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RECIPROCAL CROSS-COMPATIBILITY IN CUT ROSE BREEDING

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ABSTRACT

Rose breeding companies have developed new rose varieties in response to increasing demands for color, fragrance and shapes. Hybridization is one of the most important methods of creating new rose variations. Breeders focus on fertility, reproduction, and a high number of seeds per fruit. In the present study, four *Rosa* genotypes ('Jumilia', 'Black Magic', 'Tineke', 'Black Baccara') were crossed to assess genetic compatibility, seed formation potential and germination rate. The results showed that all genotypes were tetraploid, and pollen germination varied from 11.36% to 23.41%. The highest crossability rate (94.44%) was found in the 'Black Baccara' × 'Jumilia' combination, followed by 'Black Magic' × 'Jumilia' (60%). The highest seed yields were obtained in 'Jumilia' × 'Tineke' (60.50). 'Tineke' × 'Jumilia' (43.74) showed the second highest number of seeds per fruit, whereas limited success was determined in cross 'Jumilia' × 'Black Magic (2.25). The maximum germination percentage was found in 'Jumilia' when crossed with 'Tineke'. Significant variations were recorded for the weight of hips and weight of fruit. The PCA-biplot results indicated a positive correlation between crossability rate and seed production efficiency. Overall, the choice of parents was crucial for the crossability indices, which are the average crossability rate and seed production efficiency.

Key words: ACR (average crossability rate), compatibility, cut rose, hybridization, rose breeding

INTRODUCTION

Roses date back about 5,000 years in civilization, as shown in the history of cultivation. A wide variety of roses are grown for cut flowers, pot flowers, garden or landscape plants, perfumery, food, and medical purposes [Lawrence 1997, Liu et al. 2015, Dogan et al. 2020]. Rose breeding primarily involves cut flowers, as approximately 10 billion cut rose stems are sold annually worldwide [AIPH and Union Fleurs 2018]. However, sales of potted roses and garden or landscape roses are approximately 300 million per year. Cut roses are still the leader in rose production. Roses are known as the first non-edible species used in plant breeding with crossbreeding [Gudin 2001]. The hybrid tea rose genotype '1985' was selected as the seed parent, and genotype '1848' was selected as the pollen donor [Pipino et al. 2011]. Therefore, hybridization is the most widely used breeding method in cut flowers to obtain a new rose variety these days. The ability to produce new rose varieties is mandatory for growers to maintain and develop their market share.



The taxonomic variation in the Rosa species offers an opportunity for success in the transition [De Vries and Dubois 1996]. As with all ornamental plants, aesthetic value is at the center of attention in cut rose cultivation. The breeders desire several further characteristics, such as yield, flower colors, stem quality, tough petals, double flowers, flower opening shape, the size of the flowers, vase life, fragrance and durability. The most fertile progenitors, such as seed or/and pollen donors, are preferred in gene pools because roses are known for their difficult sexual reproduction, from pollination to seed set. Problems with germination and genetic barriers are obstacles to frequently gaining interspecific hybrids [Perez and Moore 1985, Gudin 1992, Abdolmohammadi et al. 2014, Dogan et al. 2020]. Rose breeders demand to increase the efficiency of breeding programs by producing more offspring, where hybrid genotypes producing high seed yield can be evaluated based on different characteristics. F1 hybrids are selected for commercialization by breeders, and the decision regarding which parent will serve as the male or female line influences the distribution of progeny phenotypes in plants [Oh et al. 2005, Nadeem et al. 2014]. Estimating how male or female phenotypes will manifest in the progeny is difficult. For this reason, reciprocal hybridization provides information about the heritability of phenotypes.

The present study was designed to select hybrids that show relatively good performance, offer a good seed set and gain more insight into the inheritance of traits. Therefore, the purpose of this study was to determine the crossability indices in cut rose breeding between popular hybrid rose varieties.

MATERIAL AND METHODS

Plant material

The plant materials used for this study consisted of four hybrid tea roses 'Jumilia', 'Black Magic', 'Tineke', and 'Black Baccara' (Table 1). The study was conducted in the research area of the rose breeding greenhouse, Department of Horticulture, Faculty of Agriculture, Ankara University, Ankara, Türkiye (39°57'40.2" N 32°51'51.7" E), from 1 May 2021 to March 2022.

Ploidy levels of plant materials

The ploidy levels of all cultivars under study were determined using flow cytometry and confirmed thro-

ugh chromosome counting. Initially, the core DNA contents of the plants were analyzed, followed by chromosome counting in one of the plants exhibiting a distinct DNA content. The ploidy level was then correlated with the DNA content and chromosome number [Tuna 2016].

Pollen viability and germination

Anthers of pollen donors were collected after the removal of petals in one-third to one-half open stages and stored in glass Petri dishes in an incubator at temperatures above 24 °C and with humidity equal to 60%. The pollen viability was measured using the IKI (Iodine + Potassium Iodide) test described by Eti [1991]. The IKI solution was prepared by dissolving 1 g potassium iodide and 0.5 g iodine in 100 mL water for dyeing. A drop of the solution was placed on microscope slides, and pollen grains were then sprinkled on the stain with a brush [Abejide et al. 2013]. The viability of the pollen was examined under a light microscope (×100) after 5 minutes of incubation. Pollen grains were classified as viable or non-viable based on pollen color. Brown or black grains were viable, light red or orange ones were semi-viable and yellow ones were recorded as non-viable. A medium containing 20% sucrose and 10 ppm boric acid with 1% agar was prepared for the germination of fresh pollen in Petri dishes, and the pollen was splashed uniformly on the medium with a brush. After an eight-hour incubation period (24 °C and 60-65% humidity), pollen germination was counted when a pollen tube reached a length of at least 1.5 times the pollen diameter under the light microscope (×100) [Leus 2005, Nadeem et al. 2013, Kazaz et al. 2020]. The counting was conducted in four replicates in five randomized fields, and approximately 200 pollens were counted in each area.

Hybridization

Pollination was carried out by applying pollen onto the pistil of the female parents in the early morning by brush. Pollens were collected the day before and left for 24 h (24 °C and 60–65% humidity) for dusting in a dry place, and female parents were prepared by emasculation to prevent self-pollination [Roberts 2003]. The following day, pollinations were properly performed and labelled because it is believed that a 24-hour period is needed to induce the production of exudates in the stigmas necessary for pollen germination [Jacob and Ferrero 2003]. Reciprocal hybridizations

Varieties	Fragrance	Color	Blooming	Number of petals	Number of pistil per flower	Number of anther per flower
'Jumilia'	no	bicolor	repeat	30–40	120-150	90-120
'Black Magic'	no	black	repeat	30–40	100-135	130–150
'Tineke'	no	white	repeat	80–100	230-250	230-250
'Black Baccara'	no	black	repeat	35–50	130–220	70–90

Table 1. Quantitative characteristics of plant materials

were performed from 1 May to 15 June 2021. At least 30 hybridizations were obtained for each of the six combinations. The fruit set started after eight weeks of pollination, and mature fruits were harvested from the end of October until the beginning of December. An electric balance was used to measure the fresh weight of the fruit. Afterwards, seeds were extracted from the fruits, and the number of seeds per fruit, the total number of seeds and the weight of seeds were counted. Seeds were kept in bags and stored at a moderate moisture level at 4 °C for about 12 weeks in the peat. Following this, seeds were sown in mixed ingredients (cocopeat and peat 1:1), and germinated seeds were counted and recorded.

Moreover, the data on the number of flowers crossed, fruit set and seed set were used to calculate the ACR (Average Crossability Rate) and SPE (Seed Production Efficiency), which are cross-compatibility indices. The cross-compatibility rate of a cross was calculated using the following formula:

Crossability rate (%) =
$$\frac{\text{Number of fruits set}}{\text{Number of flowers pollinated}} \times 100$$

ACR for a parent was calculated as the sum of cross-compatibility rates in specific crosses divided by the number of cross-combinations involving that particular parent:

$$ACR = \sum \frac{Crossability rates}{Number of cross combinations}$$

The SPE for a cross was calculated as the number of viable seeds divided by the number of stigmas of the seed parents in that cross-combination (the expected number of seeds in a rose fruit is equal to the number of stigmas), and the number of pollinated flowers multiplied by 100:

 $SPE = \frac{Number of viable seeds set}{Number of flowers pollinated x number of stigma} \times 100$

The sorted F₁ hybrid seeds were subjected to cold moist stratification at 4 ± 1 °C for 100 days to eliminate the germination barrier [Gudin et al. 1990, Debener and Mattiesch 1995]. Perlite was used for the stratification medium, and seeds were treated with a fungicide with 25% tebuconazole as an active ingredient against fungal diseases. After cold moist stratification, the seeds were sown in vials containing peat and germinated in a plastic-covered greenhouse maintained at a temperature range of 18-21 °C to ensure optimal conditions for germination. The seeds were irrigated by the fogging method during the germination process. The operation of the fogging system, which maintains the greenhouse humidity level between 60-80% [Jones 2004, Kazaz et al. 2010] to accelerate seed germination, was adjusted based on internal humidity levels monitored by sensors using a stop-and-start mechanism. The germinated seeds (with the distinct formation of cotyledon leaves and the emergence of the shoot above the soil surface) were counted, and the seed germination rate (%) was determined by the following formula:

Seed germination rate (%) =
$$\frac{\text{Number of seeds germinated}}{\text{Number of seeds sown}} \times 100$$

RESULTS

Ploidy levels

Ploidy levels were determined by analyzing the core DNA contents of genotypes and were found to

Varieties	DNA (pg/2C)	Ploidy level
'Jumilia'	2.33	tetraploid
'Black Magic'	2.42	tetraploid
'Tineke'	2.36	tetraploid
'Black Baccara'	2.34	tetraploid

 Table 2. Ploidy level of rose varieties

Table 3. Pollen viability and germination of rose genotypes

varieties Polien vlability (%) Polien germination (%)	
'Jumilia' 43.28 b 21.60 a	
'Black Magic' 47.25 a 11.36 b	
'Tineke' 33.29 c 20.50 a	
'Black Baccara' 48.76 a 23.41 a	

Statistically significant differences at $P \le 0.05$

vary between 2.33 pg/2C and 2.42 pg/2C. All genotypes were identified as tetraploid (2n = 4x) with 2n = 28 chromosomes (Table 2).

Pollen viability and germination

The viability rate varied between 33.29% and 48.76%. Significant statistical differences ($P \le 0.05$) were observed between varieties in pollen viability and pollen germination rates. The viability rate of 'Black Baccara' was the highest and reached 48.76%, followed by 47.25% in 'Black Magic' and 39.28% in 'Jumilia', respectively (Table 3). The lowest percentage of pollen viability was detected in 'Tineke' with a value of 33.29%. The percentage of pollen germination rate was measured in 'Tineke' (25.79%), while the minimum value in 'Black Magic' (11.36%) (Table 3).

Crossability rate, seed set, and seed germination

Significant statistical differences ($P \le 0.05$) were observed between crossability rate, number of seeds per fruit, germination of seed and seed production efficiency. As a male parent, 'Jumilia' excelled in the percentage of crossability rate (94.44%) when crossed with 'Black Baccara' followed by 'Black Magic' (seed parent) (60.0%) However, as a seed parent, 'Jumilia' showed limited success, achieving a crossability rate of only 14.44% when crossed with 'Tineke' and 20% with 'Black Magic'. As a female, 'Jumilia' showed a good number of seeds per fruit (60.50 seeds) when crossed with 'Tineke', while 'Tineke' × 'Jumilia' (43.74 seeds) showed the second highest value for a number of seeds per fruit, whereas a limited success was found in the cross 'Jumilia' × 'Black Magic' (2.25 seeds). The maximum average fruit weight was found in 'Jumilia' when crossed with 'Tineke' (13.66 g), although the minimum value was observed in 'Jumilia' when crossed with 'Black Magic' (4.08 g). 'Jumilia' also excelled in the average weight of seed when crossed with 'Black Magic' (14.85 mg), although the lowest value was recorded for 'Black Baccara' when crossed with 'Jumilia' (0.31 mg) (Table 4). As a female parent, 'Black Baccara' showed the highest germination percentage. The germination percentage of 'Black Baccara' as a male parent of 'Jumilia' reached 41.27%, followed by 'Jumilia' × 'Black Baccara' combination at 37.86%. However, the lowest value was recorded for 'Jumilia' when crossed with 'Tineke' (11.27%). As a female parent, 'Black Baccara' excelled in seed production efficiency (5.05%) when crossed with 'Jumilia' followed by 'Tineke' \times 'Jumilia' (1.56%), although as a seed parent 'Jumilia' when crossed with 'Black Magic' showed limited success in the percentage of seed production efficiency (0.073%) (Table 4).

Doğan Meral, E., Kiliç, T., Kirbay, E., Kazaz, S., Gözen, V. (2025). Reciprocal cross-compatibility in cut rose breeding. Acta Sci. Pol. Hortorum Cultus, 24(1), 51–60. https://doi.org/10.24326/asphc.2025.5390

Cross combination	Crossability rate (%)	Seed number per fruit	Average fruit weight (g)	Average seed weight (mg)	Seed germination rate (%)	SPE (%)
'Jumilia' × 'Black Magic'	20.00 cd	2.25 d	4.08 c	14.85 a	20.63 ab	0.073 c
'Black Magic' × 'Jumilia'	60.00 b	6.88 d	5.07 c	1.57 b	31.53 ab	1.02 bc
'Jumilia' × 'Tineke'	14.44 d	60.50 a	13.66 a	0.71 b	11.27 b	0.74 bc
'Tineke' × 'Jumilia'	45.60 bc	43.74 b	13.46 a	0.34 b	22.66 ab	1.56 b
'Jumilia' × 'Black Baccara'	23.68 cd	12.37 cd	7.70 b	2.20 b	37.86 a	0.79 bc
'Black Baccara' × 'Jumilia'	94.44 a	22.94 c	12.85 a	0.31 b	41.27 a	5.05 a

Table 4. Crossability rate, number of seeds per fruit, germination and seed production efficiency from reciprocal crosses in some cut roses

 $P \le 0.05$, SPE: seed production efficiency

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Table 5. Interspecific cross-compatibility indices among Rosa hybrida cultivar

Varieties	ACR (%)
'Tineke'	30.00 c
'Jumilia'	42.77 b
'Black Magic'	50.00 ab
'Black Baccara'	58.33 a

 $P \le 0.05$, ACR: average cross-compatibility/crossability rate



BM - 'Black Magic', J - 'Jumilia', BB - 'Black Baccara', T - 'Tineke'

Fig. 1. Principal component analysis

Cross-compatibility indices

Significant statistical differences ($P \le 0.05$) were observed between average cross-compatibility rates. The average crossability rate (ACR) is presented in Table 5. The ACR of these genotypes ranged from 30% for 'Tineke' to 58.33% for 'Black Baccara'.

Principal component analysis

Principal component analysis (PCA) was performed, and the biplot was established for a greater approximation compared with the coefficient of correlation to describe the crossability success between rose varieties. Given the eigenvalue higher than 1, the first (F1) and second (F2) principal components explained 48.57% and 33.17% of the total variation, cumulatively accounting for 81.74% (Fig 3). The PCA-biplot results indicated a positive correlation between crossability rate and seed production efficiency because they were placed on the same side and had similar vector lengths. Average fruit weight, pollen germination rate and seed number per fruit also positively correlated (Fig. 3). Among all the cross-combinations, 'Black Baccara' × 'Jumilia' was found to have a higher crossability rate and seed production efficiency. 'Tineke' \times 'Jumilia' and 'Jumilia' × 'Tineke' combinations were classified as the best based on average fruit weight, pollen germination rate, and seed number per fruit (Table 4).

DISCUSSION

Controlled hybridization has been used in cut rose breeding. The most important step in cross-breeding is to include genotypes in breeding programs to ensure high pollen viability/germination and a high seed set. Breeders are interested in enhancing the number of seeds per fruit. Therefore, fertile progenitors also yield high seeds, and due to the heterozygosity in roses, new rose varieties can be obtained more easily with the characteristics desired by breeders. Problems in rose hybridization arise from ploidy differences [Leus et al. 2018]. The base chromosome numbers of rose were reported as 2n = 2x, 3x, 4x, 6x, 8x, and 10x [Jian et al. 2010]. The ploidy levels of all genotypes used in the current study were found to be 2n = 4x (tetraploid). These results were compatible with research showing that the 2C/DNA levels of tetraploid roses varied from 1.85 pg/2C to 2.71 pg/2C [Yokoya et al. 2000]. According to reports, commercial-cut roses are usually tetraploid, while garden roses are either diploid or tetraploid [Datta 2018]. Tetraploid (2n = 4x) roses are more frequently utilized in breeding programs because of their beneficial production performance [Zlesak 2007]. However, it was found that different hybrid combinations produced different types of fruit and seeds. This variation results from the fact that plants with differing DNA contents but the same ploidy levels (e.g., tetraploid) can become incompatible with one another. This could be because variations in DNA content impact both physiological and genetic processes [Morey 1959, Rajapakse et al. 2001, Kazaz et al. 2020, Dogan et al. 2022]. Nadeem et al. [2013] reported that most Rosa hybrida cultivars are tetraploid and self-fertilized. For this reason, the low fruit set could be explained as cross incompatibility and ploidy level. In the present study, the findings are consistent with the findings of other researchers [Täckholm 1923, Erlanson 1938, Krussmann 1981, de Vries and Dubois 1996, Crespel et al. 2002, Zlesak 2007]. Although crossing efficiency typically remains consistent, with the number of fruits or seeds per fruit being similar regardless of whether the tetraploid parent is used as seed or pollen donor, the current study observed variations in fruit or seed formation. These differences can be attributed to the physiological and genetic factors of the parent plant.

The pollen germination rate in the current study ranged from 11.36% to 23.41%, whereas the pollen viability rate ranged from 33.29% to 47.25%. The lower and upper limit values varied among the investigations despite the fact that the results of the current study were largely consistent with the previous studies. The genotype, ploidy levels [Ueckert 2014], methods [Sulusoglu and Cavusoglu 2014], climate, plant nutritional status, pollen collection time (season, flowering period, and flower development period) [Martins et al. 2017], storage conditions, and storage duration are all thought to affect pollen quality [Miler and Wozny 2021]. Furthermore, it has been reported that wild and ancient garden roses produce higher-quality pollen than hybrid roses, which is consistent with the findings of the current study [Ueda and Hirata 1989, Gudin and Arene 1991, Meral 2023, Kılıç 2023]. According to Nadeem et al. [2013], interspe-

56

cific hybridizations, meiotic anomalies, heterozygous polyploidy parents, and the buildup of lethal recessive alleles may all contribute to the reduced pollen fertility of hybrid roses. High fertility in pollen enhances the efficiency of breeding programs and decreases the risk of infertile pollen related to using of new pollen donors. In the current study, differences in fruit set, seed formation per fruit, weight of fruit and weight of seed were observed. 'Jumilia' showed a higher crossability rate as a male parent than when it used as a maternal parent because 'Jumilia' featured high pollen viability and pollen germination. 'Black Baccara' achieved a good ACR of 58.33%, but the combination of 'Black Magic' × 'Jumilia' obtained 6.88 seeds per fruit. These reciprocal crossings showed that not all combinations were successful and some preferential crossing directions were observed (Table 3). However, the efficiency depended on the specific cross combination and varied between 2.25 and 60.50 seeds per fruit. The current study indicated the maximum crossability rate in 'Black Baccara' × 'Jumilia' (94.44%), while the ineffective result in crossability rate (23.68%) was obtained in 'Jumilia' × 'Black Baccara'. 'Black Baccara' showed a better SPE ratio than 'Jumilia', and this situation was paralleled by the success of crossability. The maximum number of seeds per fruit was obtained from the 'Jumilia' × 'Tineke' (60.50 seeds) combination, followed by 'Tineke' × 'Jumilia' (43.74 seeds). Regardless of the combination, Khan et al. [2021] found that the fruit set rate was 63.33% in their crossbreeding investigation. According to Abdolmohammadi et al. [2014], the combinations' fruit set rates ranged from 0% to 80.00%. It varied between 0% and 100.0% in the Atram et al. [2015] study and between 30.00% and 83.00% in the Nadeem et al. [2015] trials. According to research that determined the average number of seeds per fruit, roses typically had between 0 and 50.0 seeds per fruit [Zlesak 2007]. Abdolmohammadi et al. [2014] found that crosses between wild and old garden roses and modern roses resulted in an average of 0-35.30 seeds per fruit. Using contemporary roses as parents, Nadeem et al. [2015] found that the average number of seeds per fruit varied from 15.0 to 33.0. According to Farooq et al. [2016], crosses between five distinct rose species showed average numbers of seeds per fruit ranging from 0 to 17.0. According to Khan et al. [2020], hybrid roses had seed numbers ranging from 0.0 to 15.0 per fruit.

The complex genetic structures of genotypes [Ueckert 2014], parental fertility [Nadeem et al. 2015], incompatibility [MacPhail and Kevan 2009], meiotic abnormalities, and the accumulation of lethal alleles [Ogilvie et al. 1991, Nadeem et al. 2015] may all contribute to the variation in crossability rate among combinations. Furthermore, a poor crossability rate may result from hormonal regulation that affects the embryo and hip formation [Cruden and Lyon 1989, Stone et al. 1995]. According to Gudin [2001], fruit set in roses appears to be regulated by embryo development. The crossability rate and seed production efficiency were shown to be positively correlated in the current study. Zlesak [2007] asserts that hybrid roses are primarily self-pollinating and that the ability of the female gametes to accept foreign pollen is what determines whether the crossover is successful. The differences in seed set and crossability rate could also be attributed to petal counts [Nadeem 2012]. In the wild, there are more fruits and seeds, while old garden roses have fewer petals because of increased infertility. It has also been claimed that roses with fewer petals produce more fruits than those with more petals [Baydar et al. 2016]. Additionally, researchers found that sterility caused fewer fruits and seeds, which were correlated with fewer anthers as the number of petals increased. Other studies reported that the number of seeds per fruit may differ depending on pollination, fertilization, embryogenesis, ploidy levels and pollen viability and germination [Gudin and Arene 1992, Zlesak 2007, Farooq et al. 2016, Kazaz et al. 2020]. These differences were due to ACR, SPE, meiotic abnormality and accumulation of recessive alleles [Zlesak 2007]. The germination percentage differed for each combination. The low seed germination percentage could be attributed to a lack of a good seed set or viable embryos [Fagerlind 1954]. In addition, environmental factors such as daylight or daily temperature affect crossability rates and germination. A physiological dormancy, which is under hormonal control, may affect rose seeds [Semeniuk et al. 1963, Gudin 1995, Finch-Savage and Leubner-Metzger 2006]. Hence, the rose embryo may force the seed coat to open. Zlesak [2005] reported that hybrid tea roses demonstrate between 38.6% and 64.4% germination rates as these genotypes feature high germination rates. This confirms the findings of the current study that hybrid tea roses show different germination characteristics of tetraploid genotypes as a result of different crosses. In the current study, the fertility status of genotypes varied from low to high.

CONCLUSIONS

Production and breeding in cut roses are continuously advancing, however, due to the limited scope of current rose breeding efforts, breeders are focused on increasing seed production to develop new rose varieties. The current study aimed to assess the compatibility among several Rosa varieties used in commercial cut rose breeding programs. It was found that 'Black Baccara' and 'Jumilia' exhibited excellent crossability rates and seed germination rates, with 'Jumilia' proving to be a superior male parent for all crosses. The findings emphasize the importance of compatible parent pairs in improving crossability indices (ACR, SPE), suggesting that further combinations of parents should be tested to fully explore their breeding potential. By improving crossability and seed sets, which are crucial for creating commercially viable rose varieties, this study provides valuable insights into current breeding strategies. The results offer practical applications that can guide future rose breeding programs. Moreover, further research is recommended into the effects of different ploidy levels across various cross combinations to optimize breeding outcomes and enhance the development of new rose varieties.

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