

Plant mating systems: self-incompatibility and evolutionary transitions to self-fertility in the mustard family

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Flowering plants have evolved diverse mechanisms that promote outcrossing. The most widespread of these outbreeding devices are self-incompatibility systems, the highly selective prefertilization mating barriers that prevent self-fertilization by disrupting pollen–pistil interactions. Despite the advantages of outcrossing, loss of self-incompatibility has occurred repeatedly in many plant families. In the mustard family, the highly polymorphic receptors and ligands that mediate the recognition and inhibition of self-pollen in self-incompatibility have been characterized and the 3D structure of the receptor–ligand complex has been solved. Sequence analyses and empirical studies in self-incompatible and self-compatible species are elucidating the genetic basis of switches from the outcrossing to selfing modes of mating and beginning to provide clues to the diversification of the self recognition repertoire.

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Introduction

In plants as in other organisms, mating system determines patterns of genetic variation and has profound consequences for the rate and mode of evolutionary change. Outcrossing is advantageous because it can produce new combinations of different sequence variants, thus resulting in the high levels of genetic variability required for adaptation in the face of a wide range of environmental challenges. Yet, the transition from an outcrossing to a selfing mating system is one of the most prevalent evolutionary transitions in flowering plants [1]. This transition occurred repeatedly in many plant families likely because selfing provides transmission advantage over outcrossers

as well as reproductive assurance when mating partners or pollinators are scarce [2,3].

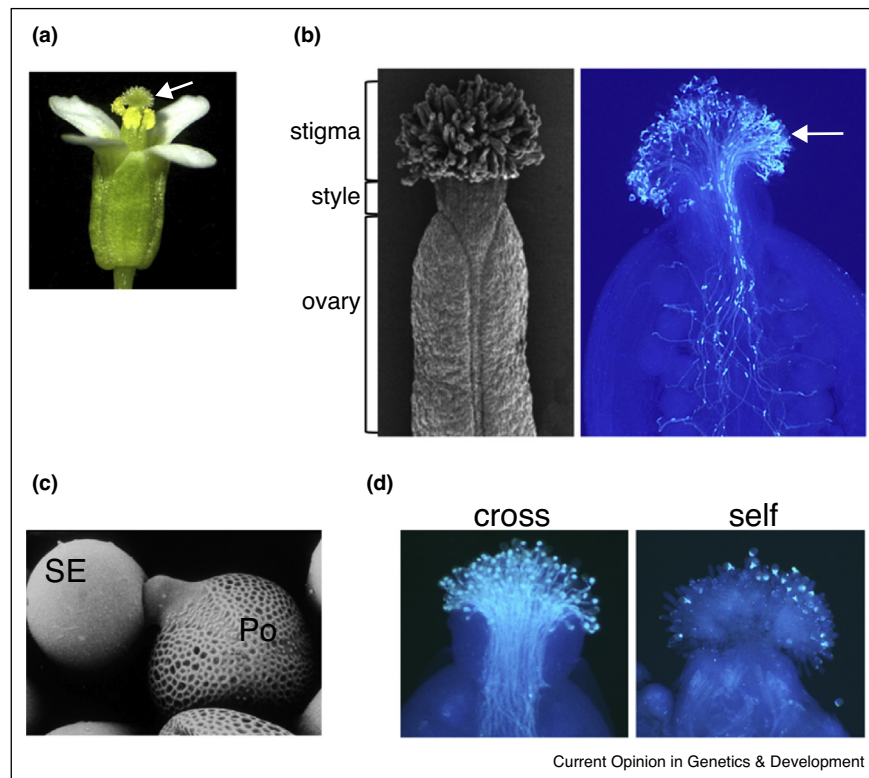
Consistent with the advantages provided by an outcrossing mode of mating, flowering plants have evolved an extraordinary variety of adaptations that promote outcrossing. These adaptations include physical separation of the sexes in different individual plants or of male and female flowers on the same plant, or temporal separation in the maturation of male and female reproductive structures [3]. However, most flowering plants have hermaphroditic flowers, in which the sperm-carrying pollen grains are in close proximity to the pistil, the female reproductive structure that harbors the egg cell-containing ovules (Figure 1). Nevertheless, many of these plants are obligate or predominant outcrossers, often due to the operation of a genetically determined physiological prefertilization barrier to self-pollination known as self-incompatibility (SI). SI systems, which occur in approximately half of flowering plant taxa, allow cells of the pistil to discriminate between ‘self’ and ‘non-self’ pollen grains or pollen tubes. The result is a highly specific disruption of pollen germination at the stigma surface or of pollen tube growth within the pistil (Figure 1), which precludes fertilization and seed production in self-pollinations but not in cross-pollinations. Despite these similar outcomes, the underlying mechanisms and the genes responsible for pollen recognition and inhibition can differ in different plant families [4]. Thus, SI refers to a group of independently evolved and molecularly unrelated mechanisms for preventing self-fertilization in hermaphroditic plants.

Here, the focus is on the molecular genetic analysis of SI and mating system transitions in the mustard (Brassicaceae) family. This family includes self-incompatible obligate outcrossers, such as the economically important *Brassica oleracea* and *B. rapa* crop species and wild *Arabidopsis lyrata* and *A. halleri*, as well as predominantly selfing species, such as the model plant *Arabidopsis thaliana*. The review summarizes our current understanding of the molecular basis of self-pollen recognition and of the genetic basis of switches from SI to self-fertility in the family, and presents data related to the diversification of the SI recognition repertoire.

SI in the mustard family

The features of SI in the mustard family have been extensively reviewed [5]. In brief, a distinctive feature of SI in this family is that self-pollination is inhibited at

Figure 1



Pollination responses in the mustard family. **(a)** An *Arabidopsis thaliana* flower showing the four petals that are characteristic of the overwhelming majority of species in the family. The arrow points to the stigma, which is the structure that interacts with incoming pollen grains. **(b)** Structure of the pistil and the path of pollen tube growth. The panel on the left shows a Scanning Electron Microscopy (SEM) image of the *A. thaliana* pistil, which consists of a stigma, style, and ovary. The panel on the right shows a UV fluorescence microscopic image of a pollinated pistil with fluorescent tubes growing through pistil tissues. For successful fertilization to occur, a pollen grain, which is released in a desiccated state from the anthers, must hydrate at the stigma surface and germinate to produce a pollen tube that grows into the wall of a stigma epidermal cell and within the extracellular matrix of the style and ovary. In the ovary, the pollen tube is guided toward an ovule into which it releases its sperm cells, resulting in fertilization and seed production. **(c)** An SEM image showing the interaction of a germinated pollen grain (Po) with a stigma epidermal cell (SE). Image courtesy of M.K. Kandasamy. **(d)** The outcomes of cross-pollination and self-pollination in a self-incompatible plant. Note that upon cross-pollination (left), large numbers of elongated pollen tubes are produced. By contrast, upon self-pollination (right), pollen grains are arrested at the stigma surface and any pollen tubes that do form fail to elongate and grow into the pistil.

the surface of stigma epidermal cells within minutes of pollen-stigma contact, primarily due to the failure of self-pollen grains to hydrate and germinate (Figure 1). Consistent with this rapid and specific inhibition of self-pollen, two self-recognition genes have been identified at the locus, designated 'S', which determines pollen recognition specificity: one gene encodes the S-locus receptor kinase (SRK), a single-pass transmembrane serine/threonine kinase displayed on the plasma membrane of stigma epidermal cells; and the second gene encodes the S-locus cysteine-rich protein SCR (also designated SP11), a small (~50 amino acids) diffusible component of the pollen coat that is the ligand for SRK. Together, SRK and SCR comprise the SI specificity-determining S haplotype and are the sole determinants of specificity in the SI response. The SRK and SCR proteins exhibit extraordinarily high levels of polymorphism and their genes

show clear signs of co-evolution [6]. The interaction between SRK and SCR is haplotype-specific and it is this interaction that determines specificity in the SI response and triggers a cascade of events within the stigma epidermal cell that culminates in the inhibition of self-pollen (Figure 1 [7]). Thus, the persistence of SI depends on the maintenance of co-adapted SRK and SCR alleles in a tightly linked genetic unit. This linkage appears to be maintained by small physical distances between the two genes in some cases [8], or more frequently, by suppressed recombination in the S-locus region. Indeed, S haplotypes typically differ in overall size and organization, they contain haplotype-specific sequences, and they accumulate transposable element sequences, similar to other chromosomal regions that exhibit suppressed recombination due to long-term independent evolution [9,10].

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