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Review

Self/non-self recognition mechanisms in sexual reproduction: New insight into the self-incompatibility system shared by flowering plants and hermaphroditic animals

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ABSTRACT

Sexual reproduction is an essential process for generating a genetic variety in the next generation. However, most flowering plants and hermaphroditic animals potentially allow self-fertilization. Approximately 60% of angiosperms possess a self-incompatibility (SI) system to avoid inbreeding. The SI system functions at a process of interaction between pollen (or pollen tube) and the pistil. These SI-responsible factors (*S*-determinants) in pollen and the pistil are encoded by highly polymorphic multiallelic genes in the *S*-locus, which are tightly linked making a single haplotype. Different taxonomic families utilize different types of *S*-determinant proteins.

In contrast to the plant system, the mechanisms of SI in simultaneously hermaphroditic animals are largely unknown. Among them, promising candidates for SI in ascidians (primitive chordates) were recently identified. The SI system in the ascidian *Ciona intestinalis* was found to be very similar to those in flowering plants: The products of sperm- and egg-side multiallelic SI genes, which are tight linked and highly polymorphic, appear to be responsible for the SI system as revealed by genetic analysis. These findings led us to speculate that the SI systems in plants and animals evolved in a manner of convergent evolution. Here, we review the current understanding of the molecular mechanisms of the SI system in flowering plants, particularly Brassicacea, and in ascidians from the viewpoint of common mechanisms shared by plants and animals.

Contents

Abbreviations: SI, self-incompatibility; VC, vitelline coat.

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1. Introduction

Most living organisms undergo sexual reproduction as a reproductive strategy. This enables them to make a genetic variety in the next generation. In contrast to most animals, flowering plants and hermaphroditic marine animals releasing gametes may allow self-fertilization under natural conditions. In order to avoid inbreeding, many flowering plants possess a self-incompatibility (SI) system, which eventually prevents self-fertilization. There are several SI systems to block self-fertilization depending on the taxonomic family [1–3]. In this review, the SI systems of flowering plants, particularly that in Brassicaceae, are described in detail.

Most terrestrial and aquatic hermaphroditic animals exhibit reproductive behaviors. Therefore, a self-gamete recognition system is not necessarily required to avoid inbreeding. However, in hermaphroditic marine animals that release sperm and eggs to the surrounding seawater, a self/non-self-recognition system between sperm and eggs (or the egg investments) is indispensable to avoid self-fertilization. There are several gamete proteins involved in species specificity and in self/non-self-recognition (or SI) during fertilization. The molecular mechanism of SI, which is also referred to as self-sterility, was a long-standing enigma in animals. However, a recent discovery in the ascidian SI system provided a new insight: the SI system in *Ciona intestinalis* appears to be very similar to those in flowering plants [4–6]. This discovery was surprising, since it had long been believed that the SI system in ascidians might be similar to that of adaptive immunity. Before describing the SI system in ascidians and other animals, we will summarize the current understanding in flowering plants.

2. Self-incompatibility in flowering plants

A SI system in angiosperms has been found in more than 250 of the 600 genera, which occupy about 60% of angiosperms [7]. In many angiosperms, self/non-self recognition of SI is controlled by pollen-*S* determinant and pistil-*S* determinant encoded at the *S* loci. Recent genetic, molecular biological and biochemical analyses of Brassicaceae, Papaveraceae and Solanaceae have suggested that angiosperms have developed diverse SI systems, which can be classified into two fundamentally different systems, self-recognition and non-self recognition systems: the SI systems in Brassicaceae and Papaveraceae are classified into a self-recognition system, while the SI system in Solanaceae is classified into a non-self recognition system (see Table 1) [1,2]. In Papaveraceae, self-pollen undergoes apoptosis elicited by an intracellular increase in Ca^{2+} concentration in pollination after being recognized as self [1–3]. On the other hand, pollen tube elongation is inhibited by degrading RNA with *S*-RNase of the self-pistil in Solanaceae, resulting in the avoidance of self-fertilization. This is a non-self recognition system, in which non-self S-RNase in the pistil is recognized by a ubiquitin ligase E3 (SLF/SBP) and then degraded by the ubiquitin–proteasome system in a pollen tube (Table 1) [1–3]. For Brassicaceae, we will describe recent progress made forward elucidation of the mechanism of the SI system.

In Brassicaceae, SI is controlled by a self-recognition system. The stigma is covered by a layer of epithelial cells, called papilla cells. When a cross pollen grain lands on a papilla cell, the pollen grain hydrates and geminates a pollen tube. The pollen tube then invades the papilla cell wall and grows toward the ovule cells to achieve fertilization. On the other hand, when a self pollen grain lands on a papilla cell, pollen hydration and germination are inhibited, and then self-fertilization is arrested.

The pistil-*S* determinant encoded at the *S* locus is *S*-locus receptor kinase (SRK), which localizes to the plasma membrane of stigmatic papilla cells [8]. The pollen-*S* determinant is *S*-locus protein 11 (SP11, or *S*-locus cysteine-rich protein: SCR), which is a small basic protein secreted from the anther tapetum and transferred to the pollen coat during pollen maturation [9,10]. *S*-haplotype-specific binding of SP11 to SRK induces autophosphorylation of SRK to elicit a self-incompatible reaction for rejecting self-pollen (Fig. 1) [11,12].

Thus far, two candidate molecules, *M*-locus protein kinase (MLPK) and Arm-Repeat Containing 1 (ARC1), have been identified as direct downstream factors of the SRK signaling pathway in *Brassica* species. MLPK is a membrane-anchored cytoplasmic protein kinase that co-localizes and interacts with SRK on the papilla cell membrane [13,14]. Recent studies have suggested that MLPK is also related to intra-species unilateral incompatibility of *Brassica rapa* [15], but it remains controversial whether MLPK is required for SI throughout the Brassicaceae [16]. ARC1 is a U-box protein with E3 ubiquitin ligase activity, phosphorylated by the kinase domain of SRK in *Brassica napus* [17–19], and interacts with Exo70A1, a putative component of the exocyst complex [20,21]. Suppression of *ARC1* expression results in incomplete breakdown of SI in both *B. napus* and *Arabidopsis lyrata* [18,22]. However, the precise role of ARC1 in the signaling pathway downstream of SRK that leads to self-pollen rejection remains controversial [16].

Physiological studies during cross- and self-pollination in *B. rapa* showed that actin bundles were concentrated at the cross-pollen attachment site, while actin reorganization occurs at the self-pollen attachment site. Additionally, electron tomography revealed attachment of the actin cytoskeleton with an apical vacuole network. Self-pollination disrupted the vacuole network, while cross-pollination led to vacuolar rearrangements toward the site of pollen attachment. These findings suggested that self-pollination and cross-pollination differently affect the dynamics of the actin cytoskeleton, leading to changes in vacuolar structure that might be associated with hydration and germination.

A recent biological assay using water-soluble Calcium Green showed that Ca^{2+} is exported from the papilla cell during cross-pollination and that the cross pollen coat alone elicits the Ca^{2+} transport [23]. In contrast, neither a self-pollen grain nor the self-pollen coat in *B. rapa* induced Ca^{2+} transport. These findings led us to speculate that Ca^{2+} is transported from the papilla cell to the cell wall and then transferred from the cell wall to the pollen

Table 1
Male and female determinants in self-incompatibility of plants and animals.

Family	Female determinant	Male determinant	Self or non-self recognition
Flowering plants (Angiosperms)			
Brassicaceae	SRK	SP11/SCR	Self
Papaveraceae	PrsS	PrpS	Self
Solanaceae/Rosaceae	S-RNase	SLF/SBP	Non-self
Animals (Ascidians)			
Cionidae (*C. intestinalis*)	v-Themis-A, -B	s-Themis-A, -B	Self
Pyuridae (*H. roretzi*)	VC70	(TTSP1, Urabin)?	Non-self ?

See Refs. [1–6], [25], [27–28].