Introduction

Many fruit trees of Rosaceae, such as Japanese pear (Pyrus pyrifolia), apple (Malus × domestica), sweet cherry (Prunus avium), almond (Prunus dulcis), mume (Prunus mume), and apricot (Prunus armeniaca), exhibit self-incompatibility (SI) and require pollination with pollen from compatible SI genotypes for stable fruit production. Aside from this practical importance, SI of Rosaceae is interesting from an evolutionary point of view, because the common ancestor of Asterid and Rosid is thought to exhibit S-RNase-based gametophytic self-incompatibility (GSI, see below, Igic and Kohn 2001) which is suggestive of a common origin. To date, S-RNase has been characterized in two families of Asterid, Solanaceae and Plantaginaceae, while it is known in only one family of Rosid, Rosaceae (de Nettancourt 2001, Franklin-Tong 2008, Sassa et al. 2010, Fig. 1). In addition, Rosaceae is likely to include two different systems of SI: a self-recognition system of Prunus of tribe Amygdaleae of subfamily Spiraeoideae (cherry, almond, and apricot), and a non-self-recognition system of tribe Pyraeae of subfamily Spiraeoideae (pear and apple). This review focuses on recent findings on different mechanisms of SI in Rosaceae.

Key Words: Rosaceae, self-incompatibility, pistil, pollen, S locus, S-RNase, F-box.

Review

Molecular mechanism of the S-RNase-based gametophytic self-incompatibility in fruit trees of Rosaceae

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Self-incompatibility (SI) is a major obstacle for stable fruit production in fruit trees of Rosaceae. SI of Rosaceae is controlled by the S locus on which at least two genes, pistil S and pollen S, are located. The product of the pistil S gene is a polymorphic and extracellular ribonuclease, called S-RNase, while that of the pollen S gene is a protein containing the F-box motif, SFB (S haplotype-specific F-box protein)/SFBB (S locus F-box brothers). Recent studies suggested that SI of Rosaceae includes two different systems, i.e., Prunus of tribe Amygdaleae exhibits a self-recognition system in which its SFB recognizes self-S-RNase, while tribe Pyraeae (Pyrus and Malus) shows a non-self-recognition system in which many SFBB proteins are involved in SI, each recognizing subset of non-self-S-RNases. Further biochemical and biological characterization of the S locus genes, as well as other genes required for SI not located at the S locus, will help our understanding of the molecular mechanisms, origin, and evolution of SI of Rosaceae, and may provide the basis for breeding of self-compatible fruit tree cultivars.

Key Words: Rosaceae, self-incompatibility, pistil, pollen, S locus, S-RNase, F-box.

Products of the S locus of Rosaceae: pistil determinant S-RNase and pollen determinant F-box proteins SFB and SFBB

Genetically, SI of Rosaceae is controlled by a single S locus with multiple alleles (for Fragaria of subfamily Rosoideae, in addition to the S locus, involvement of another locus was suggested (Bošković et al. 2010)), and when one of the two S alleles of the pistil matches that of a pollen, the pollen is recognized as self, and is rejected (de Nettancourt 2001, Franklin-Tong 2008). However, the S locus contains at least two genes tightly linked with each other, pistil S and pollen S genes, and the pair of pistil S and pollen S alleles is called the S haplotype (de Nettancourt 2001, Franklin-Tong 2008).

The pistil S gene of Rosaceae encodes a polymorphic and highly expressed extracellular ribonuclease called S-RNase, similar to Solanaceae and Plantaginaceae (de Nettancourt 2001, Franklin-Tong 2008). S-RNase acts as a cytotoxin in self-pollen tubes; however, it is taken up in both self- and non-self-pollen tubes in Solanaceae (Goldraij et al. 2006, Luu et al. 2000), suggesting a mechanism in which the pollen S gene plays a pivotal role in detoxifying non-self-S-
RNases. Although identification of the pollen $S$ gene had been challenging probably because of its low expression level, chromosome walking from the $Prunus$ $S$-RNase gene identified polymorphic and pollen-specific F-box gene called $SFB$ ($S$-haplotype-specific F-box protein) as a good candidate for pollen $S$ (Entani et al. 2003, Ushijima et al. 2003). F-box proteins have also been identified as pollen candidates in other plants, e.g., SLF of Solanaceae and Plantaginaceae, and SFBB of Pyreae of Rosaceae; however, further analyses suggested that the function of $SFB$ may be different from these F-box proteins, coinciding with their differing $S$ locus duplication effects on their pollen SI function.

**Effects of $S$ locus duplication on SI in Pyreae and Prunus**

In many SI species, tetraploidy has been associated with the loss of SI function in pollen (de Nettancourt 2001). Genetic analyses have revealed that diploid heteroallelic pollen, such as $S^1S^2$, loses SI function and is compatible with pistils with any $S$ genotype, while homoallelic pollen retains SI function. This phenomenon, called ‘competitive interaction’ (CI) (de Nettancourt 2001), was also observed in haploid pollen with a translocated chromosome segment harboring the $S$ locus of $Nicotiana$ (Solanaceae) and $Antirrhinum$ (Plantaginaceae) (Golz et al. 2001, Xue et al. 2009). Golz et al. (2001) conducted a large-scale screening of mutagenized pollen for self-compatible (SC) mutants by incompatible pollination, and recovered SC mutants caused by CI and not by pollen $S$ deletion, suggesting that pollen $S$ is essential for pollen tube growth. In Rosaceae, CI has been well documented in Pyreae, i.e., tetraploids of pear and apple (Adachi et al. 2009, Crane and Lewis 1942) and diploid mutants with translocated $S$ locus fragment of Japanese pear (Mase et al. 2014), although this has not been observed to occur in Prunus (Hauck et al. 2006, Tao and Iezzoni 2010). Naturally occurring tetraploid sour cherry ($Prunus cerasus$) includes both SI and SC plants (Lansari and Iezzoni 1990), and genetic analyses have shown that heteroallelic pollen is rejected by the pistil with a matching $S$ haplotype, leading to a ‘one-allele-match’ model hypothesizing that the SC of sour cherry is caused by the accumulation of mutations in $S$ genes, but not by CI (Hauck et al. 2006, Tao and Iezzoni 2010). This ‘one-allele-match’ model is consistent with the findings of other studies showing pollen-part SC mutants of cherry ($P. avium$) with deletion or insertion within the $SFB$ (Sonneveld et al. 2005, Ushijima et al. 2004). These differences in the effect of $S$ locus duplication on pollen SI function suggest differing pollen $S$ functions in Prunus and Pyreae.

**Self-recognition by a single pollen $S$ protein in Prunus**

In Rosaceae, the pollen-part determinant was first identified in Prunus species by chromosome walking from the
The chromosome walking strategy was also adopted to identify the pollen S gene in apple (M. × domestica) and Japanese pear (Pyrus pyrifolia), which belong to tribe Pyraceae, and detected pollen-specific F-box genes at the S locus region, similar to Prunus. However, unlike Prunus, more than two pollen-specific F-box genes, homologous with each other, were identified and named SFBB (S locus F-box brothers) (Sassa et al. 2007). Further analyses showed that more than ten SFBB genes are clustered at the S locus region of Pyraceae (De Franceschi et al. 2011, Minamikawa et al. 2010, Okada et al. 2011, 2013). Genetic analysis showed tight linkage of these genes with the S-RNase, consistent with the heterochromatic nature of the S locus region (Minamikawa et al. 2010), which may contribute to suppress recombination in this region (Wang et al. 2012).

Multiple F-box genes at the S locus were also characterized in the solanaceous plant, Petunia (Kubo et al. 2010, 2015). The function of SLF, a pollen S F-box gene of Petunia, was revealed by CI when transgenic pollen with introduced heteroallelic SLF gene showed breakdown of SI (Sijacic et al. 2004). However, further analysis showed that transformation of SLF does not always cause breakdown of SI (e.g., S5-SLF causes CI for S6 and S7 pollen, but not for S5 and S11 pollen) suggesting that SLF is not the sole determinant of pollen specificity, and other factors may also be involved in SI (Kubo et al. 2010). Kubo et al. (2010) cloned five additional types of SLF-like F-box genes, and named SLF2-SLF6. These genes were expressed in pollen and linked to the S-RNase. Functional analysis showed that the newly identified SLF genes induced CI for particular S haplotypes (e.g., S5-SLF2 causes CI for S6, S11, and S15 pollen, but not for S5 and S7 pollen). Based on these findings, the ‘collaborative non-self recognition’ model was proposed for SI of Petunia, i.e., multiple SLF proteins are involved in pollen specificity, and each targets a subset of non-self-S-RNases for detoxification (Kubo et al. 2010). This discovery in Petunia hinted at the significance of the SFBB cluster at the S locus of Pyraceae. Kakui et al. (2011) cloned eight types of SFBB genes from S1~S10 haplotypes, and showed that the allelic sequence diversity within the same SFBB type is very low, while the sequence diversity of SFBB genes within the same S haplotype is high and comparable to the allelic diversity of the S-RNase. This is consistent with the hypothesis that multiple SFBB genes are involved in pollen specificity in SI of Pyraceae, with each SFBB targeting a subset of non-self-S-RNases. This hypothesis was supported by findings from a mutant haplotype, S5sm, which lacks S5-RNase and an SFBB gene, S4-F-box0/SFBB1-S4 (Kakui et al. 2011, Okada et al. 2008, Sassa et al. 1997). The S5sm pollen was rejected not only by S5 pistils, but also by S5 pistils, while it was accepted by pistils of other S haplotypes. This suggests that S4-F-box0/SFBB1-S4 is the only factor in the S5 haplotype to detoxify S1-RNase, and that it is not involved in targeting other non-self-S-RNases (Kakui et

Table 1. Different systems of the S-RNase based GSI

| Family     | Tribe     | Genus       | CI  | Copy number of pollen S | Effect of deletion of pollen S               | Type of SI              |
|------------|-----------|-------------|-----|------------------------|---------------------------------------------|-------------------------|
| Rosaceae   | Pyraceae  | Pyrus, Malus| +   | multiple               | Incompatibility to non-self pistils          | Non-self-recognition    |
| Amygdaleae | Prunus    | Prunus      | +   | multiple               | Incompatibility to non-self pistils          | Self-recognition        |
| Solanaceae | Petunia,  | Nicotiana   | -a  | single                 | SC6                                         | Non-self-recognition    |
|            | Solanum   |             |     | multiple               |                                             |                        |
| Plantaginaceae | Antirrhinum |            | +   | multiple?              | ?                                           | Non-self-recognition?   |

*S-RNase* gene and subsequent sequence analyses of the region (Entani et al. 2003, Ushijima et al. 2003). The identified gene *SFB* (S haplotype-specific F-box protein) encodes an F-box protein, is specifically expressed in pollen, and shows high allelic polymorphism, comparable to that of the S-RNase. Analyses of pollen-part SC mutants identified 4 bp deletion in the *SFB* gene of cherry (P. avium) and 6.8 kb insertion in the *SFB* gene of Japanese apricot (P. mume), further supporting the involvement of SFB in pollen SI function (Ushijima et al. 2004). Given that the major role of the F-box proteins is, as a component of SCF ubiquitin ligase, recognition of target proteins to be ubiquitinated for degradation by the 26S proteasome, SFB was initially assumed to mediate ubiquitination and degradation of non-self-S-RNases while differentially interacting with self-S-RNase and leaving it intact (Ushijima et al. 2003). However, a pollen-part SC haplotype of cherry, S9', was found to lack the SFB-containing genomic region. This suggested that ubiquitination of non-self-S-RNases by SCF-SFB was unlikely; deletion of SFB would result in the inability to degrade non-self-S-RNases, arresting pollen tube growth in pistils with any S haplotype (Sonneveld et al. 2005). Instead, it is likely that non-self-S-RNases taken up by the pollen tube are detoxified by an unidentified ‘general inhibitor’, while self-S-RNase is protected from the ‘general inhibitor’ by the function of SFB as a ‘blocker’, and acts as a cytotoxin to arrest the growth of a self-pollen tube (Luu et al. 2001, Sonneveld et al. 2005). This model suggests that SI of Prunus is of the ‘self recognition by a single factor’ type, and is consistent with the probable absence of CI in Prunus. Non-self-recognition by multiple pollen S proteins in Pyraceae
The SI of Rosaceae is intriguing due to the coexistence of different SI types such as the self-recognition system of *Prunus* and non-self-recognition system of Pyreae. However, the self-recognition model of SI of *Prunus* is based on the analyses of naturally occurring tetraploids (Tao and Iezzoni 2010), and previous studies of another natural tetraploid, *Prunus pseudocerasus*, suggested the possibility of CI in this species (Gu et al. 2013, Huang et al. 2008). Analyses of artificial tetraploids may further clarify the self-recognition model of SI of *Prunus*.

Biochemical analyses have identified several probable components involved in the SI systems of Rosaceae. Interestingly, both the SFB of *Prunus* and SFBB of Pyreae have been suggested to form similar SCF complexes, in which an Skp1-like protein, SSK1, bridges SFB/SFBB and Cullin (Matsumoto et al. 2012, Minamikawa et al. 2014, Yuan et al. 2014). Yeast two-hybrid screening using S-RNase as the bait identified actin and an ABC transporter as probable interacting partners of the cherry and apple S-RNases, respectively (Matsumoto and Tao 2012, Meng et al. 2014). However, the biological significance of these protein-protein interactions observed in these *in vitro* experiments remains to be elucidated. Further biochemical and biological analyses may clarify the molecular bases for the self-recognition and non-self-recognition of the *Prunus* and the Pyreae systems, respectively.

The products of the S locus have been shown to be not sufficient for SI function, and other factors not linked to the S locus may also be required. Such non-S-specific factors have been characterized in Solanaceae, e.g., HT-B and 120 k proteins (McClure et al. 2011), but not in Rosaceae. Furthermore, non-S locus pollen-part mutations (PPM) have been reported in *Prunus avium* (sweet cherry) and *P. armeniaca* (apricot) (Cachi et al. 2011, Zuriaga et al. 2012). Interestingly, the two non-S locus PPM have been mapped to a similar region of linkage group 3 (LG3), which shows synteny to apple (*M. domestica*) LG17, where the apple S locus is located. Although it is not clear if the two non-S locus PPMs of sweet cherry and apricot are due to the same gene, identification of the gene(s) will help our understanding of the SI mechanism. Further characterization of the S and non-S locus SI genes, together with evolutionary studies (Aguir et al. 2015, Morimoto et al. 2015), will shed light on the origin and evolution of self-recognition and non-self-recognition SI systems in Rosaceae.

**Literature Cited**

Adachi, Y., S. Komori, Y. Hoshikawa, N. Tanaka, K. Abe, H. Bessho, M. Watanabe and A. Suzuki (2009) Characteristics of fruited and pollen tube growth of apple autotetraploid cultivars showing self-compatibility. J. Japan Soc. Hort. Sci. 78: 402–409.

Aguir, B., J. Vieira, A.E. Cunha, N.A. Fonseca, D. Reboiro-Jato, M. Reboiro-Jato, F. Fdez-Riverola, O. Raspé and C.P. Vieira (2013) Patterns of evolution at the gametophytic self-incompatibility *Sorbus aucuparia* (Pyrinae) S pollen genes support the non-self recognition by multiple factors model. J. Exp. Bot. 64: 2423–2434.

Aguir, B., J. Vieira, A.E. Cunha, N.A. Fonseca, A. Iezzoni, S. van Nocker and C.P. Vieira (2015) Convergent evolution at the gametophytic self-incompatibility system in *Malus* and *Prunus*. PLoS ONE 10: e0126138.

Bosković, R.I., D.J. Sargent and K.R. Tobutt (2010) Genetic evidence that two independent S-loci control RNase-based self-incompatibility in diploid strawberry. J. Exp. Bot. 61: 755–763.

Cachi, A.M. and A. Wünsch (2011) Characterization and mapping of non-S gametophytic self-compatibility in sweet cherry (*Prunus avium* L.). J. Exp. Bot. 62: 1847–1856.

Crane, M.B. and D. Lewis (1942) Genetical studies in pears III. Incompatibility and sterility. J. Genet. 43: 31–43.

De Franceschi, P., L. Piertantoni, L. Dondini, M. Grandi, J. Sanzol and S. Sansavini (2011) Cloning and mapping multiple S-locus F-box genes in European pear (*Pyrus communis* L.). Tree Genet. Genomes 7: 231–240.

de Nettancourt, D. (2001) Incompatibility and incongruity in wild and cultivated plants. Berlin: Springer.

Entani, T., M. Iwano, H. Shiba, F.S. Che, A. Isogai and S. Takayama (2003) Comparative analysis of the self-incompatibility (S-) locus region of *Prunus mume*: identification of a pollen-expressed F-box gene with allelic diversity. Genes Cells 8: 203–213.

Franklin-Tong, V.E.E. (2008) Self-Incompatibility in Flowering Plants: Evolution, Diversity, and Mechanisms: Springer-Verlag, Berlin.

Goldraij, A., K. Kondo, C.B. Lee, C.N. Hancock, M. Sivaguru, S. Vasquez-Santana, S. Kim, T.E. Phillips, F. Cruz-Garcia and B. McClure (2006) Compartmentalization of S-RNase and HT-B degradation in self-incompatible *Nicotiana*. Nature 439: 805–810.

Golz, J.F., H.Y. Oh, V. Su, M. Kusaba and E. Newbigin (2001) Genetic analysis of *Nicotiana* pollen-part mutants is consistent with the presence of an S-ribonuclease inhibitor at the S locus. Proc. Natl. Acad. Sci. USA 98: 15372–15376.

Gu, C., Q.-Z. Liu, Y.-N. Yang, S.-J. Zhang, M.A. Khan, J. Wu and S.-L. Zhang (2013) Inheritance of hetero-diploid pollen S-haplotypes in self-compatible tetraploid Chinese cherry (*Prunus pseudocerasus* Lindl.). PLoS ONE 8: e61219.

Hauck, N.R., H. Yamane, R. Tao and A.F. Iezzoni (2006) Accumulation of nonfunctional S-haplotypes results in the breakdown of gametophytic self-incompatibility in tetraploid *Prunus*. Genetics 172: 1191–1198.

Huang, S.-X., H.-Q. Wu, Y.-R. Li, J. Wu, S.-J. Zhang, W. Heng and S.-L. Zhang (2008) Competitive interaction between two functional
S-haplotypes confer self-compatibility on tetraploid Chinese cherry (Prunus pseudocerasus Lindl. cv. Nanjing Chuisi). Plant Cell Rep. 27: 1075–1085.

Igic, B. and J.R. Kohn (2001) Evolutionary relationships among self-incompatibility RNases. Proc. Natl. Acad. Sci. USA 98: 13167–13171.

Kakui, H., M. Kato, K. Ushijima, M. Kitaguchi, S. Kato and H. Sassa (2011) Sequence divergence and loss-of-function phenotypes of S locus F-box brothers genes are consistent with non-self recognition by multiple pollen determinants in self-incompatibility of Japanese pear (Pyrus pyrifolia). Plant J. 68: 1028–1038.

Kato, M., S. Kato and H. Sassa (2012) Polyacrylamide gel electrophoresis of S-RNase fragments for identification of S-genotypes of Japanese pear (Pyrus pyrifolia). Breed. Sci. 62: 348–351.

Kubo, K., T. Entani, A. Takara, N. Wang, A.M. Fields, Z. Hua, M. Toyoda, S. Kawashima, T. Ando, A. Isoi and et al. (2010) Collaborative non-self recognition system in S-RNase-based self-incompatibility. Science 330: 796–799.

Kubo, K., T. Paape, M. Hatakeyama, T. Entani, A. Takara, K. Kajihara, R. Shimizu-Inatsugi, K.K. Shizu and S. Takayama (2015) Gene duplication and genetic exchange drive the evolution of S-RNase-based self-incompatibility in Petunia. Nature Plants 1: 14005.

Lansari, A. and A. Iezzoni (1990) A preliminary analysis of self-incompatibility in sour cherry. HortScience 25: 1636–1638.

Luu, D.T., X. Qin, D. Morse and M. Cappadocia (2000) S-RNase uptake by compatible pollen tubes in gametophytic self-incompatibility. Nature 407: 649–651.

Luu, D.T., X. Qin, G. Laublin, Q. Yang, D. Morse and M. Cappadocia (2001) Rejection of S-heteroallelic pollen by a dual-specific S-RNase in Solanum chacoense predicts a multimeric SI pollen component. Genetics 159: 329–335.

Mase, N., Y. Sawamura, T. Yamamoto, N. Takada, N. Shishio, T. Saito and H. Iketani (2014) A segmental duplication encompassing S-haploype triggers pollen-part self-compatibility in Japanese pear (Pyrus pyrifolia). Mol. Breeding. 33: 117–128.

Matsumoto, D. and R. Tao (2012) Isolation of pollen-expressed actin as an actin and F-box protein gene, with haplotype-specific polymorphism. Journal of Agricultural Science 43: 1559–1566.

McClure, B., F. Cruz-Garcia and C. Romero (2011) Compatibility and self-incompatibility in S-RNase-based systems. Amer. Bot. 108: 647–658.

Meng, D., Z. Gu, W. Li, A. Wang, H. Yuan, Q. Yang and T. Li (2014) Apple MdABCF assists in the transportation of S-RNase into pollen tubes. Plant J. 78: 990–1002.

Minamikawa, M., H. Kakui, S. Wang, N. Kotoda, S. Kikuchi, T. Koba and H. Sassa (2010) Apple S locus region represents a large cluster of related, polymorphic and pollen-specific F-box genes. Plant Mol. Biol. 74: 143–154.

Minamikawa, M.F., R. Koyano, S. Kikuchi, T. Koba and H. Sassa (2014) Identification of SFBB-containing canonical and non-canonical SCF complexes in pollen of apple (Malus × domestica). PLoS ONE 9: e97642.

Morimoto, T., T. Akagi and R. Tao (2015) Evolutionary analysis of genes for S-RNase-based self-incompatibility reveals S locus duplications in the ancestral Rosaceae. Hort. J. 84: 233–242.

Nowak, M.D., A.P. Davis, F. Anthony and A.D. Yoder (2011) Expression and trans-specific polymorphism of self-incompatibility RNases in Coffea (Rubiaceae). PLoS ONE 6: e21019.

Okada, K., N. Tonaka, Y. Moriya, N. Natorioka, Y. Sawamura, T. Matsumoto, T. Nakanishi and T. Takasaki-Yasuda (2008) Deletion of a 236 kb region around S4-RNase in a stylar-part mutant S4–haplotype of Japanese pear. Plant Mol. Biol. 66: 389–400.

Okada, K., N. Tonaka, T. Taguchi, T. Ichikawa, Y. Sawamura, T. Nakanishi and T. Takasaki-Yasuda (2011) Related polymorphic F-box protein genes between haplotypes clustering in the BAC contig sequences around the S-RNase of Japanese pear. J. Exp. Bot. 62: 1887–1902.

Okada, K., S. Moriya, T. Haji and K. Abe (2013) Isolation and characterization of multiple F-box genes linked to the Sf and Sf-RNase in apple (Malus × domestica Borkh.). Plant Reprod. 26: 101–111.

Okada, K. (2015) DNA markers and the molecular mechanism of self-incompatibility in Japanese pear (Pyrus pyrifolia Nakai). Hort. J. 84: 183–194.

Saito, T., Y. Sato, Y. Sawamura, M. Shoda, T. Takasaki-Yasuda and K. Kobotuki (2012) Dual recognition of Sf and Sf pistils by Sf± pollen in self-incompatibility of Japanese pear (Pyrus pyrifolia Nakai). Tree Genet. Genomes 8: 689–694.

Sassa, H., H. Hirano, T. Nishino and T. Koba (1997) Style-specific self-compatible mutation caused by deletion of the S-RNase gene in Japanese pear (Pyrus pyrifolia). Plant J. 12: 223–227.

Sassa, H., H. Kakui, M. Miyamoto, Y. Suzuki, T. Hanada, K. Ushijima, M. Kusaba, H. Hirano and T. Koba (2007) S locus F-box brothers: multiple and pollen-specific F-box genes with S haploype-specific polymorphisms in apple and Japanese pear. Genetics 175: 1869–1881.

Sassa, H., H. Kakui and M. Minamikawa (2010) Pollen-expressed F-box gene family and mechanism of S-RNase-based gametophytic self-incompatibility (GSI) in Rosaceae. Sex. Plant Reprod. 23: 39–43.

Sijacic, P., X. Wang, A.L. Skirpan, Y. Wang, P.E. Dowd, N.G. McBubb, S. Huang and T.H. Kao (2004) Identification of the pollen determinant of S-RNase-mediated self-incompatibility. Nature 429: 302–305.

Sonneveld, T., K.R. Tobutt, S.P. Vaughan and T.P. Robbins (2005) Loss of pollen-S function in two self-compatible selections of Prunus avium is associated with deletion/mutation of an S haploype-specific F-box gene. Plant Cell 17: 37–51.

Tao, R. and A.F. Iezzoni (2010) The S-RNase-based gametophytic self-incompatibility system in Prunus exhibits distinct genetic and molecular features. Sci. Hortic. 124: 423–433.

The Angiosperm Phylogeny Group (2009) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. Bot. J. Linn. Soc. 161: 105–121.

Ushijima, K., H. Sassa, A.M. Dandekar, T.M. Gradziel, R.Tao and H. Hirano (2003) Structural and transcriptional analysis of the self-incompatibility locus of almond: Identification of a pollen-expressed F-box gene with haplotype-specific polymorphism. Plant Cell 15: 771–781.

Ushijima, K., H. Yamae, A. Watari, E. Kakehi, K. Ikeda, N.R. Hauck, A.F. Iezzoni and R. Tao (2004) The S haploype-specific F-box protein gene, SFB, is defective in self-compatible haplotypes of Prunus avium and P. mume. Plant J. 39: 573–586.

Wang, S., H. Kakui, S. Kikuchi, T. Koba and H. Sassa (2012) Interhaploypic heterogeneity and heterochromatic features may contribute to recombination suppression at the S locus in apple (Malus × domestica). J. Exp. Bot. 63: 4983–4990.

Xue, Y., Y. Zhang, Q. Yang, Q. Li, Z. Cheng and H.G. Dickinson (2009) Genetic features of a pollen-part mutation suggest an inhibitory...
role for the *Antirrhinum* pollen self-incompatibility determinant. Plant Mol. Biol. 70: 499–509.

Yamane, H. and R. Tao (2009) Molecular basis of self-(in)compatibility and current status of S-genotyping in rosaceous fruit trees. J. Japan. Soc. Hort. Sci. 78: 137–157.

Yuan, H., D. Meng, Z. Gu, W. Li, A. Wang, Q. Yang, Y. Zhu and T. Li (2014) A novel gene, *MdSSK1*, as a component of the SCF complex rather than *MdSBP1* can mediate the ubiquitination of S-RNase in apple. J. Exp. Bot. 65: 3121–3131.

Zuriaga, E., L. Molina, M.L. Badenes and C. Romero (2012) Physical mapping of a pollen modifier locus controlling self-incompatibility in apricot and synteny analysis within the Rosaceae. Plant Mol. Biol. 79: 229–242.