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Interspecific Hybridization Characteristics of Pumpkin (*Cucurbita moschata* Duch.) and Winter Squash (*Cucurbita maxima* Duch.)

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ABSTRACT

This experiment focused on the production and evaluation of interspecies hybrids of Cucurbita (*Cucurbita maxima* × *Cucurbita moschata*) for use as rootstocks in cucurbit crops such as cantaloupe. The study involved cultivating and crossing various pumpkin and squash varieties under both controlled and field conditions, assessing germination viability and pollen fertility, and evaluating the morphological traits of the rootstocks. These evaluations were conducted over two years (2019 and 2020) at the research field and greenhouse of the University of Tehran, Iran. A total of 307 crosses were performed, of which 17 successfully formed fruit and produced seeds. The results indicated that characteristics such as hypocotyl length and diameter, germination percentage, and pollen fertility are critical factors influencing transplant success. Notably, the hybrids MB525×SI8910 and MB525×SB409 demonstrated strong performance in terms of morphological indices. For instance, MB525×SI8910 exhibited improvements of 44.26%, 22.22%, and 62.16% over the Takii rootstock in terms of hypocotyl length, diameter, and shoot dry matter, respectively. Although some hybrids showed high levels of pollen infertility, likely due to genetic incompatibility and environmental factors, several hybrids with favorable characteristics were identified. These hybrids show promise for use as commercial rootstocks. The observed traits suggest that producing well-adapted hybrids can enhance plant establishment under environmental stress and potentially increase both the yield and quality of horticultural crops. This research offers valuable insights into the application of interspecies hybrids in modern agriculture and underscores the need for future studies to focus on optimizing the genetic and environmental attributes of these rootstocks.

Introduction

The genus *Cucurbita*, belonging to the family Cucurbitaceae, comprises several economically important species such as squash (*C. moschata*), pumpkin (*C. maxima*), and zucchini (*C. pepo*). These species are valued for their high genetic diversity, broad climatic adaptability, and extensive agricultural applications. As monoecious plants, cucurbits bear separate male and female flowers, and pollination is primarily insect-mediated. They typically thrive in warm and temperate climates, showing considerable resistance to high temperatures and adaptability to soils with neutral or slightly acidic pH (Kaur et al., 2023).

Interspecies hybridization in cucurbits is an effective strategy for transferring desirable traits such as pest and disease resistance, environmental stress tolerance, and improved crop yield. However, hybridization success can be hindered by genetic distance and reproductive barriers, including insufficient pollen tube growth and the failure to develop embryos and endosperm (Kapoor et al., 2024). Despite these challenges, studies have demonstrated that hybrids derived from crosses between pumpkin and squash serve as excellent rootstocks for crops like watermelon and melon. These hybrids enhance crop performance by improving tolerance to environmental stresses and increasing the efficiency of mineral uptake.

Key morphological traits such as hypocotyl length and diameter are crucial for successful grafting and plant establishment (Fredes et al., 2017). Hybrid plant production plays a vital role in boosting yield and overall crop performance. In crop breeding programs, hybridization techniques are widely used to develop superior cultivars (Kumar et al., 2018). Hybrid rootstocks offer several advantages, including deeper root penetration and greater drought tolerance, making them suitable for cultivation in arid and semi-arid regions. As interspecific hybrids, they also promote genetic diversity and improved adaptability to diverse environmental conditions.

Additional benefits of using hybrid rootstocks include enhanced stem growth regulation, improved fruit quality and early maturity, controlled plant size, extended harvest periods, reduced drought-related damage, and increased economic returns. These rootstocks also induce stress tolerance in grafted plants, making them an efficient tool for managing abiotic stress and enhancing the productivity of horticultural crops (del-Canto et al., 2023).

Numerous studies have highlighted the benefits of grafted seedlings. Vakili Moghadam et al. (2022) reported that grafting watermelon (*Crimson Sweet*) onto Shintosa rootstock (*C. maxima* × *C. moschata*) increased yield, fruit number, fruit firmness, and leaf area by 30.37%, 31.02%, 8.88%, and 11.32%, respectively, compared to ungrafted controls. Similarly, watermelon (*TAMU Mini*) grafted onto the Strong Tosa rootstock (*C. maxima* × *C. moschata*) exhibited a 64.30% increase in fruit weight and a 65.29% increase in soluble solids (°Brix) compared to ungrafted plants (Simpson et al., 2015).

Cantaloupe grafted onto Star, Cobalt, and Shintosa rootstocks showed increases in stem length by 39.86%, 32.02%, and 40.53%, stem diameter by 20%, 25.33%, and 28%, and leaf number per plant by 36.58%, 17.04%, and 29.26%, respectively, compared to ungrafted controls. Under salinity stress (150 mM NaCl), cantaloupe grafted onto Shintosa still exhibited improvements in stem length (21.21%) and stem diameter (11.67%), although leaf number remained unchanged, highlighting the positive impact of grafting even under stress conditions (El-Kafafi et al., 2017).

The success of interspecies hybridization is one of the most critical factors in parental selection. The rate of fruit set with normal seeds can vary significantly depending on the parental genotypes used. In a study by Karaagac and Balkaya (2013), this trait was reported to range from 0 to 50 percent, with the highest fruit set observed in parental lines MA9, MA4, MA11, and MA12, at rates of 50%, 33.3%, 25%, and 20%, respectively. The present experiment aimed to cross pumpkin and squash species to produce hybrid rootstocks and evaluate their performance in comparison with existing commercial varieties.

Materials and Methods

Plant materials and growth condition

In order to carry out this project, 26 varieties of cucurbit seeds were obtained from the National Gene Bank of Iran, 5 varieties from a commercial company, as well as some local varieties from different parts of Iran (Rasht, Kermanshah, Mashhad) (Table 1).

This study was conducted over two years (2019 and 2020) at the research field and greenhouse of the University of Tehran, Iran. Seeds of the selected cucurbit genotypes were surface-disinfected using sodium hypochlorite and rinsed twice with distilled water, following the method described by Arab Salmani and Hakimi (2024). For each planting, ten seeds from various pumpkin and squash samples were sown in 50-well seedling trays filled with a cocopeat-to-perlite substrate in a 3:1 ratio, at a depth of approximately 2 cm. Once the seedlings emerged and developed to the two- or three-leaf stage, they were transplanted to the main experimental site.

Measurement of rootstock hybrids characteristics

At the flowering stage, one day prior to crossing, the male pumpkin flowers were secured using a clamp, and the female winter squash flowers were isolated with a bag to prevent unintended pollination. Hybridization was performed at 7:00 a.m. the following day. After pollination, the flowers were labeled and re-isolated with bags for several days to ensure successful fertilization. Once the fruits resulting from successful crosses reached maturity and were ready for harvest, the number of seeds per fruit was counted, and their germination status was assessed (Table 2).

Measurement of pollen characteristics

To assess the fertility status of hybrid pollen in comparison to that of the parental lines, selected hybrid seeds (intended for use as rootstock) were cultivated simultaneously with their respective paternal and maternal parents. After germination and flowering, flower buds of various sizes were collected for cytogenetic analysis and placed in Falcon tubes containing Carnoy’s solution (prepared in advance using 25 mL glacial acetic acid and 75 mL 96% ethanol per 100 mL). After 24 h in Carnoy’s solution, the buds were removed, washed three times with distilled water, and stored in 70% ethanol to stabilize the pollen grains. Prior to examination, the buds were removed from ethanol and again rinsed three times with distilled water. The length of the buds and anthers was measured using an ocular micrometer under a stereomicroscope (10× magnification). The sepals of each bud were carefully removed using a razor blade, and the anther was placed on a microscope slide (75 × 25 mm). To release the pollen grains, the anther was split and gently crushed, followed by staining with Aceto Orcein. Residual tissue was then removed from the slide, and the sample was covered with a No. 1.5 coverslip (22 × 22 mm). To ensure even distribution of pollen and eliminate air bubbles, the coverslip was lightly tapped using the end of a pencil, and the slide was gently squashed between two pieces of filter paper. For each hybrid and its parents, three slides of pollen grains were prepared. To evaluate pollen fertility and infertility based on morphology (with fertile pollen being larger and more spherical), each slide was examined under a light microscope using a 40× objective lens. A total of 24 randomly selected images were captured per slide, and the percentages of fertile and infertile pollen grains were calculated accordingly.

Table 1. List of varieties and origin of cucurbit seeds.

Code	Origin	Variety	Code	Origin	Variety	Code	Origin	Variety
C. maxima	Iran gene bank	MB596	*C. maxima*	Iran gene bank	MB370	*C. moschata*	gene bank	SB477
C. maxima	Iran gene bank	MB525	*C. maxima*	Iran gene bank	MB2021	*C. moschata*	gene bank	SB320
C. maxima	Iran gene bank	MB582	*C. maxima*	Iran gene bank	MB2094	*C. moschata*	gene bank	SB381
C. maxima	Iran gene bank	MB668	*C. maxima*	Suttons Co.	MI5580	*C. moschata*	gene bank	SB684
C. maxima	Iran gene bank	MB201	*C. maxima*	Suttons Co.	MI5581	*C. moschata*	gene bank	SB554
C. maxima	Iran gene bank	MB646	*C. maxima*	Bazram Co.	MI5587	*C. moschata*	gene bank	SB646
C. maxima	Iran gene bank	MB545	*C. maxima*	Bazram Co.	Mid	*C. moschata*	Suttons Co.	SB8910
C. maxima	Iran gene bank	MB212	*C. maxima*	Bazram Co.	Mid	*C. moschata*	Suttons Co.	SB8869
C. maxima	Iran gene bank	MB2020	*C. maxima*	Rasht	ML1	*C. moschata*	Suttons Co.	SB8900
C. maxima	Iran gene bank	MB580	*C. maxima*	Rasht	ML2	*C. moschata*	Mashhad	SGa1
C. maxima	Iran gene bank	MB554	*C. maxima*	Kermanshah	MK1	*C. moschata*	Mashhad	SGa2
C. maxima	Iran gene bank	MB541	*C. moschata*	Iran gene bank	SB409	*C. maxima*	Rasht	MR1
C. maxima	Iran gene bank	MB536	*C. moschata*	Iran gene bank	SB441	*C. maxima*	Mashhad	MT1
C. maxima	Iran gene bank	MB277	*C. moschata*	Iran gene bank	SB440			

Table 2. Characteristics evaluated in the experiment related to cucurbit hybrids.

Character	Unit	Measurement method
Leaf length	Centimeter	Ruler
Leaf width	Centimeter	Ruler
Angle between hypocotyls	Millimeter	Digimizer
Hypocotyl length	Centimeter	Ruler
Hypocotyl diameter	Millimeter	Caliper
Root length	Centimeter	Digimizer
Leaf fresh weight	Gram	Scale
Leaf dry matter	Gram	Scale
Root fresh weight	Gram	Scale
Root dry weight	Gram	Scale
Root volume	Cubic centimeter	Graduated cylinder
Leaf area	Cubic centimeter	Digimizer

Statistical analysis
In this study, data analysis was performed using SPSS software version 26 (SPSS, Chicago, USA). Analysis of variance (ANOVA) was conducted, followed by Duncan's multiple range test (DMRT) for mean comparisons at a 5% significance level. Results were presented using well-structured tables and graphs to facilitate clear interpretation and accurate comparison of the data.

Results
Hybridization viability
Out of 307 crosses, 17 were successful and resulted in fruit formation. Fifty days after crossing, the fruits were harvested, the number of healthy and empty seeds was counted, and their germination viability was examined (Table 3).

Table 3. Count of filled and empty seeds and their Germination viability of *C. maxima* × *C. moschata* rootstock.

Hybrids	Filled Seeds	Empty Seeds	Germination viability
ML1×SI8910	64	5	No
MI8869×SB409	135	150	No
MB525×SI8910	110	15	Yes
MB596×SB440	65	23	No
MB525×SR	20	55	No
MB5580×SB409	49	42	No
MB596×SB441	22	110	No
MB596×SB409	62	60	No
MB525×SB409	98	58	Yes
MB270×SB409	30	45	No
MB582×SB409	0	0	No
MI5580×SB441	0	45	No
MI5580×SB381	0	98	No
MI5580×SB320	66	25	Yes
MD1×SB423	32	75	Yes
MK1×SB409	80	20	Yes
MI5587×SB409	72	10	Yes

According to Table 3 and Figure 1, the crosses MI8869×SB409, MB525×SI8910, and MB525×SB409 had the highest number of healthy seeds, and the crosses MB582×SB409, MI5580×SB441, and MI5580×SB381 had no healthy seeds.

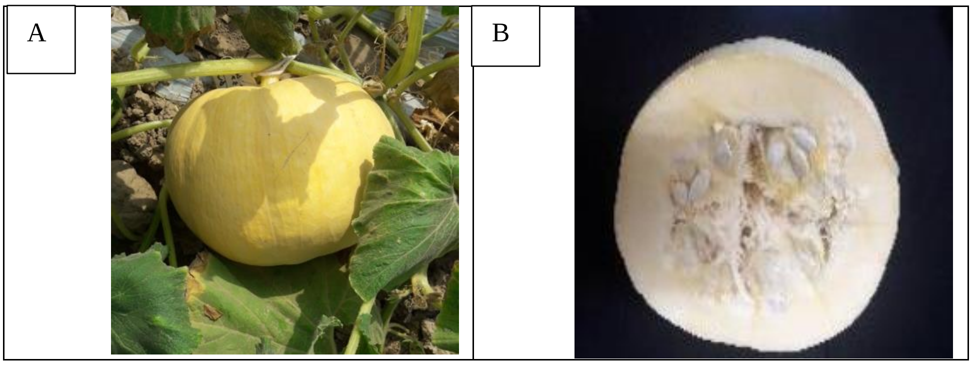

Fig. 1. (**A**) Successful fruit formation of *C. maxima* × *C. moschata*; (**B**) Successful seed formation of *C. maxima* × C. *moschata.*

Rootstock evaluation
The traits related to the rootstocks are given in Table 4. The maximum hypocotyl diameter was 4.6 mm, the length of cotyledon leaves was 6.8 cm for the rootstock Shintozwa, and in the rootstocks MB525×SB409 and MB525×SI8910, the hypocotyl diameter was 3.4 and 3.5 mm, and the leaf length was 5.3 and 6 cm, respectively. The highest hypocotyl length was 7.1 cm and the width of cotyledon leaves was 3.9 cm in the Takii rootstock, the highest cotyledon leaf area was 9.56 cm^2, root length was 25 cm, and root volume was 2 cm^3, root fresh weight was 0.6 g, root dry weight was 0.12 g in the SI8910×MB525 rootstock, and the highest root dry matter percentage was 34.6%, shoot dry weight was 0.534 g, and shoot dry matter was 59.3% in the SB409×MK1 rootstock.

Table 4. Rootstocks characteristics of *C. maxima* × *C. moschata*.

Hypocotyl diameter (mm)	Hypocotyl length (cm)	Angle between hypocotyls (mm)	Leaf length (cm)	Leaf width (cm)	Root length (cm)	Leaf area (cm^2)	Root volume (cm^3)	Root fresh weight (g)	Root dry weight (g)	Leaf fresh weight (g)	Leaf dry weight (g)
3.5	3.4	90.93	6.0	3.5	25.0	9.56	2.0	0.6	0.12	0.6	0.269
3.4	5.2	86.61	5.3	2.8	20.2	3.90	1.5	0.4	0.05	0.6	0.277
3.4	4.0	81.69	5.7	3.6	10.0	7.83	1.0	3.0	0.10	0.9	0.534
2.3	2.3	59.55	4.0	2.2	9.0	0.27	1.0	1.0	0.02	0.3	0.091
3.4	4.7	73.55	4.3	2.0	9.0	0.39	1.0	1.0	0.022	0.4	0.110
3.7	4.8	77	3.3	2.4	7.5	4.15	1.0	1.0	0.023	0.4	0.166
4.6	4.0	69.70	6.2	3.3	17.5	9.47	1.0	5.0	0.097	0.7	0.380
4.5	6.1	67.75	5.8	3.3	11.0	6.41	1.0	5.0	0.074	0.7	0.386

Pollen evaluation

According to Table 5 and Figure 2, the rootstock Shintozwa exhibited the highest percentage of infertile pollen at 32% and the lowest percentage of fertile pollen at 68%, along with the shortest bud and anther lengths. In contrast, the rootstock Takii showed the greatest bud length of 32 mm and anther length of 13 mm. Among the selected rootstocks, the hybrid SI8910×MB525 had the highest percentage of sterile pollen, accompanied by a bud length of 31 mm and an anther length of 13 mm. Additionally, among the male parents, the highest percentage of sterile pollen was observed in parent SI8910.

Table 5. Pollen characteristics of *C. maxima* × *C. moschata*.

Rootstock	Parent	Bud Length (mm)	Anther Length (mm)	Fertile Pollen (%)	Sterile Pollen (%)
SI8910×MB525	Hybrid	31	13	77.2	22.8
SB409×MB525	Hybrid	30	10	81.74	18.27
SB409	Male	30	11	95.3	4.7
SI8910	Male	28	10	93.10	6.9
MB525	Female	26	10	87.8	12.2
Takii	Control	32	12	70	30
Shintozwa	Control	15	5	68	32

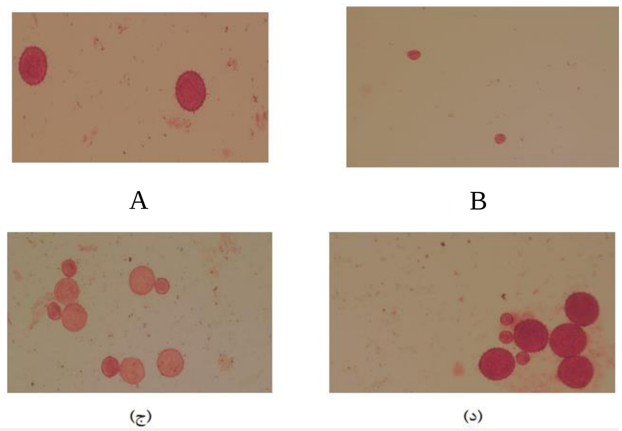

Fig. 2. (**A**) Big and fertile pollen; (**B**) Small and sterile pollen; (**C** and **D**) Sterile and fertile pollen.

Discussion

In this study, interspecific crosses between pumpkin and squash were performed to evaluate the potential for hybrid formation and to assess their characteristics based on the number of healthy seeds, number of empty seeds, and germination rates. The results revealed significant differences among the hybrids for these traits. Certain combinations, such as MB525×SI8910 and MB525×SB409, were identified as successful hybrids due to their higher production of healthy seeds, better germination success, and more desirable rootstock characteristics. These hybrids show strong potential for use as effective grafting rootstocks in horticultural crops. Out of 307 crosses involving 26 pumpkin and 16 squash genotypes, only 17 resulted in successful fruit formation and seed production. Numerous factors contributed to the low success rate, including genotypic incompatibilities, adverse environmental conditions, pre-fertilization barriers (such as insufficient pollen tube growth), post-fertilization barriers (including failure of egg cell formation or embryo abortion), lack of fruit set, development of weak or seedless fruits, and production of wrinkled or non-viable seeds. These issues substantially reduced the overall crossing success (Sasaki and Tanaka, 2023). Supporting these findings, Coşkun (2022) reported that among 234 crosses performed, only 79 fruits were obtained, attributing the high failure rate to extensive genetic diversity in pumpkins. Nonetheless, pumpkins remain more effective as parental lines for hybrid seed production. Similarly, Maekawa et al. (2022) found that out of 43 successful crosses, only 23 resulted in fruit formation, with observed inconsistencies in the growth and germination of the resulting hybrid seeds.

Studies have shown that the number and quality of seeds produced from crosses between pumpkin and squash are generally compatible. The formation of healthy seeds can be influenced by the presence and balance of essential nutrients—including low- and high-consumption elements—as well as carbohydrates, proteins, enzymes, and hormones in the pollen. Deficiencies in any of these components can lead to reduced fertilization, impaired seed formation, and lower germination rates (Vendruscolo et al., 2024). In another study, only six types of seeds from the obtained hybrids successfully germinated. Evaluation of aerial and root traits of these hybrids highlighted the critical importance of hypocotyl length and diameter for grafting success. Specifically, the hypocotyl length should neither be too long nor too short, and an excessively large hypocotyl diameter results in a larger internal pith cavity. This can disrupt vascular connections between the rootstock and scion, leading to graft failure (Kan et al., 2023).

In this research, the rootstocks MB525×SI8910 and MB525×SB409 showed no significant differences compared to commercial rootstocks (Takii and Shintozwa) in terms of hypocotyl length (3.4 cm and 5.2 cm) and hypocotyl diameter (3.5 mm and 3.4 mm), respectively. Genotypic compatibility between pumpkin and squash plays a crucial role in successful hybrid rootstock seed production, with selection criteria focusing on seed yield, plant vigor, and hypocotyl traits (Fogliata et al., 2019). Most *Cucurbita* hybrids are preferred as rootstocks because they exhibit robust performance, producing long and thick hypocotyl tracheas that facilitate grafting. Additionally, these hybrids have a strong ability to delay flowering and fruit ripening in grafted plants, enhancing crop management (Zhou et al., 2008). Interspecific hybridization among ten *Cucurbita* species confirmed that stem hypocotyl characteristics are critical to grafting success. Hypocotyls that are too long can block vascular connections at the graft junction, while overly short hypocotyls complicate the grafting process (Sekino et al., 2023). Furthermore, the structural condition of the pith cavity diameter and hypocotyl also influences grafting outcomes. Even in hybrids with similar vascular bundle counts and hypocotyl thickness, an excessively large pith cavity can prevent proper reconnection between vascular bundles, negatively affecting graft and seedling success rates (Bengtsson et al., 2008). Studies on pollen fertility showed that hybrids from interspecific crosses, such as MB525×SI8910 and MB525×SB409, exhibited lower fertility percentages compared to their maternal and paternal parents. Among the hybrids, Shintozwa displayed the highest pollen infertility rate. A higher rate of pollen infertility is often associated with interspecific hybridization. In a study on *Cucurbita pepo*, hybridization was found to reduce pollen fertility without affecting pollen performance metrics such as germination, pollen tube growth rate, or fertilization capability, while simultaneously increasing heterozygosity (Stephenson et al., 2001).

Conclusions

The results of this study demonstrated that crosses between squash and pumpkin species often led to successful hybrid formation and production of filled seeds, supporting the research hypothesis. Certain hybrids, such as SI8910×MB525, showed promising potential as grafting rootstocks for horticultural crops like cucumber, melon, and watermelon due to their superior root and shoot growth characteristics. However, some crosses either failed or produced seeds incapable of germination, highlighting the need for further research into the genetic and environmental factors influencing crossing success. Based on the morphological data collected, it can be concluded that the hybrid rootstocks exhibited superior morphological traits compared to the standard commercial varieties.

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Author Contributions

Conceptualization, ML and RS; methodology, MP; software, MP; validation, ML and RS; formal analysis, MP; investigation, MP; resources, JK; data curation, ML; writing—original draft preparation, YH; writing—review and editing, YH; supervision, ML and RS; project administration, ML. All authors have read and agreed to the published version of the manuscript.

Conflict of Interest

The authors indicate no conflict of interest in this work.

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