

· 评述 · 饲草生物学专辑

## 饲草自交不亲和性与近交衰退

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**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生殖障碍, 在防止植物近交衰退并促进其异交中发挥重要作用。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、菊科与禾本科植物自交不亲和的分子机制尚不明确, 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。现有研究已经揭示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。该文简要综述五类自交不亲和机制, 以及豆科、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

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被子植物约有30万种, 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40%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交授粉后不能产生合子的现象(de Nettancourt, 2001)。作为一种种内生生殖隔离机制, 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1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1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, 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 (heteromorphic SI)。基于花粉自交不亲和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植株(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)。现有研究已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1类(Type 1) SI, 十字花科(Brassicaceae)的孢子体2类

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(Type 2) SI, 罂粟科(Papaveraceae)的配子体3类(Type 3) SI, 以及分别发现于报春花科(Primulaceae)和时钟花科(Turneraceae)的异型花柱4类(Type 4)和5类(Type 5) 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(*Zea mays*)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(*Medicago sativa*) 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, 从而不能有效利用杂种优势, 使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和机制相同。因此, 解析豆科、菊科与禾本科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, 以及豆科、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等(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)。

### 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并且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泛素连接酶泛素化胞外复合体亚基Exo70A1、乙二醛酶GLO1 (Glyoxalase 1)和磷脂酶PLD $\alpha$ 1 (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1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;

PLD $\alpha$ 1 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(reactive oxygen species, ROS)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)。

### 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,  $\text{Ca}^{2+}$ 和 $\text{K}^{+}$ 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 $\text{Ca}^{2+}$ 浓度瞬时升高,导致无机焦磷酸酶(inorganic pyrophosphatases, 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)。

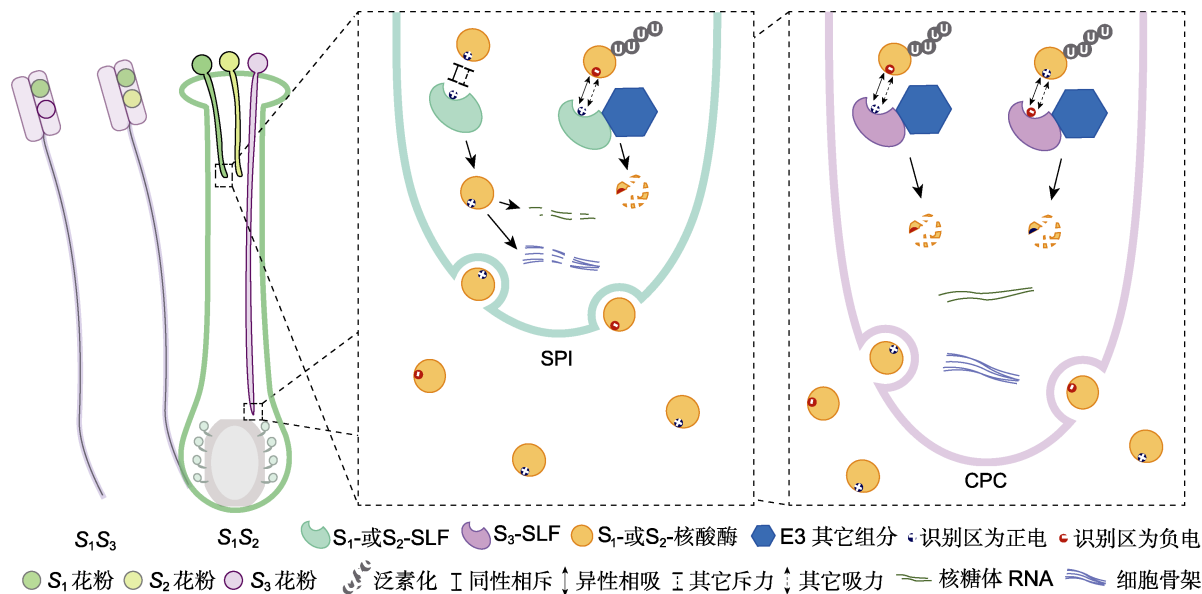
### 1.4 Type 4和Type 5自交不亲和性

Type 4 SI由1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,使得将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受精并抑制长花柱花的花粉受精,因此将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3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*仅在花药中表达,*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)。

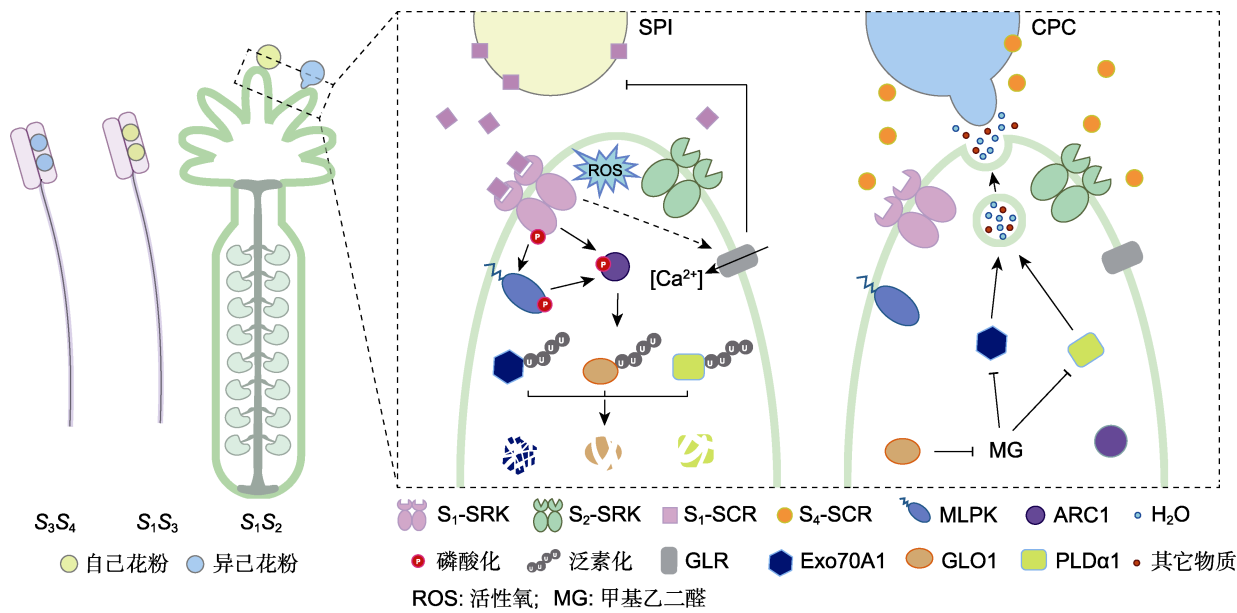
## 2 SI的起源与演化

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会频繁地丢失和重获(de Nettancourt, 2001; Franklin-Tong, 2008)。然而,关于SI如何起源和演化以及五类SI机制的演化关系一直是未解之谜。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



**图1** 1类自交不亲和性(SI)的分子与生化机制  
图示车前科、茄科、蔷薇科和芸香科1类自交不亲和性的分子与生化机制。 $S$ 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 and biochemical mechanisms of Type 1 self-incompatibility (SI)  
Schematic diagram illustrating the molecular and biochemical mechanisms 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 self-pollen incompatibility (SPI) and cross-pollen compatibility (CPC) reactions occurring in pollen tubes on the right dashed boxes.



**图2** 2类自交不亲和性(SI)的分子与生化机制  
图示十字花科2类自交不亲和性的分子与生化机制。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含义同图1。

**Figure 2** Molecular and biochemical mechanisms of Type 2 self-incompatibility (SI)  
Schematic diagram illustrating the molecular and biochemical mechanisms 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 those described in Figure 1.

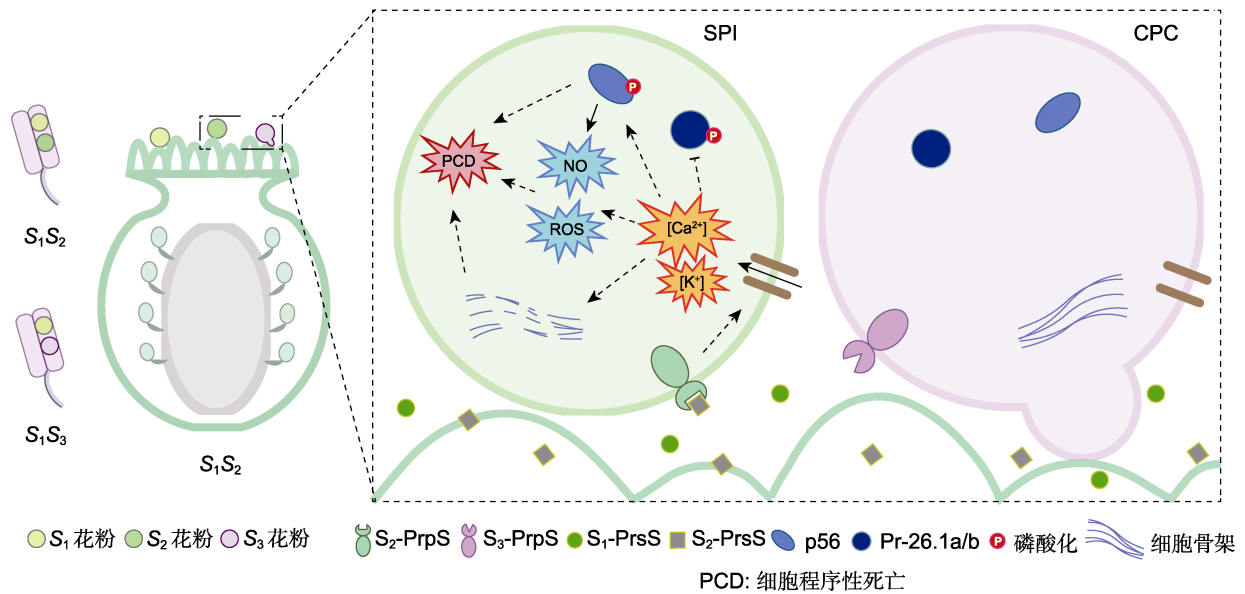


图3 3类自交不亲和性(SI)的分子与生化机制

图示罂粟科3类自交不亲和性的分子与生化机制。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。SPI和CPC同图1, ROS同图2。

Figure 3 Molecular and biochemical mechanisms of Type 3 self-incompatibility (SI)

Schematic diagram illustrating the molecular and biochemical mechanisms 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 SPI and CPC are identical to those described in Figure 1, and ROS is the same as shown in Figure 2.

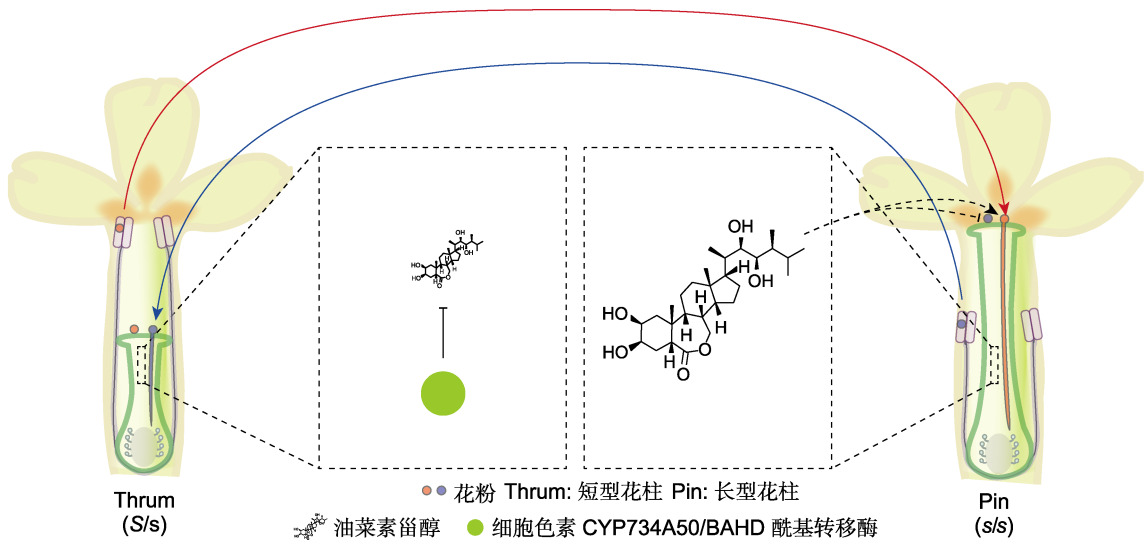
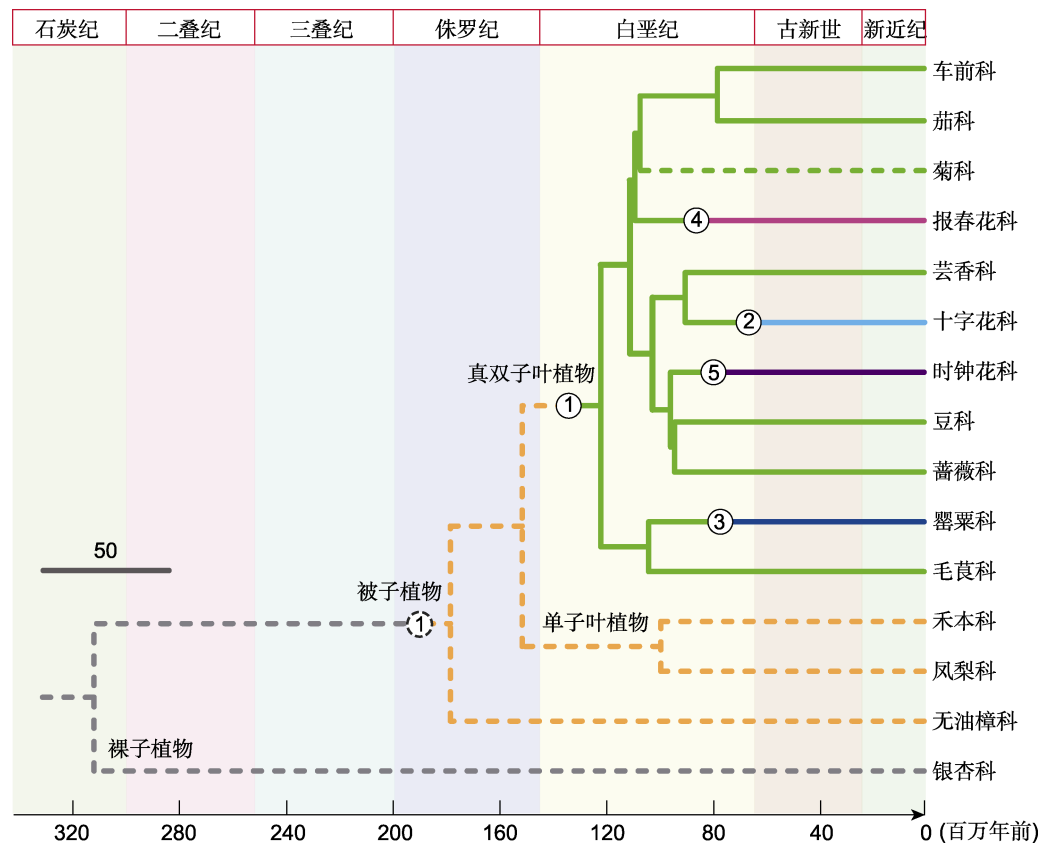


图4 4类和5类自交不亲和性(SI)的分子与生化机制

图示报春花科和时钟花科4类和5类自交不亲和性的分子机制。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油菜素甾醇(BR)对异交和自交花粉的促进和抑制作用。黑色实线平末端箭头表示CYP734A50/BAHD对BR含量的抑制作用。

Figure 4 Molecular and biochemical mechanisms of Type 4 and Type 5 self-incompatibility (SI)

Schematic diagram of Type 4 and Type 5 SI in Primulaceae and Turneraceae. Short style with long anther and long style with short anther are separately 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 brassinosteroid (BR) on the cross and self pollen, respectively. The black solid arrow with a flat end indicates the inhibition on BR content by CYP734A50/BAHD.



**图5** 1–5类自交不亲和性(SI)的起源与演化机制  
图示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1–5类SI。绿色、浅蓝色、深蓝色、玫红色和深紫色实线分别指示1–5类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 self-incompatibility (SI)  
Phylogenetic tree constructed with TimeTree (<http://www.timetree.org/>) showing several representative families/species separately possessing Type 1–5 SI. The axis under the tree indicates the evolutionary time. The serial numbers in the circles represent 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 dotted line represents Type 1 S-like structure encoding Class I/II T2 RNase and FBA/FBK domain proteins and the green dotted line represents no Type 1 S-locus containing Class III T2 RNase/S-RNase tightly linked to FBA/FBK.

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)。

### 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属18 000种, 是被子植物中仅次于菊科和兰科的第3大科。其中, 紫花苜蓿、白车轴草(*Trifolium repens*) (俗名白三叶)和红车轴草(*T. pratense*) (俗名红三叶)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、含羞草亚科及蝶形花亚科中分别有62.3%、66.7%和22.1%的物种具有自交不亲和现象(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, 因而对杂交育种及野生种质资源保存和利用均造成严重限制。因此, 对豆科特别是豆科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,均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*)和百脉根属(*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,被称为“牧草之王”的紫花苜蓿还具有部分自交不亲和性,其自交结实率在不同品种或个体间差异较大,平均为27.6% (Brink and Cooper, 1938; 何咏松和吴仁润, 1987)。

关于豆科自交不亲和性的详细分子机制目前尚未见报道。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)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号染色体存在共线性,但并未明确其中是否包含S-RNase和SLF。Aguilar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蛋白能够分别与S-RNase和SLF聚为一支,但其均能在除雌蕊和雄蕊以外的其它组织中表达。此外,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甚至豆科都可能不具备Type 1 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1 000属30 000种,是被子植物的第一大科,其中串叶松香草(*Silphium perfoliatum*)、苦苣菜(*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),如松香草属全叶松香草(*S. integrifolium*)、向日葵属向日葵(*Helianthus annuus*)、莴苣属生菜(*L. sativa*)和菊苣属菊苣。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。Tabah等(2004)尽管克隆到了糙叶千里光(*Senecio squalidus*)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位点定位至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 lycopersicum*)中最初发现于柱头分泌物中,可以通过结合花粉特异表达的激酶促进花粉管生长(Huang et al., 2014)。更有趣的是,在该基因下游109 kb处存在1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。但值得一提的是,由于在该位点及其与菊科其它物种的共线性区域中并未发现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



人员还在向日葵17号染色体与全叶松香草的假定S位点共线性区域中发现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、丢失与重获的动态进化过程相一致(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

禾本科是被子植物第四大科,单子叶植物的第二大科,约有660属11 000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,如黑麦草属多年生黑麦草(*Lolium perenne*)、赖草属羊草(*Leymus chinensis*)、大麦属球茎大麦(*Hordeum bulbosum*)和稻属长雄蕊野生稻(*Oryza longistaminata*)。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,花粉管则不能在柱头表面正常生长,进而产生SPI。此外,双位点控制的特性使得禾本科植物经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20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(*Secale cereale*)中,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), $\beta$ -葡萄糖苷酶(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,在天蓝薊草(*Phalaris coerulescens*)中,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并不在S位点内(Li et al., 1994, 1995; Baumann et al., 2000)。Kakeda (2009)在球茎大麦中发现2个花药表达的*F-box*基因与S位点紧密连锁,但其生物学功能尚未见报道。Shinozuka等(2010)基于SNP分子标记和BAC测序,定位到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10 177个个体进行定位并结合BAC测序和转录组分析,发现1个编码DUF247 (domain of unknown function 247)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1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2个花粉基因*OISS1*和*OISS2*和1个花柱基因*OISP*,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以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进行研究有望提升我们对禾本科SI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的SI,其中二氧化碳处理法最为有效,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衣草菌素A (lavendustin A)也可促使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基因或其它不亲和相关基因从而获得稳定遗传的自交亲和植株。例如,从二倍体野生马铃薯(*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 Han-neman, 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。然而,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则更加简单有效(Ye et al., 2018; Enciso-Rodriguez et al., 2019),但是该方法也受到遗传转化条件的限制。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、菊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。

## 参考文献

- 何咏松, 吴仁润 (1987). 苜蓿自交不亲和性研究. 中国草业科学 (4), 6–12.
- Aguiar B, Vieira J, Cunha AE, Vieira CP (2015). No evidence for Fabaceae gametophytic self-incompatibility being determined by Rosaceae, Solanaceae, and Plantaginaceae S-RNase lineage genes. *BMC Plant Biol* 15, 129.
- Allen AM, Thorogood CJ, Hegarty MJ, Lexer C, Hiscock SJ (2011). Pollen-pistil interactions and self-incompatibility in the Asteraceae: new insights from studies of *Senecio squalidus* (Oxford ragwort). *Ann Bot* 108, 687–698.
- Anderson MA, Cornish EC, Mau SL, Williams EG, Hoggart R, Atkinson A, Bonig I, Grego B, Simpson R, Roche PJ, Haley JD, Penschow JD, Niall HD, Tregear GW, Coghlan JP, Crawford RJ, Clarke AE (1986). Cloning of cDNA for a stylar glycoprotein associated with expression of self-incompatibility in *Nicotiana glauca*. *Nature* 321, 38–44.
- Arroyo MTK (1981). Breeding systems and pollination biology in Leguminosae. In: Polhill RM, Raven PH, eds. *Advances in Legume Systematics*. Kew: Royal Botanic Gardens. pp. 723–769.
- Atwood SS (1940). Genetics of cross-incompatibility among self-incompatible plants of *Trifolium repens*. *Agron J* 32, 955–968.
- Baumann U, Juttner J, Bian XY, Langridge P (2000). Self-incompatibility in the grasses. *Ann Bot* 85, 203–209.
- Brewbaker JL (1954). Incompatibility in autotetraploid *Trifolium repens* L. I. Competition and self-compatibility. *Genetics* 39, 307–316.
- Brewbaker JL (1957). Pollen cytology and self-incompatibility systems in plants. *J Hered* 48, 271–277.
- Brink RA, Cooper DC (1938). Partial self-incompatibility in *Medicago sativa*. *Proc Natl Acad Sci USA* 24, 497–499.
- Cabrillac D, Cock JM, Dumas C, Gaude T (2001). The S-locus receptor kinase is inhibited by thioredoxins and activated by pollen coat proteins. *Nature* 410, 220–223.
- Casey NM, Milbourne D, Barth S, Febrer M, Jenkins G, Abberton MT, Jones C, Thorogood D (2010). The genetic location of the self-incompatibility locus in white clover (*Trifolium repens* L.). *Theor Appl Genet* 121, 567–576.
- Chen JQ, Wang P, de Graaf BHJ, Zhang H, Jiao HJ, Tang C, Zhang SL, Wu JY (2018). Phosphatidic acid counteracts S-RNase signaling in pollen by stabilizing the actin cytoskeleton. *Plant Cell* 30, 1023–1039.
- Chen SY, Jia JT, Cheng LQ, Zhao PC, Qi DM, Yang WG, Liu H, Dong XB, Li XX, Liu GS (2019). Transcriptomic analysis reveals a comprehensive calcium- and phytohormone-dominated signaling response in *Leymus chinensis* self-incompatibility. *Int J Mol Sci* 20, 2356.
- Cornish MA, Hayward MD, Lawrence MJ (1980). Self-incompatibility in ryegrass. *Heredity* 44, 55–62.
- de Graaf BHJ, Rudd JJ, Wheeler MJ, Perry RM, Bell EM, Osman K, Franklin FCH, Franklin-Tong VE (2006). Self-incompatibility in *Papaver* targets soluble inorganic pyrophosphatases in pollen. *Nature* 444, 490–493.
- de Nettancourt D (2001). *Incompatibility and Incongruity in Wild and Cultivated Plants*, 2nd edn. Berlin: Springer. pp. 1–356.
- Delaney LE, Igić B (2022). The phylogenetic distribution and frequency of self-incompatibility in Fabaceae. *Int J Plant Sci* 183, 30–42.

- Do Canto J, Studer B, Frei U, Lübberstedt T (2018). Fine mapping a self-fertility locus in perennial ryegrass. *Theor Appl Genet* **131**, 817–827.
- Duvick DN (2005). The contribution of breeding to yield advances in maize (*Zea mays* L.). *Adv Agron* **86**, 83–145.
- Enciso-Rodriguez F, Manrique-Carpintero NC, Nadakuduti SS, Buell CR, Zarka D, Douches D (2019). Overcoming self-incompatibility in diploid potato using CRISPR-Cas9. *Front Plant Sci* **10**, 376.
- Entani T, Kubo KI, Isogai S, Fukao Y, Shirakawa M, Isogai A, Takayama S (2014). Ubiquitin-proteasome-mediated degradation of S-RNase in a Solanaceous cross-compatibility reaction. *Plant J* **78**, 1014–1021.
- Ferrer MM, Good-Avila SV (2007). Macrophylogenetic analyses of the gain and loss of self-incompatibility in the Asteraceae. *New Phytol* **173**, 401–414.
- Foote HC, Ride JP, Franklin-Tong VE, Walker EA, Lawrence MJ, Franklin FC (1994). Cloning and expression of a distinctive class of self-incompatibility (S) gene from *Papaver rhoeas* L. *Proc Natl Acad Sci USA* **91**, 2265–2269.
- Franklin-Tong VE (2008). Self-incompatibility in Flowering Plants. Berlin: Springer. pp. 1–313.
- Fujii S, Kubo KI, Takayama S (2016). Non-self- and self-recognition models in plant self-incompatibility. *Nat Plants* **2**, 16130.
- Gertz A, Wricke G (1989). Linkage between the incompatibility locus Z and  $\beta$ -glucosidase locus in rye. *Plant Breed* **102**, 255–259.
- Gonthier L, Blassiau C, Mörchen M, Cadalen T, Poiret M, Hendriks T, Quillet MC (2013). High-density genetic maps for loci involved in nuclear male sterility (*NMS1*) and sporophytic self-incompatibility (S-locus) in chicory (*Cichorium intybus* L., Asteraceae). *Theor Appl Genet* **126**, 2103–2121.
- Gu TS, Mazzurco M, Sulaman W, Matias DD, Goring DR (1998). Binding of an arm repeat protein to the kinase domain of the S-locus receptor kinase. *Proc Natl Acad Sci USA* **95**, 382–387.
- Gu ZY, Meng D, Yang Q, Yuan H, Wang AD, Li W, Chen QJ, Zhang Y, Wang DM, Li TZ (2015). A CBL gene, *MdCBL5*, controls the calcium signal and influences pollen tube growth in apple. *Tree Genet Genomes* **11**, 27.
- Hayman DL (1956). The genetical control of incompatibility in *Phalaris coerulescens* Desf. *Aust J Biol Sci* **9**, 321–331.
- Heslop-Harrison Y, Shivanna KR (1977). The receptive surface of the angiosperm stigma. *Ann Bot* **41**, 1233–1258.
- Hiscock SJ (2000). Genetic control of self-incompatibility in *Senecio squalidus* L. (Asteraceae): a successful colonizing species. *Heredity* **85**, 10–19.
- Hiscock SJ, McInnis SM, Tabah DA, Henderson CA, Brennan AC (2003). Sporophytic self-incompatibility in *Senecio squalidus* L. (Asteraceae)—the search for S. *J Exp Bot* **54**, 169–174.
- Hosaka K, Hanneman RE Jr (1998a). Genetics of self-compatibility in a self-incompatible wild diploid potato species *Solanum chacoense*. 1. Detection of an S locus inhibitor (Sli) gene. *Euphytica* **99**, 191–197.
- Hosaka K, Hanneman RE Jr (1998b). Genetics of self-compatibility in a self-incompatible wild diploid potato species *Solanum chacoense*. 2. Localization of an S locus inhibitor (Sli) gene on the potato genome using DNA markers. *Euphytica* **103**, 265–271.
- Huang J, Zhao L, Yang QY, Xue YB (2006). AhSSK1, a novel SKP1-like protein that interacts with the S-locus F-box protein SLF. *Plant J* **46**, 780–793.
- Huang WJ, Liu HK, McCormick S, Tang WH (2014). Tomato pistil factor STIG1 promotes *in vivo* pollen tube growth by binding to phosphatidylinositol 3-phosphate and the extracellular domain of the pollen receptor kinase LePRK2. *Plant Cell* **26**, 2505–2523.
- Huu CN, Kappel C, Keller B, Sicard A, Takebayashi Y, Breuninger H, Nowak MD, Bäurle I, Himmelbach A, Burkart M, Ebbing-Lohaus T, Sakakibara H, Altschmied L, Conti E, Lenhard M (2016). Presence versus absence of *CYP734A50* underlies the style-length dimorphism in primroses. *eLife* **5**, e17956.
- Huu CN, Keller B, Conti E, Kappel C, Lenhard M (2020). Supergene evolution via stepwise duplications and neofunctionalization of a floral-organ identity gene. *Proc Natl Acad Sci USA* **117**, 23148–23157.
- Huu CN, Plaschil S, Himmelbach A, Kappel C, Lenhard M (2022). Female self-incompatibility type in heterostylous *Primula* is determined by the brassinosteroid-inactivating cytochrome P450 *CYP734A50*. *Curr Biol* **32**, 671–676.
- Iwano M, Ito K, Fujii S, Kakita M, Asano-Shimosato H, Igarashi M, Kaothien-Nakayama P, Entani T, Kanatani A, Takehisa M, Tanaka M, Komatsu K, Shiba H, Nagai T, Miyawaki A, Isogai A, Takayama S (2015). Calcium signaling mediates self-incompatibility response in the Brassicaceae. *Nat Plants* **1**, 15128.
- Kakeda K (2009). S locus-linked F-box genes expressed in anthers of *Hordeum bulbosum*. *Plant Cell Rep* **28**, 1453–

1460.

- Kakita M, Murase K, Iwano M, Matsumoto T, Watanabe M, Shiba H, Isogai A, Takayama S** (2007). Two distinct forms of *M*-locus protein kinase localize to the plasma membrane and interact directly with *S*-locus receptor kinase to transduce self-incompatibility signaling in *Brassica rapa*. *Plant Cell* **19**, 3961–3973.
- Klaas M, Yang BC, Bosch M, Thorogood D, Manzanares C, Armstead IP, Franklin FCH, Barth S** (2011). Progress towards elucidating the mechanisms of self-incompatibility in the grasses: further insights from studies in *Lolium*. *Ann Bot* **108**, 677–685.
- Lai Z, Ma WS, Han B, Liang LZ, Zhang YS, Hong GF, Xue YB** (2002). An F-box gene linked to the self-incompatibility (*S*) locus of *Antirrhinum* is expressed specifically in pollen and tapetum. *Plant Mol Biol* **50**, 29–41.
- Lao XT, Suwabe K, Niikura S, Kakita M, Iwano M, Takayama S** (2014). Physiological and genetic analysis of CO<sub>2</sub>-induced breakdown of self-incompatibility in *Brassica rapa*. *J Exp Bot* **65**, 939–951.
- Lewis D, Jones DA** (1992). The genetics of heterostyly. In: Barrett SCH, ed. *Evolution and Function of Heterostyly*. Berlin: Springer. pp. 129–150.
- Li JH, Cocker JM, Wright J, Webster MA, McMullan M, Dyer S, Swarbreck D, Caccamo M, Oosterhout CV, Gil-martin PM** (2016). Genetic architecture and evolution of the *S* locus supergene in *Primula vulgaris*. *Nat Plants* **2**, 16188.
- Li JH, Zhang Y, Song YZ, Zhang H, Fan JB, Li Q, Zhang DF, Xue YB** (2017). Electrostatic potentials of the *S*-locus F-box proteins contribute to the pollen *S* specificity in self-incompatibility in *Petunia hybrida*. *Plant J* **89**, 45–57.
- Li ST, Šamaj J, Franklin-Tong VE** (2007). A mitogen-activated protein kinase signals to programmed cell death induced by self-incompatibility in *Papaver* pollen. *Plant Physiol* **145**, 236–245.
- Li XM, Nield J, Hayman D, Langridge P** (1994). Cloning a putative self-incompatibility gene from the pollen of the grass *Phalaris coerulescens*. *Plant Cell* **6**, 1923–1932.
- Li XM, Nield J, Hayman D, Langridge P** (1995). Thioredoxin activity in the C terminus of *Phalaris S* protein. *Plant J* **8**, 133–138.
- Lian XP, Zhang SL, Huang GF, Huang LY, Zhang J, Hu FY** (2021). Confirmation of a gametophytic self-incompatibility in *Oryza longistaminata*. *Front Plant Sci* **12**, 576340.
- Liang M, Cao ZH, Zhu AD, Liu YL, Tao MQ, Yang HY, Xu Q Jr, Wang SH, Liu JJ, Li YP, Chen CW, Xie ZZ, Deng CL, Ye JL, Guo WW, Xu Q, Xia R, Larkin RM, Deng XX, Bosch M, Franklin-Tong VE, Chai LJ** (2020). Evolution of self-compatibility by a mutant *S<sub>m</sub>-RNase* in citrus. *Nat Plants* **6**, 131–142.
- Lundqvist A** (1954). Studies on self-sterility in rye, *Secale cereale* L. *Hereditas* **40**, 278–294.
- Manzanares C, Barth S, Thorogood D, Byrne SL, Yates S, Czaban A, Asp T, Yang BC, Studer B** (2016). A gene encoding a DUF247 domain protein cosegregates with the *S* self-incompatibility locus in perennial ryegrass. *Mol Biol Evol* **33**, 870–884.
- Matzke CM, Hamam HJ, Henning PM, Dougherty K, Shore JS, Neff MM, McCubbin AG** (2021). Pistil mating type and morphology are mediated by the brassinosteroid inactivating activity of the *S*-locus gene *BAHD* in heterostylous *Turnera* species. *Int J Mol Sci* **22**, 10603.
- Matzke CM, Shore JS, Neff MM, McCubbin AG** (2020). The *Turnera* style *S*-locus gene *TsBAHD* possesses brassinosteroid-inactivating activity when expressed in *Arabidopsis thaliana*. *Plants* **9**, 1566.
- McClure BA, Gray JE, Anderson MA, Clarke AE** (1990). Self-incompatibility in *Nicotiana glauca* involves degradation of pollen rRNA. *Nature* **347**, 757–760.
- McClure BA, Haring V, Ebert PR, Anderson MA, Simpson RJ, Sakiyama F, Clarke AE** (1989). Style self-incompatibility gene products of *Nicotiana glauca* are ribonucleases. *Nature* **342**, 955–957.
- Mcinnis SM, Costa LM, Gutiérrez-Marcos JF, Henderson CA, Hiscock SJ** (2005). Isolation and characterization of a polymorphic stigma-specific class III peroxidase gene from *Senecio squalidus* L. (Asteraceae). *Plant Mol Biol* **57**, 659–677.
- Parajuli A, Yu LX, Peel M, See D, Wagner S, Norberg S, Zhang ZW** (2021). Self-incompatibility, inbreeding depression, and potential to develop inbred lines in alfalfa. In: Yu LX, Kole C, eds. *The Alfalfa Genome*. Cham: Springer. pp. 255–269.
- Phumichai C, Mori M, Kobayashi A, Kamijima O, Hosaka K** (2005). Toward the development of highly homozygous diploid potato lines using the self-compatibility controlling *Sli* gene. *Genome* **48**, 977–984.
- Price JH, Raduski AR, Brandvain Y, Van Tassel DL, Smith KP** (2022). Development of first linkage map for *Silphium integrifolium* (Asteraceae) enables identification of sporophytic self-incompatibility locus. *Heredity* **128**, 304–312.
- Qiao H, Wang F, Zhao L, Zhou JL, Lai Z, Zhang YS, Robbins TP, Xue YB** (2004a). The F-box protein

- AhSLF-S<sub>2</sub> controls the pollen function of S-RNase-based self-incompatibility. *Plant Cell* **16**, 2307–2322.
- Qiao H, Wang HY, Zhao L, Zhou JL, Huang J, Zhang YS, Xue YB** (2004b). The F-box protein AhSLF-S<sub>2</sub> physically interacts with S-RNases that may be inhibited by the ubiquitin/26S proteasome pathway of protein degradation during compatible pollination in *Antirrhinum*. *Plant Cell* **16**, 582–595.
- Qu HY, Guan YQ, Wang YZ, Zhang SL** (2017). PLC-mediated signaling pathway in pollen tubes regulates the gametophytic self-incompatibility of *Pyrus* species. *Front Plant Sci* **8**, 1164.
- Samuel MA, Chong YT, Haasen KE, Aldea-Brydges MG, Stone SL, Goring DR** (2009). Cellular pathways regulating responses to compatible and self-incompatible pollen in *Brassica* and *Arabidopsis* stigmas intersect at Exo-70A1, a putative component of the exocyst complex. *Plant Cell* **21**, 2655–2671.
- Samuel MA, Mudgil Y, Salt JN, Delmas F, Ramachandran S, Chilleli A, Goring DR** (2008). Interactions between the S-domain receptor kinases and AtPUB-ARM E3 ubiquitin ligases suggest a conserved signaling pathway in *Arabidopsis*. *Plant Physiol* **147**, 2084–2095.
- Sankaranarayanan S, Jamshed M, Kumar A, Skori L, Scandola S, Wang TN, Spiegel D, Samuel MA** (2017). Glyoxalase goes green: the expanding roles of glyoxalase in plants. *Int J Mol Sci* **18**, 898.
- Sankaranarayanan S, Jamshed M, Samuel MA** (2015). Degradation of glyoxalase I in *Brassica napus* stigma leads to self-incompatibility response. *Nat Plants* **1**, 15185.
- Sassa H, Kakui H, Miyamoto M, Suzuki Y, Hanada T, Ushijima K, Kusaba M, Hirano H, Koba T** (2007). *S* locus *F-box* brothers: multiple and pollen-specific *F-box* genes with *S* haplotype-specific polymorphisms in apple and Japanese pear. *Genetics* **175**, 1869–1881.
- Sassa H, Nishio T, Kowiyama Y, Hirano H, Koba T, Ikehashi H** (1996). Self-incompatibility (*S*) alleles of the Rosaceae encode members of a distinct class of the T<sub>2</sub>/S ribonuclease superfamily. *Mol Gen Genet* **250**, 547–557.
- Scandola S, Samuel MA** (2019). A flower-specific phospholipase D is a stigmatic compatibility factor targeted by the self-incompatibility response in *Brassica napus*. *Curr Biol* **29**, 506–512.
- Schopfer CR, Nasrallah ME, Nasrallah JB** (1999). The male determinant of self-incompatibility in *Brassica*. *Science* **286**, 1697–1700.
- Shinozuka H, Cogan NOI, Smith KF, Spangenberg GC, Forster JW** (2010). Fine-scale comparative genetic and physical mapping supports map-based cloning strategies for the self-incompatibility loci of perennial ryegrass (*Lolium perenne* L.). *Plant Mol Biol* **72**, 343–355.
- Shore JS, Hamam HJ, Chafe PDJ, Labonne JDJ, Henning PM, McCubbin AG** (2019). The long and short of the *S*-locus in *Turnera* (Passifloraceae). *New Phytol* **224**, 1316–1329.
- Sijacic P, Wang X, Skirpan AL, Wang Y, Dowd PE, McCubbin AG, Huang S, Kao TH** (2004). Identification of the pollen determinant of S-RNase-mediated self-incompatibility. *Nature* **429**, 302–305.
- Stone SL, Anderson EM, Mullen RT, Goring DR** (2003). ARC1 is an E3 ubiquitin ligase and promotes the ubiquitination of proteins during the rejection of self-incompatible *Brassica* pollen. *Plant Cell* **15**, 885–898.
- Suzuki T, Kusaba M, Matsushita M, Okazaki K, Nishio T** (2000). Characterization of *Brassica* *S*-haplotypes lacking *S*-locus glycoprotein. *FEBS Lett* **482**, 102–108.
- Tabah DA, Mcinnis SM, Hiscock SJ** (2004). Members of the *S*-receptor kinase multigene family in *Senecio squalidus* L (Asteraceae), a species with sporophytic self-incompatibility. *Sex Plant Reprod* **17**, 131–140.
- Takasaki T, Hatakeyama K, Suzuki G, Watanabe M, Isogai A, Hinata K** (2000). The *S* receptor kinase determines self-incompatibility in *Brassica* stigma. *Nature* **403**, 913–916.
- Takayama S, Isogai A** (2005). Self-incompatibility in plants. *Annu Rev Plant Biol* **56**, 467–489.
- Takayama S, Shimosato H, Shiba H, Funato M, Che FS, Watanabe M, Iwano M, Isogai A** (2001). Direct ligand-receptor complex interaction controls *Brassica* self-incompatibility. *Nature* **413**, 534–538.
- Thomas SG, Franklin-Tong VE** (2004). Self-incompatibility triggers programmed cell death in *Papaver* pollen. *Nature* **429**, 305–309.
- Thomas SG, Huang SJ, Li ST, Staiger CJ, Franklin-Tong VE** (2006). Actin depolymerization is sufficient to induce programmed cell death in self-incompatible pollen. *J Cell Biol* **174**, 221–229.
- Thorogood D, Armstead IP, Turner LB, Humphreys MO, Hayward MD** (2005). Identification and mode of action of self-compatibility loci in *Lolium perenne* L. *Heredity* **94**, 356–363.
- Ushijima K, Sassa H, Dandekar AM, Gradziel TM, Tao R, Hirano H** (2003). Structural and transcriptional analysis of the self-incompatibility locus of almond: identification of a

- pollen-expressed F-box gene with haplotype-specific polymorphism. *Plant Cell* **15**, 771–781.
- Wehling P, Hackauf B, Wricke G** (1994). Phosphorylation of pollen proteins in relation to self-incompatibility in rye (*Secale cereale* L.). *Sex Plant Reprod* **7**, 67–75.
- Wheeler MJ, de Graaf BHJ, Hadjiosif N, Perry RM, Poulter NS, Osman K, Vátovec S, Harper A, Franklin FCH, Franklin-Tong VE** (2009). Identification of the pollen self-incompatibility determinant in *Papaver rhoeas*. *Nature* **459**, 992–995.
- Wilkins KA, Bancroft J, Bosch M, Ings J, Smirnov N, Franklin-Tong VE** (2011). Reactive oxygen species and nitric oxide mediate actin reorganization and programmed cell death in the self-incompatibility response of *Papaver*. *Plant Physiol* **156**, 404–416.
- Wricke G, Wehling P** (1985). Linkage between an incompatibility locus and a peroxidase isozyme locus (*Prx 7*) in rye. *Theor Appl Genet* **71**, 289–291.
- Xu C, Li MF, Wu JK, Guo H, Li Q, Zhang YE, Chai JJ, Li TZ, Xue YB** (2013). Identification of a canonical SCF<sup>SLF</sup> complex involved in S-RNase-based self-incompatibility of *Pyrus* (Rosaceae). *Plant Mol Biol* **81**, 245–257.
- Xue YB, Carpenter R, Dickinson HG, Coen ES** (1996). Origin of allelic diversity in *Antirrhinum* S locus RNases. *Plant Cell* **8**, 805–814.
- Yang BC, Thorogood D, Armstead I, Barth S** (2008). How far are we from unravelling self-incompatibility in grasses? *New Phytol* **178**, 740–753.
- Yang Q, Meng D, Gu ZY, Li W, Chen QJ, Li Y, Yuan H, Yu J, Liu CS, Li TZ** (2018). Apple S-RNase interacts with an actin-binding protein, MdMVG, to reduce pollen tube growth by inhibiting its actin-severing activity at the early stage of self-pollination induction. *Plant J* **95**, 41–56.
- Ye MW, Peng Z, Tang D, Yang ZM, Li DW, Xu YM, Zhang CZ, Huang SW** (2018). Generation of self-compatible diploid potato by knockout of *S-RNase*. *Nat Plants* **4**, 651–654.
- Zhang LL, Huang JB, Su SQ, Wei XC, Yang L, Zhao HH, Yu JQ, Wang J, Hui JY, Hao SY, Song SS, Cao YY, Wang MS, Zhang XW, Zhao YY, Wang ZY, Zeng WQ, Wu HM, Yuan YX, Zhang XS, Cheung AY, Duan QH** (2021). FERONIA receptor kinase-regulated reactive oxygen species mediate self-incompatibility in *Brassica rapa*. *Curr Biol* **31**, 3004–3016.
- Zhang YJ, Zhao ZH, Xue YB** (2009). Roles of proteolysis in plant self-incompatibility. *Annu Rev Plant Biol* **60**, 21–42.
- Zhao H, Song YZ, Li JH, Zhang Y, Huang HQ, Li Q, Zhang Y, Xue YB** (2021). Primary restriction of S-RNase cytotoxicity by a stepwise ubiquitination and degradation pathway in *Petunia hybrida*. *New Phytol* **231**, 1249–1264.
- Zhao H, Zhang Y, Zhang H, Song YZ, Zhao F, Zhang Y, Zhu SH, Zhang HK, Zhou ZD, Guo H, Li MM, Li JH, Gao Q, Han QQ, Huang HQ, Copsey L, Li Q, Chen H, Coen E, Zhang YJ, Xue YB** (2022). Origin, loss, and regain of self-incompatibility in angiosperms. *Plant Cell* **34**, 579–596.
- Zhao L, Huang J, Zhao ZH, Li Q, Sims TL, Xue YB** (2010). The Skp1-like protein SSK1 is required for cross-pollen compatibility in S-RNase-based self-incompatibility. *Plant J* **62**, 52–63.

## Self-incompatibility and Inbreeding Depression of Forage Crops

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**Abstract** Self-incompatibility (SI) is an intraspecific reproductive barrier widely occurring in flowering plants to prevent inbreeding depression by promoting outcrossing. However, this trait severely restricts the production of homozygous lines in 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 major barriers limiting the development of forage industry in China and even in the world. So far, large progresses have been made in the biochemical and evolutionary mechanisms of five different SI types, 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 SI types and the research progress of SI and inbreeding depression in Fabaceae, Asteraceae and Poaceae.

**Key words** self-incompatibility, forage crops, inbreeding depression

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