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Self-compatibility sources as sources of variation in advanced almond introgression lines

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Abstract. Breeding for self-fruitfulness in almond requires the combination of pollen-pistil self-compatibility which is controlled by a single-major *S* gene and self-pollination or self-fertility which is controlled by multiple genes. Important sources for self-compatibility include *Prunus webbii* and its derivatives such as *cv. Tuono* which are pistil based, and peach and its wild relatives which are pollen based. The loci controlling the pistil and pollen self-compatibility genes are tightly linked which frustrates accurate Marker Assisted Selection. Methods of Marker Assisted Breeding complemented by Pedigree Based Analysis have facilitated the introgression of self-compatibility alleles from multiple independent sources including *P. webbii,* cv. 'Tuono', *P. mira,* and peach *(P. persica).* The final assessment of self-fruitfulness is determined by selfed-seed set in orchard trees where individual branches are enclosed to prohibit insect cross-pollination. The degree of self-fruitfulness under these field conditions has been found to be controlled by a major *S*-gene as well as modifier genes, often with significant environment interactions. In certain introgression lines, seedling tree age affects the expression of self-fruitfulness. Genetic background also strongly influences the level of self-fruitfulness as well as differences in branch architecture and so bearing habit. Some self-incompatible genotypes have also been found to express relatively high but inconsistent levels of self-fruitfulness. High levels of both expression and stability of self-fruitfulness is being pursued in advanced almond introgression lines by combining pistil-based and pollen-based genes with appropriate genetic backgrounds

Keywords. Self-fruitfulness – Introgression – S_f locus – Bearing – Architecture.

Les sources de auto-compatibilité comme source de variation dans des lignes avancés d'introgression d'amandier

Résumé. *L'amélioration pour l'auto-fructification chez l'amandier nécessite la combinaison d'auto-compatibilité pollen-pistil, contrôlée par un seul S-gène majeur, et d'auto-pollinisation ou auto-fertilité, contrôlée par des gènes multiples. Parmi les sources importantes pour l'auto-compatibilité figurent* Prunus webbii *et ses dérivés tels que* cv. Tuono*, qui sont basés sur le pistil, et la pêche et ses apparentés sauvages, qui sont basés sur le pollen. Les loci qui contrôlent les gènes d'auto-compatibilité du pistil et du pollen sont étroitement liés, ce qui entrave la précision d'une sélection assistée par marqueurs. Les méthodes d'amélioration assistées par marqueurs couplées à l'analyse généalogique ont facilité l'introgression d'allèles d'auto-compatibilité provenant de multiples sources indépendantes y compris* P. webbii, *cv. 'Tuono',* P. mira*, et la pêche* (P. persica)*. L'évaluation finale des graines auto-fécondées est déterminée par la fructification auto-pollinisée chez des arbres du verger où des branches individuelles sont ensachées pour empêcher la pollinisation croisée par les insectes. Le degré d'auto-fructification sous ces conditions de champs s'est avéré contrôlé par un S-gène majeur ainsi que par des gènes modificateurs, ayant souvent des interactions significatives avec l'environnement. Dans certaines lignées d'introgression, l'âge du plant d'arbre affecte l'expression de l'auto-fructification. Le fond génétique influence aussi fortement le niveau d'auto-fructification ainsi que les différences d'architecture des branches et donc le mode de fructification. Certains génotypes auto-incompatibles ont révélé exprimer des niveaux relativement élevés mais inconsistants d'auto-fructification. De hauts niveaux à la fois d'expression et de stabilité de l'auto-fructification sont recherchés dans les lignées avancées d'introgression d'amandier en combinant des gènes basés sur le pistil et des gènes basés sur le pollen avec des fonds génétiques appropriés.*

Mots-clés. *Auto-fructification – Introgression – Locus S_f – Architecture fruitière.*

I – Introduction

Almonds are naturally self-incompatible, requiring the inter-planting of often inferior pollinizer cultivars in orchards in order to set a commercial crop. Poor weather conditions and/or scarcity of required insect cross-pollinators during the short almond bloom period in early spring frequently contribute to crop reductions. Self-fruitfulness in almond is thus an important breeding objective as it could increase production uniformity while decreasing orchard inputs. Self-compatibility is controlled by a single-major *S* gene, while the capacity for self-pollination or autogamy is controlled by multiple genes affecting flower structure and development (López *et al*., 2006). Because the self-compatible allele *Sf* is not native to almond, it has to be introgressed from related self-fertile species either directly through interspecific hybridization and subsequent backcrossing or through intraspecific hybridization with self-compatible almond land races such as 'Tuono' where S_f introgression has occurred naturally. Both the inter-and intra-species origin as well as the mode-of-action of these different S_f gene sources vary. In peach species, self-fertility is determined by the pollen portion of the S_f gene, while in almond species, determination is within the pistil (Tao *et al*., 2007) though the relative performance of different S_f sources has rarely been compared. As part of a long-term cultivar development project, the almond breeding program at the University of California at Davis (UCD) has developed advanced introgression lines transferring self-fruitfulness from multiple independent sources including *P. webbii,* cv. 'Tuono', *P. mira,* and peach *(P. persica*. Field performance of some of the more promising advanced introgression breeding lines have been evaluated to assess both the magnitude and stability of different sources.

II – Materials and methods

Twelve advanced introgression lineages were evaluated, including breeding lines derived from *Prunus mira, Prunus fenzliana, P. persica,* cv. 'Tuono', and *P. webbii*. Trees were selected from seedling populations grown on their own roots under high orchard densities with standard commercial fertilizer and water inputs. Self-fruitfulness was evaluated from the 3rd or 4th year after planting up to the 10th year in the field. Self-fruitfulness was evaluated by enclosing approximately 80 cm of a flowering branch with an insect-proof mesh bag prior to flower opening. Bagged branches were self-pollinated every 3 days during bloom using an air-brush which caused self-pollen from adjacent dehisced anthers to be transferred to the stigma. Final fruit set was recorded 2 months after petal fall as the percentage of fruit that had set relative to the number of flowers estimated to be present at the time of bagging. Normal fruit-set on adjacent branches which had not been bagged were also used as controls.

III – Results and discussion

All advanced introgression lines evaluated possessed promising levels of self-fruitfulness as well as good tree productivity and kernel quality demonstrating the efficacy of simultaneous selection for these traits. More intensive selection was required for recovering commercially acceptable kernel sizes and shapes due both to the small initial sizes of most donor species as well as a greater tolerance for differences in tree architecture in commercial production (Kester and Gradziel, 1996). A consequence of the intensive effort required for foreign gene introgression, particularly the large number of recurrent backcrosses required to achieve commercially acceptable phenotypes, is that relatively few of the S_f alleles available in related germplasm is actually utilized. The current UCD almond breeding germplasm is dominated by only one source for *P. mira*, one source for *P. fenzliana*, 4 sources for *P. webbii* (including cv. 'Tuono' and 2 sources for *P. persica*. Both the magnitude and stability of self-fruitfulness varied among introgression sources within the limited breeding lines evaluated in this study (Fig. 1). The most consistent performance was observed in breeding lines derived from *P. mira*, particularly selection 2004,8-160. Good performance was also

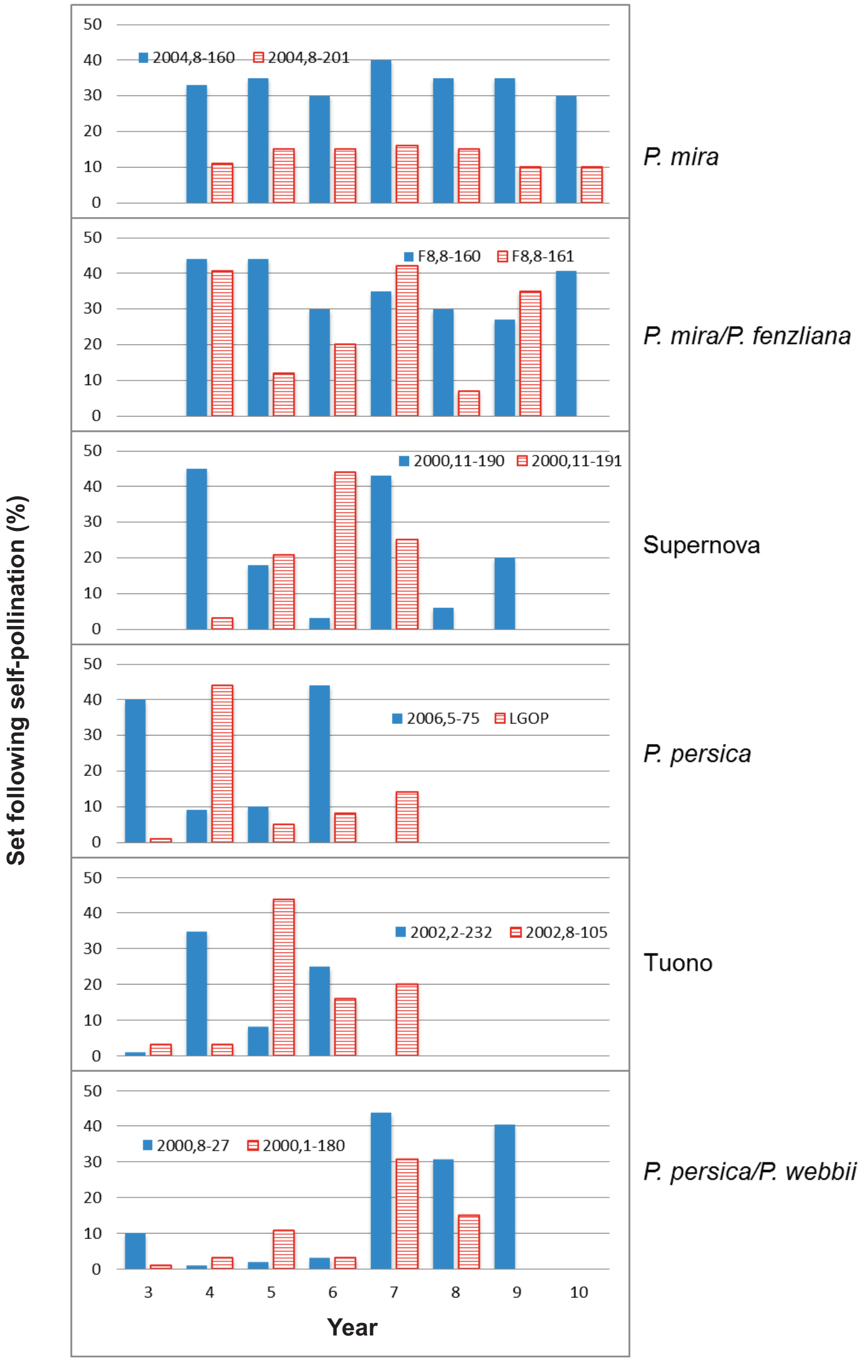

Fig. 1. Levels of self-fertility in 2 selected advanced almond selections from each of 6 separate introgression lines, with donor identity listed to the right of each plot.

observed in introgression lines derived from both *P. mira* and *P. fenzliana*. *P. fenzliana* was utilized as a source for improved tree architecture rather than self-fruitfulness since it is self-incompatible. Greater year-to-year variation was observed in breeding lines derived from *P. persica* and *P. webbii* including the cultivar's *Tuono* which appear to be derived from *P. webbii*. Of particular interest was the finding that in the breeding lines evaluated which combined sources of both *P. persica* and *P. webbii* promising levels of self-fruitfulness were only detected in mature seedling trees which were 7 years or older. Mature clonal trees, propagated on standard commercial rootstocks express more stable levels of self-fruitfulness, indicating that the variability observed is more a function of the early years of development and growth of own-rooted seedling trees. While the variability demonstrated may have implications concerning the best breeding sources for commercial production, it has more direct consequences for the initial seedling selection process since both expressivity and penetrance of the trait may vary considerably and so would confound effective response to selection. Although most traditional self-incompatible almond cultivars consistently express very low levels of self-fruitfulness (Kodad *et al*., 2008, Kodad *et al*., 2010, Martinez-Garcia *et al*., 2011), some self-incompatible genotypes such as S_1S_{14} as found in the cultivars Winters and Sweetheart can produce relatively high levels of self-seed set under conducive conditions (Gradziel *et al*., 2013) which would further confound accurate selection. In addition, the relatively late expression of self-fruitfulness in some of the introgression lines evaluated would frustrate a more efficient selection at an earlier tree age. Variations in self-fruitfulness among the different introgression lines may be as much a consequence of differences in tree growth and development as differences in Sf allele potential. Many almond seedling trees are notoriously shy-bearing in the early years even though profuse flowering may occur which is partly a result of the need to develop sustainable bearing-wood such as perennial spurs (Socias i Company *et al*., 2011). While interspecific breeding lines targeting the introgression of self-fruitfulness have the added benefits of enriching the breeding germplasm for both novel disease/pest resistance and tree architecture/productivity, modified fruit bearing habits such as shown in Fig. 2 would be expected to influence early tree cropping performance independent of self-fruitfulness, because of the differences in potential productivity as well as in bearing-wood renewal.

Fig. 2. An example of the more radial crop bearing-habit in an advanced almond introgression line derived from an initial interspecific hybridization with *Prunus webbii.*

IV – Conclusions

In the seedling selections evaluated, the degree and stability of self-fruitfulness varied among the different species sources for this trait as well as among different possible sources within species. The presence of multiple alleles for self-fruitfulness has been documented in many of the species sources including *P. persica, P. mira* and *P. webbii* (Hanada *et al.,* 2014, Tao *et al*., 2007), however the tedious and time-consuming backcrossing required for successful trait introgression has resulted in only a very small number of such alleles being transferred and tested within an almond genetic background. The more intensive selection encouraged by these more demanding recurrent backcrossing strategies also tend to limit the transfer of flower and branch development/architecture traits which could act to complement both intensity and stability of self-fruitfulness in new almond cultivars.

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