

TESTING OF SELF-(IN)COMPATIBILITY IN APRICOT CULTIVARS USING FLUORESCENCE MICROSCOPY

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Abstract. Self-incompatibility is common in apricot (*Prunus armeniaca* L.) cultivars of Central Asian and Irano-Caucasian ecogeographical groups, while cultivars of European group are traditionally considered as self-compatible. However, the number of known self-incompatible cultivars of the European group has increased rapidly over the last two decades. This can be explained by using Asian or North American self-incompatible cultivars in breeding programs that aim to create new genotypes with the traits including: *Plum Pox Virus* resistance, frost tolerance, increase of the sugar content or extending the harvest time. In this work self-(in)compatibility was tested in 38 apricot cultivars. Pollen-tube growth in pistils pollinated in laboratory was analysed using fluorescence microscopy. Cultivars were considered self-compatible if at least one pollen tube reached the ovary in the majority of pistils. In self-incompatible cultivars growth of pollen tubes in the style of pistil stopped along with formation of characteristic swellings. Of the examined cultivars, 17 were self-compatible, and 21 were self-incompatible.

Key words: *Prunus armeniaca*, pollination, pollen tube growth, pistil

INTRODUCTION

Self-incompatibility is a common evolutionary strategy in flowering plants to prevent self-fertilization and promote out-crossing. It is defined as the inability of a fertile hermaphrodite seed plant to produce zygotes after self-pollination [De Nettancourt 1977]. Fruit tree species of the *Rosaceae* family exhibit gametophytic incompatibility system (GSI), which is controlled by a single, polymorphic locus with multiple alleles (*S*-alleles). Self-incompatibility alleles stop the pollen tube growth if the same allele is present in the pollen grain and in the pistil. *S*-gene product in the style is a ribonuclease enzyme (*S*-RNase) [McClure et al. 1989], while the product in pollen is F-box protein [Entani et al. 2003].

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Self-incompatibility often occurs in fruit species of the genus *Prunus*, especially in sweet cherry (*Prunus avium* L.) and almond [*Prunus dulcis* (Mill.) D.A. Webb]. In apricot (*Prunus armeniaca* L.), it is common in cultivars of Central Asian and Irano-Caucasian ecogeographical groups. In contrast, apricot cultivars of European group are traditionally considered as self-compatible [Kostina 1970, Layne et al. 1996]. Until recently, only a few cases of self-incompatibility have been registered in apricot cultivars of this group [Schultz 1948, Nyújtó et al. 1985, Egea et al. 1991]. The number of known self-incompatible apricot cultivars of the European group has increased rapidly over the last two decades. Thus, Szabó and Nyéki [1991] reported self-incompatibility in nine cultivars, Burgos et al. [1997] in 42 cultivars, Paydas et al. [2006] in 37 cultivars and hybrids, and Milatović and Nikolić [2007] in 14 cultivars.

Self-(in)compatibility is traditionally determined by monitoring fruit set after controlled pollination under field conditions. Disadvantage of this method is that fruit set varies from year-to-year, depending on weather conditions. The second method used, is the observation of pollen tube growth in the pistil using fluorescence microscopy. It enables more reliable conclusions compared to the field tests [Viti et al. 1997]. In addition to these biological methods, two molecular methods have recently been used to determine self-(in)compatibility in apricot: detection of stelar ribonucleases (*S*-RNases) [Burgos et al. 1998, Albuquerque et al. 2002] and DNA amplification and identification by PCR analysis [Badenes et al. 2000, Halász et al. 2005].

The aim of this paper was to examine self-(in)compatibility using fluorescence microscopy in a number of apricot cultivars from different countries.

MATERIAL AND METHODS

Plant material. Plant material was taken from the apricot cultivar collection of the Faculty of Agriculture in Belgrade. Total number of analyzed cultivars was 38. The largest number of cultivars originates from Canada (10), than from Ukraine (7), USA (5), Italy and New Zealand (4). Two cultivars originate from Romania and South Africa, and one cultivar from France, Hungary, Bulgaria, and Moldova each (tab. 1).

The apricot collection orchard was established in 2007. The rootstock was Myrobalan (*Prunus cerasifera* Ehrh.) seedling, and tree spacing was 4.5×3 m. Studies were carried out over a two-year period (2010–2011).

Pollination and fixation of pistils. Shoots with flower buds at the “balloon” stage were collected in the orchard and transported to the laboratory. They were placed in jars with 5% (w/v) sucrose solution and kept at room temperature ($20 \pm 2^\circ\text{C}$). Emasculation of flowers was done immediately, and the extracted anthers were placed in open 10 cm-diameter Petri dishes to desiccate. Pistils were hand-pollinated 24 h after emasculation.

Fixation of pistils was done four days (96 h) after pollination. It was carried out in a 5 : 5 : 90 (v/v/v) mix of 40% (v/v) formaldehyde, glacial acetic acid, and 70% (v/v) ethanol [Burgos et al. 1997]. Fixed material was kept at $+4^\circ\text{C}$ in the refrigerator until staining.

Staining and microscopy of pistils. Before staining, pistils were rinsed in running water for 15 min. Thereafter, they were immersed overnight in 8 M NaOH to soften

their tissues. They were then rinsed again in running water for 2 h. Staining was done with 0.1% (w/v) aniline blue dissolved in 0.1 M K_3PO_4 for approximately 24 h. To prepare pistils for microscopic examination, the style was separated from the ovary. Pubescence of styles was not removed. The style was squashed, while the ovary was cut longitudinally with a razor blade.

Examination of pistils was carried out by fluorescence microscopy using a "Leica DM LS", (Leica Microsystems, Wetzlar, Germany), equipped with "I3" filter (wavelength 450–490 nm) or "A" filter (wavelength 340–380 nm). Only pistils with more than 20 pollen grains on the stigma were analysed.

Statistical analyses. The numbers of pollen tubes that reached the base of the style and the ovule were recorded, and standard errors were calculated for these two parameters. These data were analysed statistically using analysis of variance, and the significance of the differences between mean values was determined using Duncan's multiple range test at $P \leq 0.05$. The percentages of pistils with at least one pollen tube that had reached the base of the style and the ovule were also calculated.

RESULTS AND DISCUSSION

Pollen tube growth in the apricot cultivars studied is presented in Table 1.

Cultivars were considered self-compatible if in the majority of pistils at least one pollen tube reached the ovary within 96 h after pollination. Of the 38 apricot cultivars studied, 17 were self-compatible. They were: 'Bella d'Imola', 'Bob Cot', 'Chudovyi', 'Festivalna', 'Harlayne', 'Harogem', 'Kospotenskyi', 'Luiset', 'Magyar kajszi C235', 'Mari de Cenad', 'Moldavskyi Krupnoplodnyi', 'Palstein', 'Peeka', 'Re Umberto', 'Reale d'Imola', 'Sabbatani', and 'Tomcot'. In these cultivars, pollen tubes reached the ovary in the majority (60–100%) of pistils (fig. 1). They also often (40–95%) reached the ovule (fig. 2). The average number of pollen tubes at the base of the style ranged from 2.8 to 15.1, and at the ovule ranged from 0.5 to 3.0.

Cultivars were considered self-incompatible if the pollen tubes stopped their growth in the style, with forming swollen tips (fig. 3 and fig. 4). Other signs of incompatibility include twisted pollen tube growth (fig. 5) and bifurcation of a pollen tube (fig. 6). Self-incompatibility was found in 21 of the apricot cultivars studied: 'Agat', 'Amos', 'Aurora', 'Benmore', 'Dunstan', 'Gabriel', 'Gvardeyskyi', 'Harglow', 'Hargrand', 'Harojoy', 'Harostar', 'Laycot', 'Orangered', 'Robada', 'Sundrop', 'Sun Glo', 'Veecot', 'Velvago', 'Vognik', 'Vulcan', and 'Zorkyi'. In these cultivars pollen tubes rarely (0–25%) reached the base of the style, while no pollen tube was found in the ovules. The number of pollen tubes at the base of the style ranged from 0.0 to 0.4.

Pollen grains placed on the surface of the stigma begin to germinate and elongate in the pollen tubes that grow through the style tissue towards the ovary. The pollen tube wall consists of two main layers of polysaccharide. The inner layer contains predominantly callose or (1.3)- β -glucan [Newbigin et al. 1993]. Callose layer stained with the fluorochrome aniline blue fluoresces intensely when illuminated with ultraviolet light. The amount of callose is higher in self-incompatible pollen tubes comparing to self-compatible ones. Especially, there is a large deposit of callose close to the swollen tip of

Table 1. Pollen tube growth in the pistils of apricot cultivars 96 h after self-pollination

| Cultivar | Country of origin | Number of pistils examined | Percentage of pistils with at least 1 pollen tube | | Mean number of pollen tubes | | |
|-----------------------------|--------------------------|----------------------------|---|-------------------|-----------------------------|-------------------|-----------------|
| | | | at the base of the style | reached the ovule | at the base of the style | reached the ovule | |
| | | | | | | | |
| Self-compatible cultivars | Bella d'Imola | Italy | 20 | 100.0 | 70.0 | 7.20 ± 0.51 ef | 1.71 ± 0.30 cde |
| | Bob Cot | USA | 20 | 95.0 | 60.0 | 6.30 ± 0.80 ef | 2.00 ± 0.33 bc |
| | Chudovyi | Ukraine | 18 | 100.0 | 66.7 | 6.00 ± 0.79 efg | 1.00 ± 0.15 fgh |
| | Festivalna | Bulgaria | 20 | 100.0 | 70.0 | 9.55 ± 1.48 cd | 2.14 ± 0.23 b |
| | Harlayne | Canada | 20 | 60.0 | 40.0 | 2.80 ± 0.71 h | 0.45 ± 0.14 i |
| | Harogem | Canada | 18 | 83.3 | 72.2 | 5.23 ± 1.15 fg | 1.29 ± 0.48 ef |
| | Kospotenskiy | Ukraine | 20 | 100.0 | 80.0 | 15.10 ± 1.13 a | 3.00 ± 0.46 a |
| | Luiset | France | 20 | 100.0 | 70.0 | 6.00 ± 1.04 efg | 1.44 ± 0.25 def |
| | Magyar kajszai C 235 | Hungary | 19 | 94.7 | 78.9 | 6.53 ± 0.93 ef | 1.41 ± 0.20 def |
| | Mari de Cenad | Romania | 20 | 100.0 | 50.0 | 7.35 ± 1.12 def | 0.71 ± 0.15 hi |
| | Moldavskiy Krupnoplodnyi | Moldova | 20 | 100.0 | 65.0 | 8.05 ± 0.87 de | 2.00 ± 0.29 bc |
| | Palsteyn (Imperial) | South Africa | 20 | 95.0 | 85.0 | 14.15 ± 1.55 a | 2.89 ± 0.36 a |
| | Peeka | South Africa | 22 | 77.3 | 63.6 | 13.41 ± 2.22 ab | 1.81 ± 0.35 cd |
| | Re Umberto | Romania | 20 | 100.0 | 70.0 | 3.90 ± 0.32 gh | 0.83 ± 0.12 gh |
| | Reale d'Imola | Italy | 20 | 100.0 | 60.0 | 11.30 ± 1.11 bc | 0.67 ± 0.11 hi |
| | Sabbatani | Italy | 20 | 100.0 | 95.0 | 11.60 ± 0.90 bc | 2.32 ± 0.22 b |
| Tomcot (Toyaco) | USA | 20 | 100.0 | 60.0 | 7.35 ± 0.75 def | 1.19 ± 0.20 fg | |
| Self-incompatible cultivars | Agat | Ukraine | 20 | 0.0 | 0.0 | 0.00 ± 0.00 i | 0.00 ± 0.00 j |
| | Amos | Ukraine | 18 | 0.0 | 0.0 | 0.00 ± 0.00 i | 0.00 ± 0.00 j |
| | Aurora | Italy | 20 | 0.0 | 0.0 | 0.00 ± 0.00 i | 0.00 ± 0.00 j |
| | Benmore | New Zealand | 23 | 4.3 | 0.0 | 0.10 ± 0.07 i | 0.00 ± 0.00 j |
| | Dunstan | New Zealand | 19 | 0.0 | 0.0 | 0.00 ± 0.00 i | 0.00 ± 0.00 j |
| | Gabriel | New Zealand | 20 | 5.0 | 0.0 | 0.07 ± 0.06 i | 0.00 ± 0.00 j |
| | Gvardeyskiy | Ukraine | 20 | 0.0 | 0.0 | 0.00 ± 0.00 i | 0.00 ± 0.00 j |
| | Harglow | Canada | 20 | 5.0 | 0.0 | 0.15 ± 0.11 i | 0.00 ± 0.00 j |
| | Hargrand | Canada | 16 | 6.3 | 0.0 | 0.09 ± 0.09 i | 0.00 ± 0.00 j |
| | Harojoy | Canada | 20 | 25.0 | 0.0 | 0.35 ± 0.13 i | 0.00 ± 0.00 j |
| | Harostar | Canada | 20 | 0.0 | 0.0 | 0.00 ± 0.00 i | 0.00 ± 0.00 j |
| | Laycot | Canada | 20 | 0.0 | 0.0 | 0.00 ± 0.00 i | 0.00 ± 0.00 j |
| | Orangered (Bhart) | USA | 16 | 0.0 | 0.0 | 0.00 ± 0.00 i | 0.00 ± 0.00 j |
| | Robada | USA | 20 | 0.0 | 0.0 | 0.00 ± 0.00 i | 0.00 ± 0.00 j |
| | Sundrop | Canada | 23 | 0.0 | 0.0 | 0.00 ± 0.00 i | 0.00 ± 0.00 j |
| | Sun Glo | USA | 20 | 0.0 | 0.0 | 0.00 ± 0.00 i | 0.00 ± 0.00 j |
| | Veecot | Canada | 22 | 0.0 | 0.0 | 0.00 ± 0.00 i | 0.00 ± 0.00 j |
| | Velvaglio | Canada | 20 | 10.0 | 0.0 | 0.10 ± 0.07 i | 0.00 ± 0.00 j |
| Vognik | Ukraine | 20 | 0.0 | 0.0 | 0.00 ± 0.00 i | 0.00 ± 0.00 j | |
| Vulkan | New Zealand | 20 | 15.0 | 0.0 | 0.40 ± 0.24 i | 0.00 ± 0.00 j | |
| Zorkyi | Ukraine | 22 | 0.0 | 0.0 | 0.00 ± 0.00 i | 0.00 ± 0.00 j | |

Note: Mean values followed by different letters within a column represent significant differences at $P \leq 0.05$ according to Duncan's multiple range test

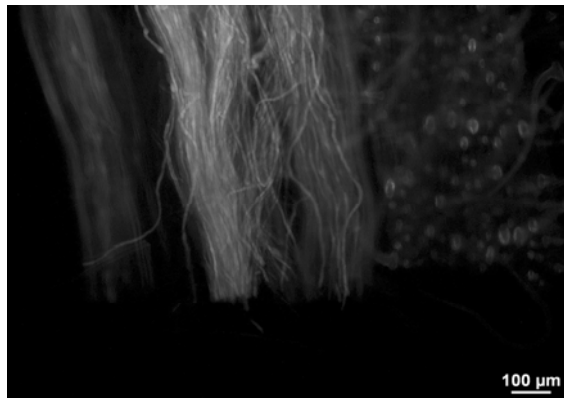


Fig. 1. The base of the style with many pollen tubes in the self-compatible apricot 'Reale d'Imola'

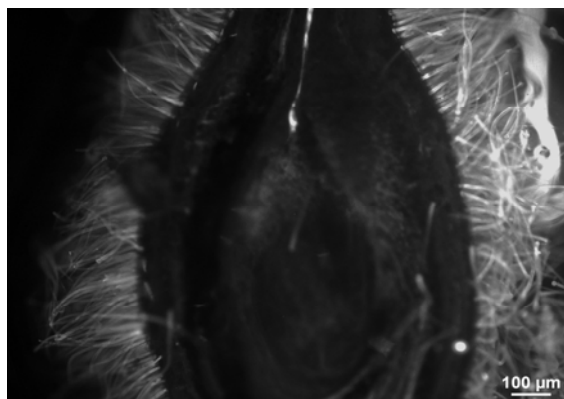


Fig. 2. Pollen tube reaching the ovule in the self-compatible apricot 'Mari de Cenad'

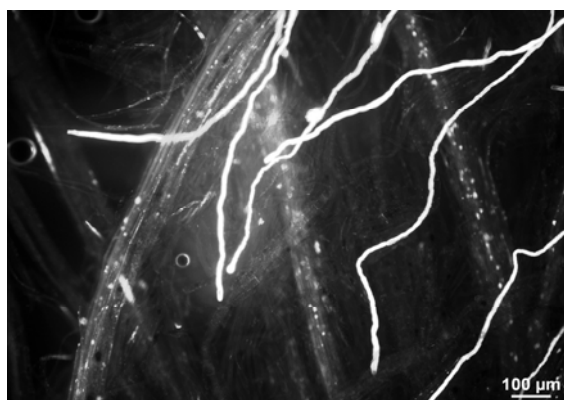


Fig. 3. Incompatible pollen tubes with swellings at the tips in the middle part of the style in the self-incompatible apricot 'Zorkyi'

the incompatible pollen tubes. Martin [1959] described the first appropriate technique for staining pollen tubes in the style. However, this method was not used in apricot until the last decade of the twentieth century [Egea et al. 1991, Egea and Burgos 1996, Burgos et al. 1997, Viti et al. 1997, Andrés and Durán 1998].

Published data on self-compatibility in apricot cultivars have been obtained mostly by studying fruit set after controlled pollination under field conditions [Kostina 1970, Nyújtó et al. 1985, Szabó and Nyéki 1991]. In their extensive study, Burgos et al. [1997] analysed self-compatibility trait of 123 apricot cultivars using both field and laboratory tests, and cultivars 'Harlayne', 'Palsteyn', and 'Tomcot' were reported as self-compatible. 'Magyar kajsz C235' and 'Mari de Cenad' were described as self-compatible based on molecular analysis [Halász et al. 2007]. Cultivars 'Aurora', 'Hargrand', 'Laycot', 'Orangered', 'Sundrop', 'Sun Glo', 'Veecot', and 'Velvaglio' were reported as self-incompatible [Burgos et al. 1997]. Our results support previous conclusions for all these cultivars.

Cultivar 'Robada' was described as self-compatible earlier [Ledbetter and Ramming 1997]. However, in the laboratory test we found that this cultivar is self-incompatible. Our data coincide with those of Drén et al. [2007] and Ghareshkeikbayat et al. [2011].

Data vary on the number of hours required for pollen tubes to reach the ovary. Thus, Egea et al. [1991] reported that pollen tubes reached the ovary in 48 h, while Guerriero and Bartolini [1995] concluded that, under ideal conditions, they reach the ovary in 48 h, but most often in 72 h. However, according to Milatović and Nikolić [2007], 72 h was insufficient for most cultivars, so they extended this period to 120 h. Viti et al. [1997] point out that, in apricot, it takes pollen tubes at least 96 h to reach the ovary. Also, Audergon et al. [1999] obtained better results when fixation of pistils was done 96 h rather than 72 h after pollination. In this study, 96 h proved to be enough time to allow compatible pollen tubes to reach the ovary and ovule.

The site of inhibition of pollen tube growth in apricot differs from that normally associated with gametophytic incompatibility. In GSI system, pollen tubes mainly stop their growth in the upper third of the style. However, in our study in most cases we observed that pollen tubes stopped growing in the lower half of the style. Our results confirm findings reported by Andrés and Durán [1998] that in apricot pollen tubes usually stop their growth in the third quarter of the style length.

The results obtained in this study lead to the conclusion that self-incompatibility is frequent among new apricot cultivars from European breeding programmes. This phenotype was found in 21 cultivars, accounting for 55% of the total number of cultivars analysed. These data outreach the results of Burgos et al. [1997], who found 42 self-incompatible cultivars in 123 cultivars studied (34%), and of Milatović and Nikolić [2007], who found 12 self-incompatible cultivars in 36 cultivars studied (39%).

The increasing number of self-incompatible cultivars in the last years can be explained by using Asian or North American self-incompatible cultivars in breeding programs that aim to create new genotypes with the traits including: *Plum Pox Virus* resistance [Badenes and Llácer 2006, Karayiannis 2006, Krška et al. 2006a], frost tolerance [Benedikova 2006, Krška et al. 2006b], increase of the sugar content [Ledbetter et al. 2006], or extending the harvest time [Pedryc and Kerek 1999, Topor et al. 2010]. Some self-incompatible cultivars are frequently used in apricot breeding programs. Thus, the

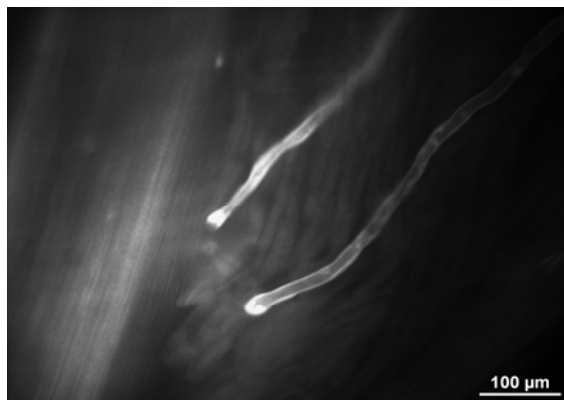


Fig. 4. Two incompatible pollen tubes with swellings at the tips in the lower half of the style in the self-incompatible apricot 'Sundrop'

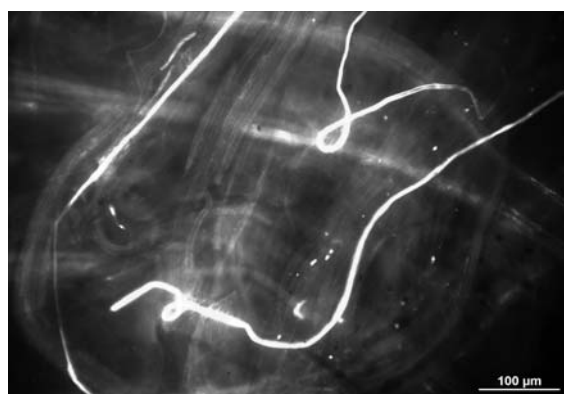


Fig. 5. Twisted pollen tube growth in the middle part of the style in the self-incompatible apricot 'Veecot'



Fig. 6. Bifurcation of the pollen tube in the lower half of the style in the self-incompatible apricot 'Dunstan'

American cultivars 'Perfection' and 'Goldrich', for example, are used in breeding for their large fruits [Layne et al. 1996], and 'Stark Early Orange' and 'Harlayne' for its resistance to *Plum Pox Virus* [Karayiannis et al. 2008]. Use of these cultivars in apricot breeding can lead to the development of new, undesirable, self-incompatible selections.

Self-incompatibility is an undesirable trait in fruit crop production, because self-incompatible cultivars cannot be grown in single-cultivar orchards, and it is necessary to provide additional pollinators. These cultivars often produce a lower yield, as fruit set depends on the abundance of pollen transfer from other trees. Apricot flowering takes place in early spring and often proceeds under unfavorable weather conditions, such as low temperatures, rainfall, and wind. Such conditions limit bees' flight and cross-pollination. Hence, when growing self-incompatible cultivars adequate pollinators should be selected. They need to be cross-compatible, because cross-incompatibility was found between some apricot cultivars [Szabó and Nyéki 1991, Egea and Burgos 1996, Jie et al. 2005, Hajilou et al. 2006, Zhang et al. 2008, Halász et al. 2005, 2010, Milatović et al. 2010].

CONCLUSIONS

1. Fluorescence microscopy provides a relatively rapid and reliable method to determine self-(in)compatible phenotype of apricot cultivars. In self-compatible cultivars, pollen tubes reach the ovary in the majority of pistils, and also often reach the ovule. In self-incompatible cultivars, growth of pollen tubes in the style stopped along with formation of characteristic swellings.

2. Of the examined 38 apricot cultivars 17 are self-compatible and 21 are self-incompatible.

3. Considering that self-incompatibility occurs frequently among new apricot cultivars, care should be taken of cultivar composition in new orchard plantings. Self-compatibility should be one of the most important objectives in apricot breeding programmes, because self-compatible cultivars can ensure more successful pollination, and thereby higher and more regular yield.

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TESTOWANIE (NIE)SAMOPŁONNOŚCI U ODMIAN MORELI PRZY UŻYCIU MIKROSKOPU FLUORESCENCYJNEGO

Streszczenie. Niesamopłonność jest powszechna u odmian moreli (*Prunus armeniaca* L.) w środkowo-azjatyckich i irańsko-kaukaskich grupach eko-geograficznych, natomiast odmiany grupy europejskiej są tradycyjnie uważane za samopłonne. Jednak liczba znanych samopłonnych odmian grupy europejskiej gwałtownie wzrosła podczas ostatnich

dwóch dziesięcioleci. Można to wyjaśnić, używając azjatyckich i północno-amerykańskich samopłonnych odmian w programach hodowlanych, które mają na celu stworzenie nowych genotypów o cechach obejmujących odporność na *Plum Pox Virus*, tolerancję na mróz, wyższą zawartość cukru czy przedłużony okres zbiorów. W niniejszej pracy testowano samo(nie)plonność u 38 odmian moreli. Przy użyciu mikroskopu fluorescencyjnego przeanalizowano wzrost łagiewki pyłkowej na słupkach zapylonych w laboratorium. Odmiany uważano za samopłonne, jeśli przynajmniej jedna łagiewka pyłkowa docierała do zalążni na większości słupków. U odmian niesamopłonnych wzrost łagiewki pyłkowej na szyjce słupka zatrzymał się wraz z wytworzeniem się charakterystycznych zgrubień. Spośród badanych odmian, 17 było samopłonne, natomiast 21 odmian było niesamopłonnych.

Słowa kluczowe: *Prunus armeniaca*, zapylenie, łagiewka pyłkowa, słupek

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