Molecular Control of S-RNase-based Self-Incompatibility

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Self-incompatibility (SI) is a genetically controlled system used by many flowering plant species to prevent inbreeding and thus promote out-crossing. Generally, self-incompatibility response involves the molecular interactions between pollen and pistil. As a result of the interactions, the self- or genetically related pollen is unable to germinate or grow in the style to complete the fertilization (de Nettancourt, 2001).

SI responses can be classified into various types based on the underlying molecular mechanisms. In most SI species, it is controlled by a single multiallelic locus known as the *S*-locus (de Nettancourt, 2001). Because recent molecular studies have revealed that more than one gene reside in the *S*-locus, they are often described as a haplotype. Since SI signaling in some species has been extensively studied at molecular level, we can define these types of self-SI as Brassicaceae-type, Solanaceae-type and Papaveraceae-type SI. In this review, we will discuss the current progress on the Solanaceae-type SI (Kao and Tsukamoto, 2004; McClure, 2004).

The Solanaceae-type SI is also often referred to as S-RNase-based self-incompatibility, since the three families (the Solanaceae, Rosaceae and Scrophulariaceae) of this type all share the similar

Z. Xu et al. (eds.), Biotechnology and Sustainable Agriculture 2006 and Beyond, 63–73.

female *S*-determinants, *S*-ribonucleases (S-RNases). These pistil-specific proteins are expressed with different molecular masses and isoelectric points that co-segregated with *S*-hapotypes, and accumulated to very high levels in the extracellular matrix. These features enabled people to identify the *S-RNase* genes through peptide sequencing and cDNA cloning, from several species in the Solanaceae and Rosaceae (Anderson et al., 1986; Ai et al., 1990; Clark et al., 1990; Sassa et al., 1993 and Ishimizu et al., 1996). Sequence alignments revealed conserved regions of *S-RNase* genes; then more *S-RNase* genes were cloned by a homology-based PCR approach, especially from *Antirrhinum hispanicum*, (Xue et al., 1996), demonstrating that the Scrophulariaceae could share the same SI mechanism with the other two families.

S-RNase was confirmed to be the sole female-specificity determinant for the SI response by gain- and loss-of-function experiments (Lee et al., 1994; Murfett et al., 1994). Other transgenic experiments revealed that the RNase activity per se of S-RNases is essential for their function in SI response, by site-directed mutagenesis of the *S-RNase* genes (Huang et al., 1994).

The determinants for SI should have haplotype diversity to ensure the specific recognition of self or non-self pollen. As one would expect, S-RNases in the Solanaceae, Rosaceae and Scrophulariaceae are all highly divergent, often with ~70% sequence identity. However, all S-RNases contained the similar conserved regions and hypervariable regions. These regions are believed to be the essential elements for ribonuclease activity or S-specificity recognition and interaction. It is notable that S-RNases in the Rosaceae appeared to have a different structure, especially in hypervariable regions, from those in the Solanaceae (Matsuura et al., 2001). This may implicate the divergence of the SI mechanisms between the Solanaceae and Rosaceae.

It is now widely accepted that S-RNases could enter the pollen cytoplasm in an *S*-haplotype-independent manner (Luu et al., 2000). Thus, whether the pollen can grow or not appears to be dependent on whether the ribonuclease activity can be inhibited in the pollen tube, since this activity had been demonstrated by McClure et al. (1990) to be cytotoxic for the pollen tube growth.