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INTERSPECIFIC HYBRID COMPATIBILITY OF HUAREN APRICOT WITH ALMOND

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Abstract

Interspecific hybridization is an effective method of fruit tree breeding for new varieties. In order to understand interspecific hybridization compatibility, abortive period, and the development of hybrid fruit from crosses between Huaren apricot and almond, we conducted crossing experiments. The growth condition of the pollen tube was observed by fluorescence electron microscopy, and the abortion rate and developmental characteristics of hybrid fruit were analyzed in different stages. The results showed that the pollen of Huaren apricot and almond were able to germinate, and that the pollen tubes can enter into the embryo sac of the other species. After four weeks of cross pollination, the average fruit-setting rate of the interspecific hybrid was 7.06% using Huaren apricot as female parent, which was 24.39% of the intraspecific hybridization rate; mature fruit accounted for 17.54% of the young fruit. When almond was used as the female parent, the average fruit-setting rate of interspecific hybridization was 6.33%, which was 46.10% of the intraspecific hybridization, and the mature fruit accounted for 5.17% of the young fruit. However, the embryos were aborted after the fruit ripened. The fruit of interspecific hybrids with Huaren apricot as the female parent grew slower than that of the intraspecific hybrid. In addition, the fruit was smaller when mature and embryo development was normal in the former as compared with that in the latter. The fruit development after interspecific hybridization using almond as the female parent was consistent with that of the intraspecific hybrids. However, the embryonic development gradually stopped, and malformed and normal embryos could not be formed. There is a high potential for interspecific hybridization between Huaren apricot and almond. Particularly, using Huaren apricot as a female parent, a well-developed embryo can be obtained.

Key words: Interspecific hybridization, Huaren apricot, Almond.

Introduction

The Huaren apricot (*Armeniaca cathayana* D.L. Fu *et al.,*) is a new species of the genus *Armeniaca* Scop. of Rosaceae. The species was found on July 11, 2008 in Zhuolu County，Hebei Province of China by Da-li Fu and mainly distributed in Zhuolu, Yu, and Xuanhua counties of Hebei province (Fu *et al*., 2011; Fu *et al*., 2010; Wang *et al*., 2016). The species appears to be similar to *A. vulgaris* Lam., however, the nuts are large and full, the shell is thin and the kernel rate is high with a sour and lesser flesh suitable for food and food processing industries based on the kernel. Huaren apricot can grow normally in arid and semi-arid areas with soil moisture content of 3–4% (v / v) (Xu *et al*., 2016). It is one of the few forest species in arid and semi-arid areas that is both economically and ecologically beneficial, and has a higher development prospects in northeast, northwest, and north China. At present, Huaren apricot mainly exists in the form of cultivated types and breeds developed by peasants. Long-term artificial selection and cultivation with the same goals has led to a similar genetic backgrounds, and the potential for intraspecific genetic improvement has become limited (Zhang *et al*., 2018; Liu *et al*., 2015). Therefore, it is an important method of improving the quality of Huaren apricot further by introducing the excellent genetic resources of the related species by means of distant hybridization.

Almond (*Prunus dulcis*) is the world famous dried fruit tree species widely planted in the United States, Central Asia and Europe. In China, almonds are mainly distributed in Shache and Yingjisha of Kashgar region, Xinjiang Autonomous Region. According to the statistics provided by Food and Agricultural Organization (FAO) of the United Nations (UN), the annual output of almond in the world in 2014 was 2.7 million tons, of which the annual output of harvested areas in China was 44,000 tons (http://www.fao.org/faostat/en/#data/ QC). Because almond has larger seed kernels and thinner shell, it has a higher market value, and the market price is 3–4 times of that of the Huaren apricot (International Nut and Dried Fruit Council, 2016; Yada *et al*., 2011). However, due to the effect of climatic factors, almonds are not suitable for planting in most parts of China and show low fruit-setting rate and serious gums in the tree, which severely affects the industry of almond. Because both Huaren apricot and almond are used for seed kernels, crossbreeding these two species might be a good approach for combining the characteristics of large seed kernel of almond with the wide adaptability of Huaren apricot into same variety with higher quality and adaptability.

Interspecific breeding of fruit trees has been considered an important means for a long time (Yamamoto *et al*., 2002; Khalid *et al*., 2010; Mehar *et al*., 2011; Wang *et al*., 2017), particularly in case of different species of Prunus; e.g., apricot and plum, apricot and mume, and plum and cherry, and some unique germplasm types have been obtained (Gomez *et al*., 1993; Foolad *et al*., 1995; Bliss *et al*., 2002; Shang *et al*., 2009; Ji *et al*., 2007). Some of these have become popular in the market, such as plumcot (Haejin *et al*., 2014). However, interspecific hybridization is more difficult than intraspecific hybridization (Vikas *et al*., 2017; Jason *et al*., 2017; Li *et al*., 2014; Tonosaki *et al*., 2013), and different degrees of incompatibility occur, such as the incompatibility between pollen and stigma, the inability of pollen tube to germinate on heterospecific stigma, inability of the germinated pollen tubes to complete fertilization, or fruit abnormalities after fertilization At present, there are few studies on crossbreeding between Huaren apricot and almond. In the process of hybrid fruit development, knowing about the occurrence of abortion and the development of the hybrid fruit is not sufficient (Cai *et al*., 2008).

Therefore, in order to explore the mechanism of incompatibility during the crossbreeding of Huaren apricot with almond and providing the theoretical basis for further work on genetic improvement, crossing experiments were carried out using Huaren apricot and almond as parent. Our aim was to understand 1) the difficulty of hybridization between Huaren apricot and almond, 2) the main period and degree of abortion of Huaren apricot and almond; 3) the developmental characteristics of the hybrid fruit of Huaren apricot and almond.

Material and Methods

Plant materials: The experiment was carried out from 2015 to 2016 in Luoyang and Yuan yang, Henan province from March 8–25, in the Collection of Apricot Genetic Resources of Luoyang Academy of Agriculture, and the Collection of Almond Genetic Resource of the Non-timber Forestry Research and Development Center, Chinese Academy of Forestry. The experimental materials included the following almond clones: Italian No. 1 (B1), Italian No. 2 (B2), Italian No. 3 (B3) and the variety of 'Shuang ruan' (B4), Huaren apricot varieties Zhongren 1 (A1), and Bai Yu Bian (A2), and clones 11D05 (A3), and 108 (A4).

Methods

Cross-pollination

Pollen collection: Huaren apricot and almond anther were collected and placed in vegetable parchment at 20–25°C until anthers released pollen. The pollen was collected in a centrifuge tube, silica gel was added to it, and placed in a refrigerator at 4°C until further use.

Pollination: Sepals, petals, and stamens were removed by hand or with tweezers. Thereafter, the stigma was smeared with a latex stick covered with pollen. After pollination, the number of pollinated flowers were counted and tagged.

Fruit-setting rate survey and statistics: The fruit setting rate statistics were divided into two. Flowers without pollination usually fall off naturally within four weeks. Therefore, data on fruit-setting rate became available at the beginning of the fifth week. The second data set was that of fruit maturity.

Fluorescence microscopic observation of fertilization process: Styles and ovaries were sampled and fixed in the FAA fixative solution for more than 24 h with five flowers per treatment, after 2, 4, 6, and 8 h, and daily morning and evening after pollination. Before the observation, the styles and ovaries were rinsed in distilled water and then placed in a 4 mol/L NaOH solution in 50ºC to soften for 3 h, and rinsed with distilled water and transferred to a 0.1% aniline blue staining solution for 12 h, After washing with distilled water, the styles and ovaries were tablets and observed with a fluorescence microscope.

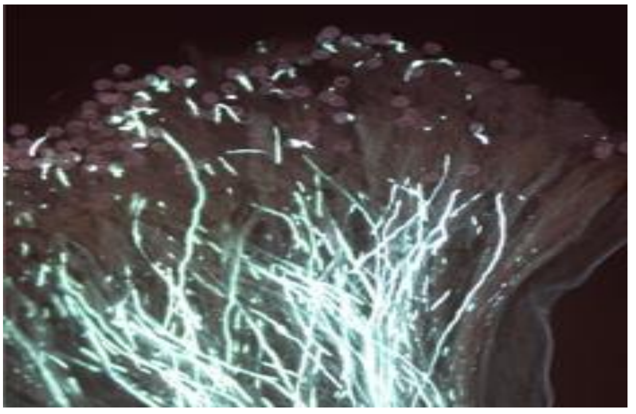
Investigation on fruit development: The size of the hybrid fruit was measured after every 5–10 d from the 5th week after pollination.

Results

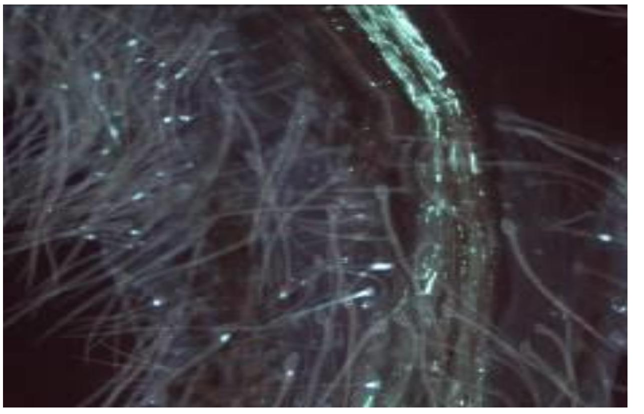
Fluorescence observation of pollen tube growth: Fluorescence microscopic observation showed that the pollen of Huaren apricot and almond could germinate and grow on each other's stigma. In the crossing combination Huaren apricot (♀) × almond (♂), the pollen tube began to germinate 8 h after pollination. The pollen tube reached half of the style on the third day after pollination and reached close to the embryo sac on the sixth day after pollination (Fig. 1). In combination of almond (♀) × Huaren apricot (♂), the pollen tube began to germinate from 6 h after pollination. The pollen tube reached half of the style on the third day after pollination and reached close to the embryo sac on the fifth day after pollination (Fig. 2). However, uneven growth of pollen tubes was visible (Fig. 3). From the overall growth of the pollen tube, it was evident that although the development of the pollen tube after hybridization will encounter some obstacles, it might still reach the embryo sac.

Fruit-setting rate in fertilization stage: The fifth week after pollination, the fruit-setting rate of each pollination combination was calculated. The average fruit-setting rate of each cross was 7.06% using Huaren apricot as the female parent, as compared with the intraspecific hybridization rate of 28.95%, the fruit-setting rate was relatively low, accounting for 24.39% of the fruit-setting rate in the intraspecific hybridizations (Table 1, Fig. 4). The average fruit-setting rate of each cross was 6.33% with almond as female parent, as compared with the intraspecific hybridization rate of 13.73%, fruit-setting rate of interspecific hybridization was relatively low, accounting for 46.10% of the fruit-setting rate in intraspecific hybridization (Table 2, Fig. 5). This indicates that the abortions caused by the distant parents in fertilization are significant.

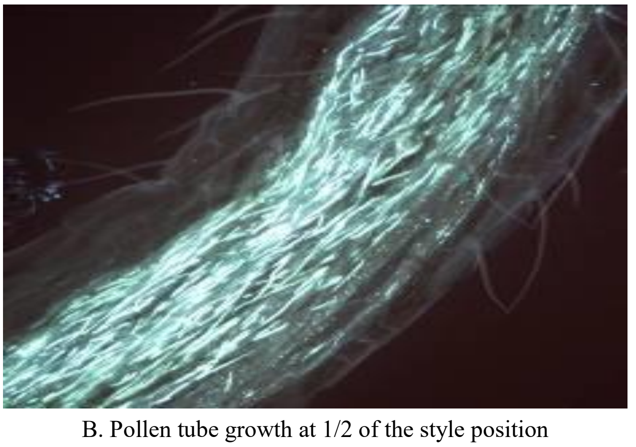
Statistics of fruit number in the ripening stage: After maturation, the number of fruits of each hybrid combination was counted. The results showed that the probability of normal embryo development with Huaren apricot as the female parent were significantly higher than that with almond as female parents. In the development process, interspecific hybridization fruit continued to abortion; 12 hybrids using almonds as the female parent eventually grew to maturity; accounting for5.17% of the proportion of young fruit, but the embryos stopped growing or deformities occurred during development (Fig. 6). Ten hybrids fruits grew to maturity with Huaren apricot as the female parent, accounting for 17.54% of the number of young fruits. The hybrid fruits obtained from crosses using almond as the female parent was significantly smaller, than those obtained from crosses using Huaren apricot as female parent, and the embryo developed normally and the kernel was full in the latter (Fig. 7).



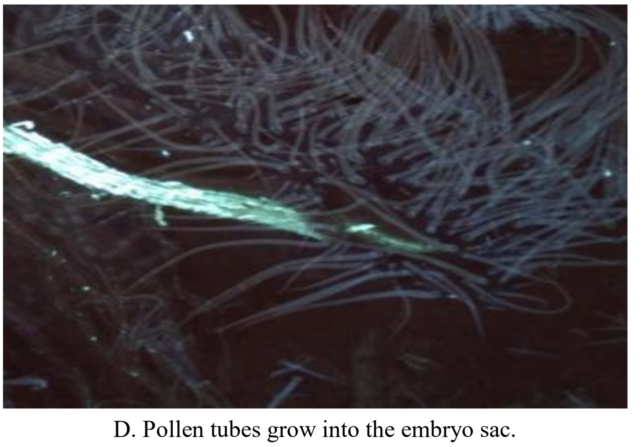
A. Pollen germination and growth in stigma



C. Pollen tube growth at 3/4 of the style position

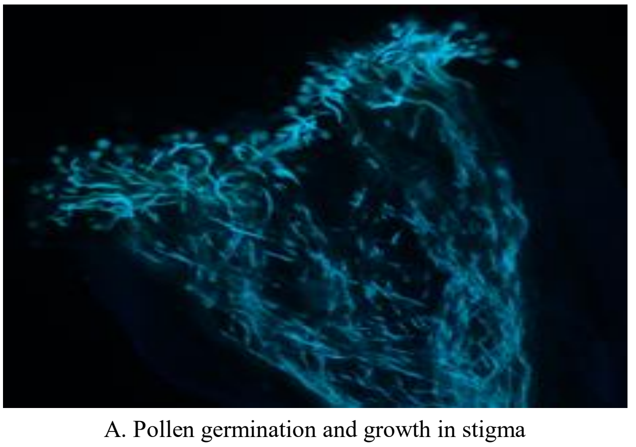


B. Pollen tube growth at 1/2 of the style position

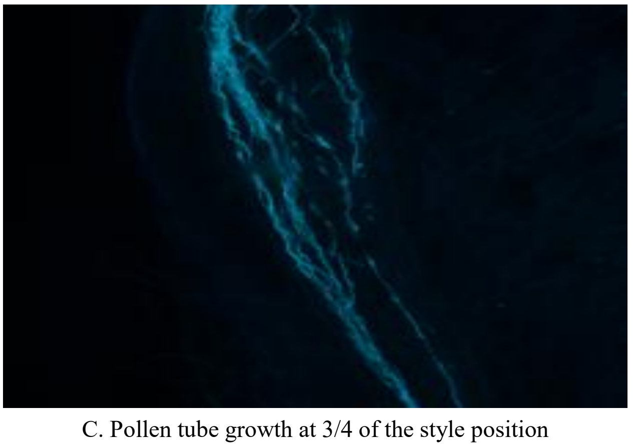


D. Pollen tubes grow into the embryo sac.

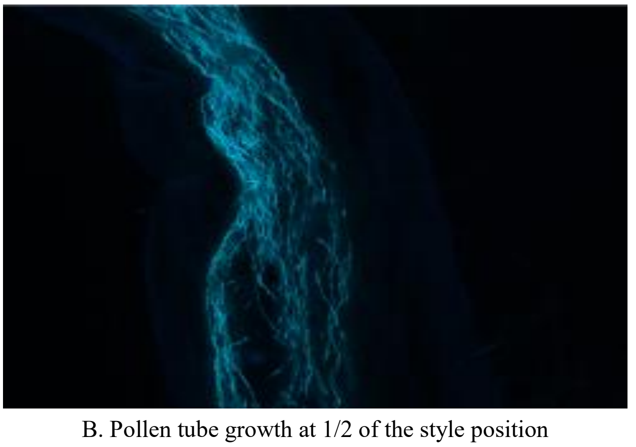
Fig. 1. Growth status of the pollen tubes in the Huaren apricot (A3) (♀) × almond (B4) (♂) cross on the sixth day after pollination.



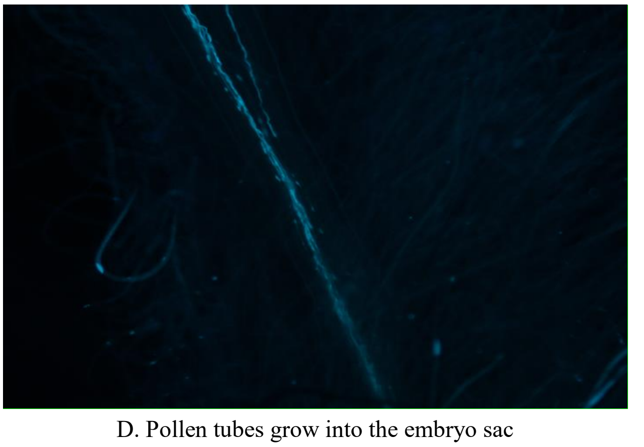
A. Pollen germination and growth in stigma



C. Pollen tube growth at 3/4 of the style position



B. Pollen tube growth at 1/2 of the style position



D. Pollen tubes grow into the embryo sac

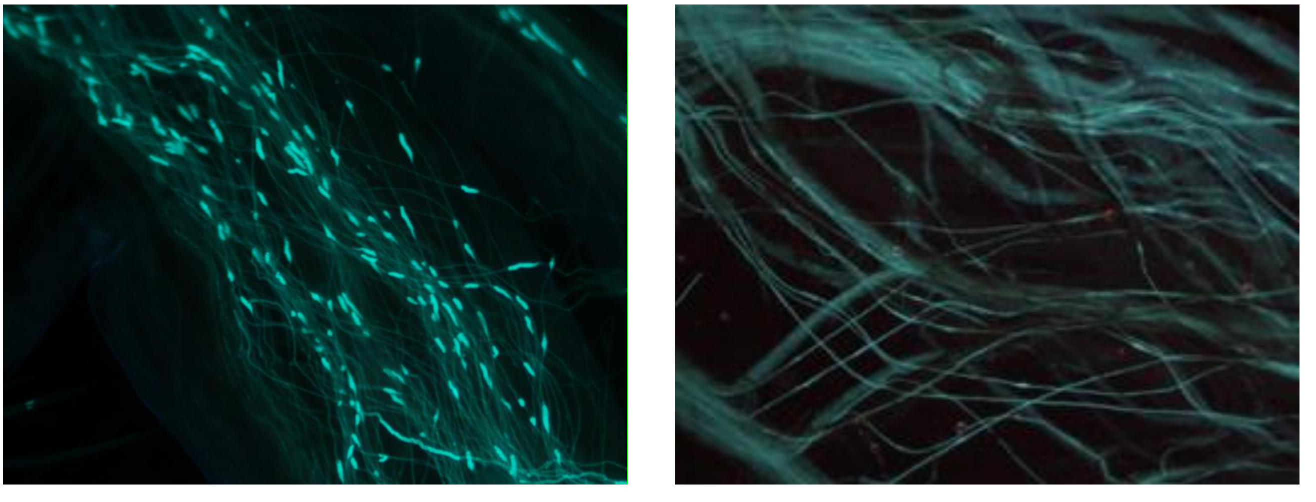
Fig. 2. Growth status of the pollen tubes in the almond (B1) (♀) × Huaren apricot (A4) (♂) on the fifth day after pollination.

Table 1. Fruit-setting rate in Huaren apricot (♀) × almond (♂).

Female parent	Male parent	Pollination number	Number of fruits	Fruit-setting rate (%)
A1	B4	252	14	5.56
	A2	171	48	28.07
A3	B4	327	15	4.59
	A2	261	63	24.14
A4	B4	228	28	12.28
	A2	245	85	34.69

Table 2. Fruit-setting rates in almond (♀) × Huaren apricot (♂).

Female parent	Male parent	Pollination number	Number of fruits	Fruit-setting rate (%)
B1	A1	264	9	3.41
	A2	349	23	6.59
	A3	329	20	6.08
	A4	390	30	7.69
	B4	357	42	11.76
B2	A1	374	17	4.55
	A2	216	9	4.17
	A3	288	15	5.21
	A4	305	20	6.56
	B4	201	26	12.93
B3	A1	266	24	9.02
	A2	345	25	7.25
	A3	267	18	6.74
	A4	272	22	8.09
	B4	294	49	16.67



A. Pollen tube growth unevenness in interspecific hybridization

B. Pollen tube grows normally

Fig. 3. The phenomenon of uneven pollen tube growth.

Growth and development of hybrid fruits: The developmental period of interspecific hybrid fruit was approximately 90 d when Huaren apricot was used as the female parent, which is consistent with the developmental period of intraspecific hybrids, but the fruit size changes (Figs. 8 and 9). The average fruit length and fruit width of interspecific hybrids were 2.9 and 2.3 cm, respectively, which were significantly smaller than those of normal fruits (3.8 and 3.3 cm, respectively; Fig. 7). Fruit development cycle and fruit size after interspecific hybridization were similar to those of the intraspecific hybrids using almonds as the female parent.

Discussions

Degree of compatibility before fertilization of Huaren apricot and almond: The mechanism of reproductive isolation between species is an important mechanism of maintaining the stability of a species. However, several studies show that this isolation mechanism is not perfect, and interspecies genetic introgression and gene exchange occur frequently, which can provide new ideas for germplasm innovation (Zhang *et al*., 2018; Zhao *et al*., 2016; Záveská *et al*., 2016; Yuri *et al*., 2013; Gerber *et al*., 2001; Xavier *et al*., 2016).

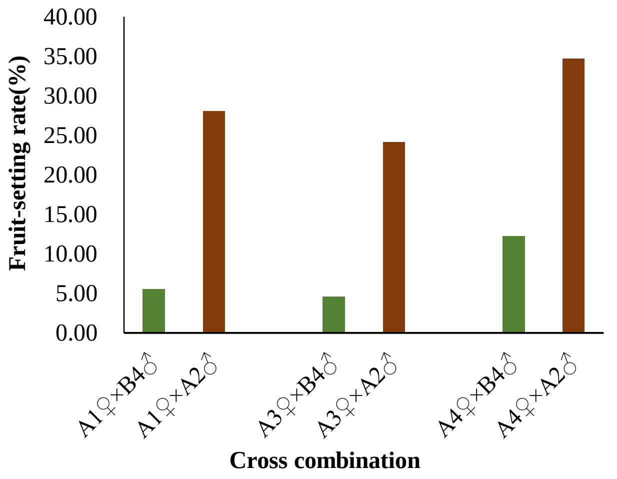


Fig. 4. Fruit-setting rate in different hybrid combinations of Huaren apricot (♀) × almond (♂).

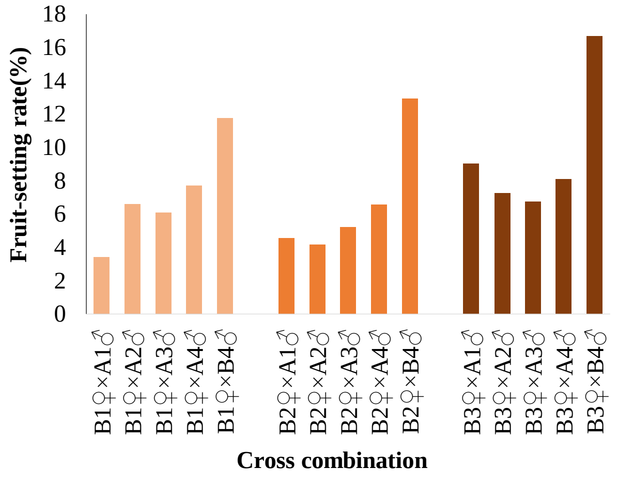
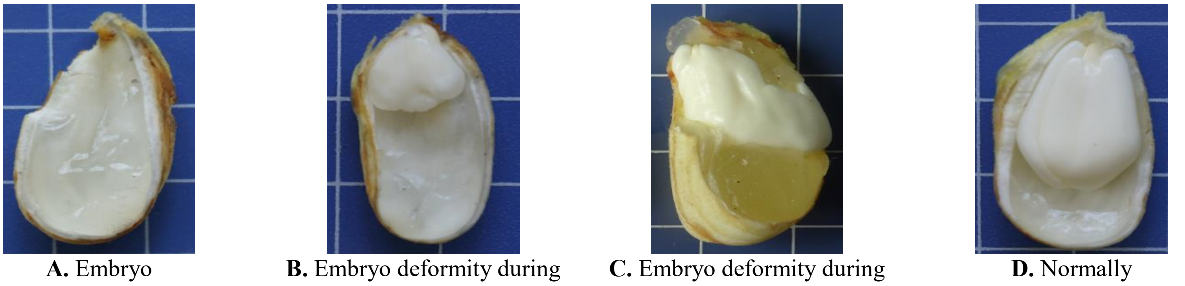
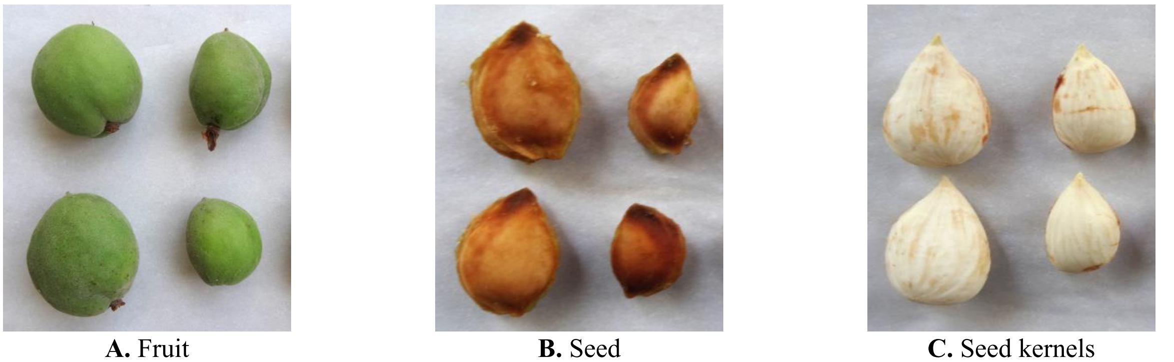


Fig. 5. Almond (♀) × Huaren apricot (♂), fruit setting rate in different hybrid combinations.



A. Embryo development stops **B.** Embryo deformity during development **C.** Embryo deformity during development **D.** Normally developing embryo

Fig. 6. Normal and abnormal embryo development in almond (♀) × Huaren apricot (♂).



A. Fruit **B.** Seed **C.** Seed kernels

Fig. 7. Comparison of fruits between interspecific and intraspecific hybrids. The column on the left shows intraspecific hybrid fruits and the column on the right shows interspecific hybrid fruits

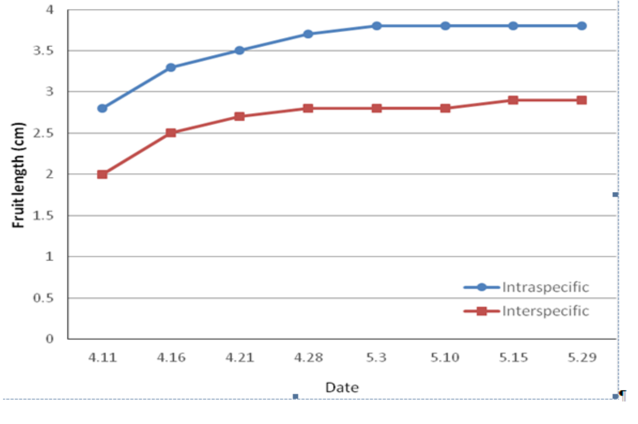


Fig. 8. Increase in fruit length with time in Huaren apricot (♀) × almond (♂).

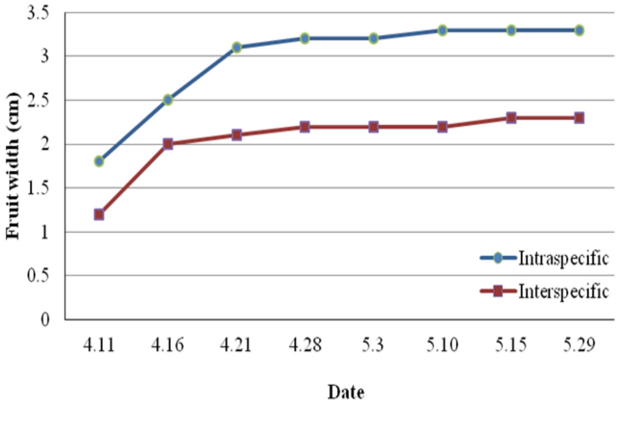


Fig. 9. Increase in fruit width with time in Huaren apricot (♀) × almond (♂).

Interspecies hybrid incompatibility can generally occur at two stages, pre-fertilization or post-fertilization (Stebbins *et al*., 1958; Wilhelmi *et al*., 1997). Incompatibility mechanism studies show that stigma has the ability to precipitate callose after pollination and reject incompatible pollen. The strength of this reaction is positively correlated with the degree of incompatibility (Van *et al*., 1997). In addition, some studies have shown that incompatibility occurs between pollen tube and style guide tissue, which leads to abnormal growth of the pollen tube due to lack of nutrition (Vervaeke *et al*., 2001). Moreover, it has been shown that the compatibility is related to the activity of protective enzymes, such as SOD, POD, CAT, and hormone content (Li *et al*., 2009; Ram *et al*., 2008). We observed that the germination of pollen tube between Huaren apricot and almond was normal during pollination, which indicated that pollen and stigma identification process was normal, and that no reproductive isolation phenomenon occured. The pollen tubes were not obstructed by callose during their growth. Uneven pollen tube growth is presumed to be affected by some incompatibility factors. However, this phenomenon did not prevent pollen tube growth, and pollen tubes could reach the embryo sac for fertilization. Fluorescence microscopy revealed that pollen tube growth of Huaren apricot and almond before fertilization is affected to some extent, but the pollen tubes can still reach the embryo sac.

Degree of compatibility during fertilization of Huaren apricot and almond: After the fertilization stage, the fruit-setting rate of the hybrid fruits did not reach 50% of the normal ratio, regardless of whether the Huaren apricot or almond was used as the female parent. This shows that during the fertilization phase, significant incompatibility occurred. This is consistent with the reports on other interspecific hybrids (Li *et al*., 2003; Wang *et al*., 2012; Zhao *et al*., 2016). This might occur because the sperm cannot fertilize the egg cells within time, thereby resulting in delayed fertilization or fertilization failure, and egg and fertilized polar nucleus cannot be fertilized simultaneously or zygotes do not split.

Degree of compatibility of Huaren apricot and almond after fertilization: Incompatibility after fertilization mainly occurs due to endosperm dysplasia or abnormal embryo development. Some studies have shown that the main reason for this phenomenon is that when endosperm degradation cannot provide enough nutrients, embryos stop developing due to lack of nutrition (Johnston *et al*., 1982; Friedman *et al*., 1998). Others argue that abortion is caused by inconsistent progression of embryos and endosperm during development (Tanaka *et al*., 1972). In the post-fertilization stage of embryo development, the reciprocal crosses between Huaren apricot and almond showed a great difference. Although the abortion phenomenon could occur continuously during the fruit developmental stages using Huaren apricot as the female parent, the final hybrid embryos could show normal growth and development. However, using almond as the female parent, the hybrid fruit embryos were completely aborted during the growth process. This phenomenon may be caused by the inconsistent process of embryo and endosperm development. Therefore, it is suggested that using Huaren apricot as female parent or embryo culture before abortion can lead to better results (Young *et al*., 2014; Shao *et al*., 2015; Saha *et al*., 2015).

Development of hybrid fruits of Huaren apricot and almond: The development of fruit is greatly affected by the parents. When Huaren apricot was used as the female parent, the interspecific hybrid fruit was smaller than that of the fruit obtained by intraspecific hybridization. When the almond was used as the female parent, the embryo developed abnormally, but the size of the hybrid fruit was the same as that of the intraspecific hybrid. The reason for this phenomenon might be related to the amount of growth hormone secreted by the embryos after fertilization.

Conclusions

The observation and statistics of the different developmental stages after the cross of Huaren apricot and almond showed that Huaren apricot and almond have high potential for distant hybridization. Particularly when the Huaren apricot is used as the female parent, a well-developed embryo can be obtained. Interspecific hybrid abortion mainly occurs in the fertilization and embryo development stages. This research provides the theoretical basis for understanding the compatibility of interspecific hybridization, the main stage and extent of abortion, and the developmental characteristics of hybrid fruit.

Acknowledgments

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