

# Molecular insights into self-incompatibility systems: From evolution to breeding

Diyang Zhang<sup>1</sup>, Yuan-Yuan Li<sup>1</sup>, Xuewei Zhao<sup>1,2</sup>, Cuili Zhang<sup>1</sup>, Ding-Kun Liu<sup>1,2</sup>, Siren Lan<sup>1,\*</sup>, Weilun Yin<sup>1,3,\*</sup> and Zhong-Jian Liu<sup>1,\*</sup>

<sup>1</sup>Key Laboratory of National Forestry and Grassland Administration for Orchid Conservation and Utilization, Fujian Agriculture and Forestry University, Fuzhou 350002, China

<sup>2</sup>College of Forestry, Fujian Agriculture and Forestry University, Fuzhou 350002, China

<sup>3</sup>College of Biological Sciences and Technology, Beijing Forestry University, Beijing 100083, China

\*Correspondence: Siren Lan ([lansiren@fafu.edu.cn](mailto:lansiren@fafu.edu.cn)), Weilun Yin ([yinweilun@fafu.edu.cn](mailto:yinweilun@fafu.edu.cn)), Zhong-Jian Liu ([lizhongjian@fafu.edu.cn](mailto:lizhongjian@fafu.edu.cn))

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## ABSTRACT

Plants have evolved diverse self-incompatibility (SI) systems for outcrossing. Since Darwin's time, considerable progress has been made toward elucidating this unrivaled reproductive innovation. Recent advances in interdisciplinary studies and applications of biotechnology have given rise to major breakthroughs in understanding the molecular pathways that lead to SI, particularly the strikingly different SI mechanisms that operate in Solanaceae, Papaveraceae, Brassicaceae, and Primulaceae. These best-understood SI systems, together with discoveries in other "nonmodel" SI taxa such as Poaceae, suggest a complex evolutionary trajectory of SI, with multiple independent origins and frequent and irreversible losses. Extensive exploration of self-/nonself-discrimination signaling cascades has revealed a comprehensive catalog of male and female identity genes and modifier factors that control SI. These findings also enable the characterization, validation, and manipulation of SI-related factors for crop improvement, helping to address the challenges associated with development of inbred lines. Here, we review current knowledge about the evolution of SI systems, summarize key achievements in the molecular basis of pollen–pistil interactions, discuss potential prospects for breeding of SI crops, and raise several unresolved questions that require further investigation.

**Key words:** self-incompatibility, *S*-RNase, evolution, genome editing, crop improvement

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## INTRODUCTION

Self-incompatibility (SI) is one of the most important reproductive innovations for prevention of self-fertilization. It enables a plant to recognize and reject self-pollen or pollen from genetically identical individuals, thereby promoting outcrossing (de Nettancourt, 2001). Particularly for many hermaphroditic species, SI represents the most widespread strategy for avoiding inbreeding depression and reduced genetic variability (Silva and Goring, 2001; Porcher and Lande, 2005). Approximately 40% of angiosperm lineages, representing at least 100 plant families, have developed SI systems (Jigic et al., 2004). The diverse forms of SI systems and their scattered phylogenetic distribution suggest that SI has evolved *de novo* many times over the course of angiosperm evolution (Allen and Hiscock, 2008). The higher diversification rate observed in species with functional SI systems than in those with self-compatibility (SC) suggests strong species-level selection favoring obligate outcrossing (Goldberg et al., 2010). SI systems also

frequently experience losses that are not subsequently regained (Barnett, 2013). Therefore, the ancestral conditions, the evolutionary dynamics of loss and gain, and the polymorphic nature of SI systems have been of long-standing interest.

In classic genetic studies, SI was classified into two homomorphic types, gametophytic self-incompatibility (GSI) and sporophytic self-incompatibility (SSI), as well as heteromorphic SI (HSI) characterized by heterostyly (de Nettancourt, 2001; Barnett and Shore, 2008). Since the advent of molecular biology, significant progress has been made in elucidating the genetic control of GSI in Solanaceae and Papaveraceae (Fuji et al., 2016), SSI in Brassicaceae (Goring et al., 2023), HSI in

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## **Table of Contents Molecular Insights Into The Living Proce**

1. Understanding the eBook Molecular Insights Into The Living Proce
  - The Rise of Digital Reading Molecular Insights Into The Living Proce
  - Advantages of eBooks Over Traditional Books
2. Identifying Molecular Insights Into The Living Proce
  - Exploring Different Genres
  - Considering Fiction vs. Non-Fiction
  - Determining Your Reading Goals
3. Choosing the Right eBook Platform
  - Popular eBook Platforms
  - Features to Look for in an Molecular Insights Into The Living Proce
  - User-Friendly Interface
4. Exploring eBook Recommendations from Molecular Insights Into The Living Proce
  - Personalized Recommendations
  - Molecular Insights Into The Living Proce User Reviews and Ratings
  - Molecular Insights Into The Living Proce and Bestseller Lists
5. Accessing Molecular Insights Into The Living Proce Free and Paid eBooks

- Molecular Insights Into The Living Proce Public Domain eBooks
- Molecular Insights Into The Living Proce eBook Subscription Services
- Molecular Insights Into The Living Proce Budget-Friendly Options
- 6. Navigating Molecular Insights Into The Living Proce eBook Formats
  - ePub, PDF, MOBI, and More
  - Molecular Insights Into The Living Proce Compatibility with Devices
  - Molecular Insights Into The Living Proce Enhanced eBook Features
- 7. Enhancing Your Reading Experience
  - Adjustable Fonts and Text Sizes of Molecular Insights Into The Living Proce
  - Highlighting and Note-Taking Molecular Insights Into The Living Proce
  - Interactive Elements Molecular Insights Into The Living Proce
- 8. Staying Engaged with Molecular Insights Into The Living Proce
  - Joining Online Reading Communities
  - Participating in Virtual Book Clubs
  - Following Authors and Publishers Molecular Insights Into The Living Proce
- 9. Balancing eBooks and Physical Books Molecular Insights Into The Living Proce
  - Benefits of a Digital Library
  - Creating a Diverse Reading Collection Molecular Insights Into The Living Proce
- 10. Overcoming Reading Challenges
  - Dealing with Digital Eye Strain
  - Minimizing Distractions
  - Managing Screen Time
- 11. Cultivating a Reading Routine Molecular Insights Into The Living Proce
  - Setting Reading Goals Molecular Insights Into The Living Proce
  - Carving Out Dedicated Reading Time
- 12. Sourcing Reliable Information of Molecular Insights Into The Living Proce
  - Fact-Checking eBook Content of Molecular Insights Into The Living Proce
  - Distinguishing Credible Sources
- 13. Promoting Lifelong Learning
  - Utilizing eBooks for Skill Development

- Exploring Educational eBooks

#### 14. Embracing eBook Trends

- Integration of Multimedia Elements
- Interactive and Gamified eBooks

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