

## SELF-COMPATIBILITY IN *PRUNUS* SPECIES: DIVERSITY OF MUTATIONS

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### Abstract

Self-compatibility (SC) is an interesting horticultural trait. Molecular approaches have been recently applied to the elucidation of the interacting pollen-pistil mechanism and to the identification of the genes involved in pistil-pollen recognition. Both mutations of the pistil *S*-RNases and the pollen *SFBs* have been reported to explain the changes in the *S* allele expression. Styler-part mutations have revealed that ribonuclease activity of the *S*-RNases is required to inhibit pollen growth. A defective function of the pollen may also give rise to SC. Breakdown of SI has also been associated with mutations affecting modifier loci unlinked to the *S*-locus. Additionally, a double phenotypic expression of the same genotype has been observed. The nature of these different mutations has only been identified in a few cases, including deletions, insertions, shift mutations and, more recently, epigenetic changes.

### Introduction

Self-incompatibility (SI) is an important biological feature from the evolutionary point of view, but it is an inconvenient attribute in most agricultural species, where the commercial part of the crop is obtained after an elaborate process of pollination, ovule fertilization and ovary growth. Thus, self-compatibility (SC) is an interesting trait from the horticultural point of view, especially in several *Prunus* species where a gametophytic SI system operates. Several breeding programmes in the past aimed at obtaining SC cultivars in mainly self-incompatible (SI) species, although the genetic basis for SI/SC was then unknown, with the founded expectation that SC would be transmitted to the offspring. Molecular approaches have been more recently applied to the elucidation of the interacting pollen-pistil mechanism and to the identification of the genes involved in pistil-pollen recognition. Genetically it has been established that SC/SI is controlled by a single polymorphic locus containing at least two linked genes, one specifically expressed in the pistil and the other in the pollen (Kao and Tsukamoto, 2004). The pistil component of SI in Rosaceae has been determined to be an *S*-RNase (Tao et al., 1997). An *SFB* was considered to be a good candidate gene for the pollen-*S*, showing a tight linkage with the *S*-RNase gene (Ikeda et al., 2005).

Our objective was to review the different mutations suggested as possible bases for the change from SI to SC in the different *Prunus* species in order better understand the possible genetic mechanisms acting in the SC/SI interaction in *Prunus* species.

### Styler-part mutations

Ribonuclease activity of the *S*-RNases is required to inhibit pollen growth (Sassa et al. 1997). In most cases no RNase activity at all was detected (Bošković et al., 1999; Kodad et al., 2009; Fernández i Martí et al., 2010), but in other cases a low level of *S*-RNase transcription has been suggested as conferring SC (Yamane et al., 2003; Watari et al., 2007; Hanada et al., 2009). A mutation or an alteration in the coding region of the *S*-

RNase gene could be the reason of the change of SI activity in *Prunus*. Bošković et al. (2007) wrongly suggested that a mutation in the C2 region of the  $S_f$ -RNase in 'Tuono' almond from histidine to arginine could be the origin of SC, although they had to correct this assertion in a note added in proof. In Japanese plum, SC was attributed to the presence of the  $S_e$  allele (Beppu et al., 2005), due to a low level of RNase accumulation (Watari et al., 2007). Although the study of SC/SI in sour cherry is somehow intricate because of the polyploid origin of this species, several mutations, including insertions and deletions, have been associated to a low expression or activity of the  $S$  protein (Yamane et al., 2003; Tsukamoto et al., 2008).

### **Pollen-part mutations**

The SC observed in some cultivars of several *Prunus* species has been reported to be due to a defective function of the pollen (Tsukamoto et al., 2006; Ushijima et al., 2004; Yamane and Tao, 2009). These modifications include mutations, deletions or insertions in the coding region of the SFB  $S$ -haplotype. The first SC mutations found in *Prunus* were artificially produced in sweet cherry by X-ray irradiation (Lewis and Crowe 1954), resulting in the  $S_3$ ' and  $S_4$ ' haplotypes, apparently mutated from the original  $SFB$ ., with a complete deletion in  $S_3$ ' (Sonneveld et al. 2005) and a frame shift mutation in  $S_4$ ' (Ushijima et al. 2004). A mutation has been reported to affect the function of the  $S$ -pollen factor in SC apricot (Vilanova et al., 2006). In *P. mume*, the  $S_f$  haplotype is a naturally occurring SC  $S$  haplotype considered to be a pollen part mutation with the presence of an insertion in the middle of the  $SFB_f$  coding region (Ushijima et al. 2004).

### **Mutations outside the $S$ locus**

Breakdown of SI has been associated with mutations affecting a modifier locus unlinked to the  $S$ -locus in sweet cherry (Wünsch and Hormaza, 2004), apricot (Vilanova et al., 2006) and almond (Fernández i Martí et al., 2009; Kodad et al., 2009). The nature of these mutations has not yet been identified, although work in progress is trying to elucidate the different possibilities of these mutations, including epigenetic changes (Fernández i Martí, 2010).

### **Double expression of the SC allele**

The almond SC  $S_f$  allele shows a double expression, one SC and the other SI (Kodad et al., 2009) despite the full genetic identity of the two expressions of this allele (Fernández i Martí et al., 2010). The double phenotypic expression of the same genotype has also been observed in Japanese plum (Watari et al., 2007; Guerra et al., 2009) and sweet cherry (Wünsch et al., 2010). The double expression of an  $S$  allele may explain the cases of unilateral incompatibility (UI), as observed in almond (Bošković et al 2007; Fernández i Martí et al., 2009) and Japanese plum (Guerra, 2011).

### **Conclusion**

The nature of the interaction of the female and male determinants of SI remains unclear. Additionally, proteins and factors besides the  $S$ -locus have been shown to play important roles in the SI system in families such as Solanaceae and Plantaginaceae (Goldraij et al., 2006). This possibility could also been present in the genus *Prunus* (Fernández i Martí et al., 2011), reinforcing the suggestion by Socias i Company (1990) that almond could be a SI species with a genetic background of pseudo-self-

compatibility (PSC). Over this background, only one  $S_f$  allele could break the SI system, but probably interacting with this background of PSC. A similar case has also been suggested in sweet cherry, as shown by the slower pollen tube growth and reduced fruit set of self-pollinated 'Cristobalina' (Cachi, 2011).

The presence of different types of mutations in the same species indicates that probably each case might be different, requiring a different approach and a closer examination of the specific change originating the shift from SI to SC. Consequently, the SI/SC scenario in *Prunus* cannot be simplified but examined as another complex situation with multiple faces.

### Acknowledgements

This research was supported by the Spanish grant AGL2010-22197-C02-01 and Research Group A12 of Aragón

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