[2], Yu'e Zhang[1], Youfa Cheng[2], Yongbiao Xue[1]*

[1]Institute of Genetics and Developmental Biology, Beijing 100101, China; [2]Institute of Botany, Beijing 100093, China

Abstract Self-incompatibility (SI) is an intraspecific reproductive barrier widely occurring in flowering plants to prevent inbreeding depression and to promote outcrossing. However, this trait has severely restricted the production of homozygous lines as well as hybrid breeding, especially for the forage crops mostly belonging to Fabaceae, Asteraceae and Poaceae with unclear molecular mechanisms of SI. Therefore, SI has become one of the main blocks limiting the development of forage industry. So far, five different types of

molecular mechanisms of SI have been reported with significant progresses made in their biochemical and evolutionary mechanisms, providing a good foundation for further exploring the SI mechanisms of Fabaceae, Asteraceae and Poaceae forage crops. Here, we briefly review the mechanisms of the five reported types of SI and the research progress of SI and inbreeding depression in Fabaceae, Asteraceae and Poaceae.
Keywords self-incompatibility, forage crops, inbreeding depression

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