Detecting Cross-incompatibility of Three North American Apricot Cultivars and Establishing the First Incompatibility Group in Apricot

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Abstract. Laboratory and orchard tests have shown that the apricot (Prunus armeniaca L.) cultivars ‘Hargrand’, ‘Goldrich’, and ‘Lambertin-1’ are cross-incompatible. All three cultivars are from North American breeding programs and have ‘Perfection’ as a common ancestor. In orchard tests, compatible pollinations resulted in 19% to 74% fruit set, while incompatible pollinations resulted in <2% fruit set. Microscopic examination showed that, in incompatible pollinations, pollen tube growth was arrested in the style, most frequently in its third quarter, and that the ovary was never reached. It is proposed that self-incompatibility in apricot is of the gametophytic type, controlled by one S-locus with multiple alleles, and that these three cultivars are $S_1S_2$.

European apricot (Prunus armeniaca) cultivars have traditionally been considered self-compatible (Mehlenbacher et al., 1991). However, self-incompatible cultivars have been described by several researchers. Schultz (1948) pointed out that ‘Riland’ and ‘Perfection’, two cultivars traditionally grown in the United States, are self-incompatible. Later, many papers confirmed that, although apricot populations in Europe and North America were mainly self-compatible, self-incompatibility was more frequent than had been thought. Lamb and Stiles (1983) found five self-incompatible cultivars in a study of 19 cultivars suitable for cultivation in New York, and Nyútjó et al. (1985) found one case of self-incompatibility among 23 tested cultivars. Most recently, several self-incompatible cultivars were found among those traditionally grown in Spain (Burgos et al., 1993; Egea et al., 1991).

Self-incompatibility in Prunus appears to be controlled by a monogenic system with a multiallelic series (De Nettancourt, 1977). Data from almond (Dicenta and García, 1993; Socias i Company, 1991) and sweet cherry (Crane and Brown, 1937) are consistent with this hypothesis. Also, preliminary results indicate that the same system operates in apricot (Burgos, 1995). The locus controls self-incompatibility and intraspecific cross-incompatibility (Kester et al., 1994; Socias i Company, 1991).

The increasingly narrow genetic base of breeding programs, a consequence of using a small number of cultivars as parents, has caused the frequent appearance of cross-incompatibility between cultivars of some species. Early work by Tufts and Philp (1922) established two incompatibility groups in almond. Much later, the work of Kester and collaborators made it possible to establish new incompatibility groups and assign additional cultivars to the groups described earlier (Kester, 1963; Kester and Asay, 1975; Kester et al., 1994). This was mainly due to the use of ‘Nonpareil’ and ‘Texas’ (‘Mission’) as common ancestors of many of these cultivars.

In apricot, only one case of cross-incompatibility has been reported between Spanish cultivars: ‘Moniquí Fino’ and ‘Moniquí Borde’ (Egea et al., 1991). The names of these cultivars indicate a probable kinship. Burgos et al. (1993) did not find cross-incompatibility after crossing other self-incompatible cultivars from the same Spanish population. Many Spanish apricot cultivars seem to have originated from crosses between north African cultivars (mainly self-incompatible) and European cultivars (mainly self-compatible) (Egea et al., 1988). Hence, a great degree of heterozygosity is to be expected and self-incompatibility might be expected.

In the present work, cross-compatibility between some North American cultivars was studied by examining pollen tube growth using fluorescence microscopy and fruit set from controlled pollinations in the orchard.

Materials and Methods

Plant material. Studies were conducted in the apricot collection at the Departamento de Mejora y Patología Vegetal, CEBAS-CSIC, Murcia, Spain. Five-year-old trees of ‘Lambertin-1’, ‘Hargrand’, ‘Harcot’, and ‘Goldrich’ were used in this study. These cultivars were obtained from breeding programs in the United States and Canada. Five-year-old trees of the self-incompatible ‘Moniquí’ (Burgos et al., 1993) and the self-compatible ‘Canino’ and ‘Bebeco’ (Audergon et al., 1988) were also used to check experimental methodology.

The parentage of the cultivars used in this study is shown in Fig. 1. ‘Goldrich’ is a seedling from ‘Sun Glo’ × ‘Perfection’ (Toyama, 1971). ‘Sun Glo’ was developed by O.H. Heider as a seedling of unknown parentage, which originated in Washington in 1942 (Brooks and Olmo, 1972a). ‘Perfection’ was introduced in 1937 in Waterville, Wash. (Brooks and Olmo, 1972a), and has been used widely in American breeding programs despite its self-incompatibility. ‘Geneva’ and ‘Naramata’ are seedlings of unknown parentage. ‘Geneva’ originated in Italy and was planted, evaluated, and selected in New York by R. Wellington in 1934 (Brooks and Olmo, 1972a). ‘Lambertin-1’ was initially selected by the U.S. Dept. of Agriculture–Agricultural Research Service at Fresno, Calif., and evaluated under the designation P32-18.

Pollen collection and controlled pollinations. Flowers in the balloon stage were collected from all cultivars to be used as male parents. Anthers were removed from the flowers and placed in a petri dish. The anthers were desiccated in a petri dish in a calcium chloride desiccator for 24 h, then the pollen was stored in small bottles and kept at 4 °C.
For controlled crosses in the orchard, several branches with a total number of about 200 flowers in the balloon stage were chosen on each parent tree. Open flowers and immature buds were removed, and flowers at the balloon stage were emasculated to prevent self- and cross-pollination. Controlled pollinations were carried out using a small brush and the corresponding pollen from each male parent. After 8 weeks, fruit were counted and fruit set percentages were determined.

For laboratory testing, branches of the cultivars to be pollinated with about 30 flowers each in the balloon stage were cut and placed in plastic bags containing water. The bags were transported to the laboratory in an insulated ice chest. Once in the laboratory, the basal ends were placed in beakers containing a 5% sucrose solution in a chamber where the temperature was maintained at 20 °C. The flowers were emasculated and 24 h later they were self- or cross-pollinated. Also, branches with a similar number of flowers in balloon stage were marked on the tree and the flowers were emasculated. After 24 h, the flowers were pollinated, for comparison with the laboratory controlled pollinations. Seventy-two hours after controlled pollination of the flowers transported to the laboratory and 192 h after controlled pollination of the flowers on the tree, 15 pistils per combination were harvested and immersed in FAA (90% alcohol at 70%, 5% formaldehyde at 40%, 5% glacial acetic acid) in small glass bottles. The pistils were stored at 4 to 5 °C in this solution. According to Williams (1970), 192 h is a sufficient time for the pollen tubes to reach the ovary in compatible Fig. 1. Parentage of the apricot cultivars used in this study (Layne, Ledbetter, and Howell, personal communication). Unless indicated otherwise, the female parent is at the top and the male parent is at the bottom. OP = open-pollination.

Table 1. Apricot pollen tube growth 72 h after self- and cross-pollinations under laboratory controlled conditions.6

| Pollinated cultivar | Pollinizing cultivar | Ovaries reached by pollen tubes (%) | Avg no. of pollen tubes penetrated by the longest pollen tube | Percent of style length |
|---------------------|----------------------|-------------------------------------|----------------------------------------------------------|------------------------|
| Lambertin-1         | Lambertin-1          | 0 ± 0.0                             | 0 ± 0.0                                                   | 76.1 ± 8.0             |
|                     | Goldrich             | 0 ± 0.0                             | 0 ± 0.0                                                   | 86.3 ± 6.1             |
|                     | Hargrand             | 0 ± 0.0                             | 0 ± 0.0                                                   | 69.7 ± 16.7            |
|                     | Harcot               | 100 ± 0.0                           | 6.2 ± 3.2                                                 | 100 ± 0.0              |
| Goldrich            | Goldrich             | 0 ± 0.0                             | 0 ± 0.0                                                   | 72.5 ± 11.9            |
|                     | Lambertin-1          | 0 ± 0.0                             | 0 ± 0.0                                                   | 54.3 ± 12.3            |
|                     | Hargrand             | 0 ± 0.0                             | 0 ± 0.0                                                   | 82.9 ± 9.0             |
|                     | Harcot               | 100 ± 0.0                           | 11.4 ± 1.5                                                | 100 ± 0.0              |
| Hargrand            | Hargrand             | 0 ± 0.0                             | 0 ± 0.0                                                   | 69.2 ± 9.8             |
|                     | Lambertin-1          | 0 ± 0.0                             | 0 ± 0.0                                                   | ---                    |
|                     | Goldrich             | 0 ± 0.0                             | 0 ± 0.0                                                   | 74.8 ± 9.9             |
|                     | Harcot               | 100 ± 0.0                           | 3.9 ± 2.0                                                 | 100 ± 0.0              |
| Harcot              | Hargrand             | 0 ± 0.0                             | 0 ± 0.0                                                   | 53.9 ± 12.7            |
|                     | Lambertin-1          | 100 ± 0.0                           | 3.7 ± 2.0                                                 | 100 ± 0.0              |
|                     | Goldrich             | 100 ± 0.0                           | 7 ± 2.9                                                   | 100 ± 0.0              |
|                     | Hargrand             | 100 ± 0.0                           | 4.2 ± 1.9                                                 | 100 ± 0.0              |

6Values are means from 10 samples ± sd.
combinations at the daily average temperatures of about 15 °C occurring during our orchard pollinations. To remove the FAA, the pistils were rinsed in distilled water for three times 1 h each, and then placed in an autoclave for 30 min at 1 atmosphere in a 5% sodium sulfite solution to soften the tissues and facilitate their staining with 0.1% aniline blue in 0.1 N potassium phosphate. The pistils were stained for 24 h. The epidermis was then removed, and the pistils squashed for observation (Linsakens and Esser, 1957).

An Olympus BH2 microscope (Olympus, Tokyo) was used with a BH2-RFL-T2 ultraviolet light source, using an Osram HBO 100 W/2 high-pressure mercury lamp (Osram GmbH, Berlin–Munich).

Results

Ten of the sixteen pollinations performed in the laboratory were incompatible (Table 1). In incompatible crosses, pollen tube growth was arrested about three-fourths of the way down the style. The percentages of fruit set following self-pollination confirm that ‘Goldrich’, ‘Hargrand’, ‘Harcot’, and ‘Lambertin-1’ are self-incompatible (Table 2) and that the first three are cross-incompatible in all possible combinations. ‘Harcot’ was compatible with the other three cultivars. No pollen tube reached the ovary in the six different combinations between ‘Lambertin-1’, ‘Hargrand’, and ‘Goldrich’ (Table 1). Orchard cross-pollination confirmed the laboratory results and no fruit set was obtained in those combinations tested except for very low fruit set (1.9%) in the combination ‘Lambertin-1’ x ‘Hargrand’ (Table 2). Results of the incompatible combinations (self- and cross-) strongly contrast, in laboratory and field pollinations, with those from the compatible ones, where 100% of the ovaries had a high average number of pollen tubes (Table 1) and large percentages of fruit set were obtained (Table 2).

Some differences were found in the length of the style that pollen tubes were able to reach in the incompatible combinations. The percentages of fruit set following self-pollination of the longest pollen tube ranged from 48.8% in the cross ‘Goldrich’ x ‘Lambertin-1’ to 86.3% in the reciprocal cross. These differences are probably genotype-combination dependent. Table 3 shows self-compatible and self-incompatible cultivars that were self-pollinated in the orchard to assess results from laboratory controlled-pollinations. Very clear differences in the growth of pollen tubes were seen. In self-compatible cultivars, pollen tubes grew the entire length of the style and entered the ovary, while in self-incompatible cultivars tube growth stopped in different parts of the style, depending on the cultivar.
been proposed as a homomorphic, monofactorial, and gametophytic system (De Nettancourt, 1977). Preliminary results in apricot (Burgos, 1995) seem to confirm this hypothesis, where a locus with a multimorphic series would control the trait. Hence, cross-incompatible cultivars would have the same genotype for the trait. We propose designating those two alleles as S1 and S2.

The three cross-incompatible cultivars have ‘Perfection’ among their ancestors. This is an old cultivar used extensively in North American breeding programs because of its large size, attractive orange color, and firm flesh. ‘Perfection’ is a parent or grandparent of some recently introduced cultivars such as ‘Rival’ (Brooks and Olmo, 1971), ‘Tracy’ (Brooks and Olmo, 1972b), ‘Skaha’, ‘Sundrop’, and ‘Westley’ (Brooks and Olmo, 1975) or ‘Castlebríte’ (Brooks and Olmo, 1978). It would be interesting to identify the alleles in ‘Perfection’, but unfortunately this cultivar was not in our apricot collection. ‘Goldrich’ (S1S2, as proposed) and ‘Perfection’ (S1S1) have an allele in common since ‘Goldrich’ was obtained from the cross ‘Sun Glo’ x ‘Perfection’. If ‘Goldrich’ or ‘Perfection’ are cross-compatible, seedlings from this cross would be of two different genotypes (i.e., two incompatibility groups) since S1 alleles would be arrested. One of these groups would be the same as the male parent (S1S1 or S1S2, if ‘Goldrich’ or ‘Perfection’ respectively, are the male parent), while the other one would be new (S1S2). These cultivars may also belong to the same incompatibility group and be cross-incompatible if ‘Perfection’ and ‘Sun Glo’ share one allele. Crosses of ‘Goldrich’ with unrelated cultivars would give genotypes representing four incompatibility groups. It is only by making controlled crosses and identifying incompatibility groups in these progenies that alleles can be assigned to groups.

The narrow genetic base resulting from using a limited number of parents has resulted in a small number of incompatibility groups in almond or cherry (Kester et al., 1994). Incompatibility is difficult to detect and is also undesirable, since incompatible clones require pollinizers and render the yield dependent on abundant pollen transfer among the trees (Frankel and Galun, 1977). The appearance of cross-incompatibility in this group of cultivars indicates that greater attention should be given to this character in breeding programs. The laboratory pollination procedure described here would allow quick and easy identification of self-incompatibility genotypes.

**Literature Cited**

Audergon, J.M., V. Signoret, J.M. Dulflil, and F. Gilles. 1988. Les variétés d'abricot. L’Arboriculture Fruitière. 403:22–56.

Brooks, R.M. and M.P. Olmo. 1971. Register of new fruit and nut varieties. List 26. HortScience 6:439–442.

Brooks, R.M. and H.P. Olmo. 1972a. Register of new fruit and nut varieties. 2nd ed. Univ. of California Press, Berkeley.

Brooks, R.M. and H.P. Olmo. 1972b. Register of new fruit and nut varieties. List 27. HortScience 7:455–460.

Brooks, R.M. and H.P. Olmo. 1975. Register of new fruit and nut varieties. List 30. HortScience 10:471–478.

Brooks, R.M. and H.P. Olmo. 1978. Register of new fruit and nut varieties. List 31. HortScience 13:523–532.

Burgos, L. 1995. Preliminary result on an inheritance study of genetic incompatibility in apricot. Acta Hort. 384:85–89.

Burgos, L., T. Berenguer, and J. Egea. 1993. Self- and cross-compatibility among apricot cultivars. HortScience 28:148–150.

Crane, M.B. and A.G. Brown. 1937. Incompatibility and sterility in the sweet cherry (Prunus avium L.). J. Pomol. 15:86–116.

De Nettancourt, D. 1977. Incompatibility in angiosperms. Monographs on theoretical and applied genetics. III. Springer-Verlag, Berlin–Heidelberg–New York.

Dicenta, F. and J.E. García. 1993. Inheritance of self-compatibility in almond. Heredity 70:313–317.

Egea, L., T. Berenguer, J. Egea, and J.E. García. 1988. Origen, situación y características de las variedades de albaricoquero de Murcia. Anales de Edafología y Agrobiología XI (5–6):999–1011.

Egea, J., J.E. García, L. Egea, and T. Berenguer. 1991. Self-incompatibility in apricot cultivars. Acta Hort. 293:285–293.

Frankel, R. and E. Galun. 1977. Pollination mechanisms, reproduction and plant breeding. Monographs on theoretical and applied genetics. II. Springer-Verlag, Berlin–Heidelberg–New York.

Hirasuoka, S., T. Tezuka, and Y. Yamaamoto. 1989. Analysis of self-incompatibility reaction in easter Lily by using heat treatments. J. Amer. Soc. Hort. Sci. 114:505–508.

Kester, D.E. 1963. California almond varieties. Calif. Agr. Ext. Serv. Lftr. 152:1–8.

Kester, D.E. and R. Asay. 1975. Almonds, p. 387–419. In: J. Janick and J.N. Moore. (eds.). Advances in fruit breeding. Purdue Univ. Press, West Lafayette, Ind.

Kester, D.E., T.M. Gradziel, and W.C. Micke. 1994. Identifying pollen incompatibility groups in California almond cultivars. J. Amer. Soc. Hort. Sci. 119:106–109.

Lamb, R.C. and W.C. Stiles. 1983. Apricots for New York state. N.Y. Food and Life Sci. Bul. (100):1–4.

Layne, R.E.C. 1978. ‘Harcot’ apricot. HortScience 13:64–65.

Layne, R.E.C. 1981. ‘Hargrand’ apricot. HortScience 16:98–100.

Linskens, H.F. and K. Esser. 1957. Über eine spezifische anfärbung der pollenblätter und der pollenflugel im fruchtknoten. Naturwissenschaften. 44:16

Meihlener, S.A., V. Cociu, and L.F. Hough. 1991. Apricots (Prunus), p. 65–107. In: J.N. Moore and J.R. Ballington. (eds.). Genetic resources of temperate fruit and nut crops. Intl. Soc. Hort. Sci., Wageningen.

Nyújtó, F., M.M. Kerek, J. Nyéki, M. Tóth, A. Pete, H. Harsányi, and E. Ifju. 1985. Introducing foreign apricot cultivars at three different areas of Hungary. Preliminary report. Acta Hort. 192:353–360.

Schultz, J.H. 1948. Self-incompatibility in apricots. Proc. Amer. Soc. Hort. Sci. 51:171–174.

Socias i Company, R. 1991. Breeding self-compatible almonds. Plant Breeding Rev. 9:313–338.

Toyama, T.K. 1971. Roza peach, Sungiant apricot and Rival apricots, new stone fruit varieties for the Pacific Northwest. Wash. Agr. Expt. Sta. Circ. 545:1–3.

Tufts, W.P. and G.L. Philp. 1922. Almond pollination. Calif. Agr. Bul. 346

Van Gastel, A.J.G. 1976. Mutability of the self-incompatibility locus and identification of the S-bearing chromosome in Nicotiana alata. PhD diss. Centre for Agricultural Publishing and Documentation, Wageningen.

Williams, R.R. 1970. Appendix, p. 57–61. In: R.R. Williams and D. Wilson (eds.). Towards regulated cropping. Univ. of Bristol, Grower Books.

Williams, R.R., P. Brain, R.M. Church, and V.A. Flook. 1984. Flower receptivity, pollen transfer and fruit set variations during a single flowering period of Cox’s Orange Pippin apple. J. Hort. Sci. 59:337–347.

Williams, R.R. and M. Maier. 1977. Pseudocompatibility after self-pollination of the apple Cox’s Orange Pippin. J. Hort. Sci. 52:475–483.