

RESEARCH ARTICLE OPEN ACCESS

Comparative Studies on Fertility Traits of CMS Eggplants (*Solanum melongena* L.) Using Cytoplasms from Five Wild *Solanum* Species

Shiro Isshiki¹ | Takashi Arita¹ | Masaki Iwayoshi¹ | Kenji Ureshino² | Md. Mizanur Rahim Khan² 

¹Vegetable and Flower Horticulture Laboratory, Faculty of Agriculture, Saga University, Saga, Japan | ²Laboratory of Horticulture, Faculty of Agriculture, University of the Ryukyus, Okinawa, Japan

Correspondence: Md. Mizanur Rahim Khan (khan@cs.u-ryukyu.ac.jp)

Received: 1 April 2025 | **Revised:** 27 June 2025 | **Accepted:** 1 July 2025

Keywords: cytoplasmic male sterile | eggplant | fertility traits | seed parents of F₁ | wild *Solanum* species

ABSTRACT

Five cytoplasmic male sterile (CMS) lines of eggplant “Uttara” (*Solanum melongena* L.) with the cytoplasms of *S. kurzii* (KUR), *S. violaceum* (VIO), *S. aethiopicum* (AET), *S. anguivi* (ANG), and *S. grandifolium* (GRA) and three restorers of fertility (RF) lines of CMS from AET, ANG, and GRA were compared for the fertility traits to determine which CMS are effective as seed parents of F₁ hybrids and/or as seedless cultivars of eggplant. The CMS lines of KUR and VIO showed functional male sterility and AET, ANG, and GRA showed pollen nonformation type sterility. While the RF lines of CMS from AET, ANG, and GRA showed a normal release of pollen grains. The CMS lines KUR, VIO, and all RF lines exhibited significantly lower pollen staining with acetocarmine and pollen germination rates on artificial media compared to “Uttara.” The number of seeds per fruit of CMS and RF lines of ANG was significantly lower than “Uttara,” while those of other CMS and RF lines were not. The lines of CMS KUR, VIO, AET, and GRA produced relatively good fruit sets and high seed numbers similar to “Uttara.” This indicates their strong potential as seed parents for F₁ hybrids and seedless eggplant cultivars.

1 | Introduction

Eggplant (*Solanum melongena* L.) is an important and popular vegetable crop, especially in Asia (Yamaguchi 1983). Most commercial cultivars of eggplants are F₁ hybrids (Kakizaki 1931; Sambandum 1962) because interbreed hybrids of eggplant develop considerable heterosis, especially in yield. Producing seeds for F₁ hybrid eggplant is a labor-intensive process as it necessitates manual emasculation, pollination, and bagging. Developing a useful male sterility system for eggplant can reduce the effort needed to produce F₁ hybrid seed.

On the other hand, in many fruit crops and trees, seedlessness is desirable for consumers and growers, as it enhances fruit quality and shelf life. In the case of eggplant, it helps to improve the quality of pickles (Donzella et al. 2000). Usually, the area around the

seeds of eggplant pickles turns brown and is not preferred by consumers. Using seedless fruit prevents this browning.

To produce completely seedless fruits in eggplant, parthenocarpy and male sterility is required to be expressed simultaneously. Commercial varieties, such as ‘Anomimori,’ ‘Anomimori 2 gou,’ and ‘PC Chikuyo,’ have been introduced as parthenocarpic cultivars (Saito et al. 2019). Combining these cultivars with promising male-sterile lines is crucial for producing completely seedless fruit.

In previous reports, we developed several cytoplasmic male sterile (CMS) lines by substituting the cytoplasm of eggplant with that of wild *Solanum* species, *S. violaceum* Ort. (VIO) (Isshiki and Kawajiri 2002), *S. kurzii* (KUR) Brace & Prain (Khan and Isshiki 2009), *S. aethiopicum* L. (AET) Aculeatum Group (Khan and Isshiki 2010), *S. anguivi* Lam. (ANG) (Khan and Isshiki 2011), and *S. grandifolium* (GRA) (*S. integrifolium* = *S. aethiopicum*

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2026 The Author(s). *New Zealand Journal of Crop and Horticultural Science* published by John Wiley & Sons Australia, Ltd on behalf of The Royal Society of New Zealand.

Aculeatum Group) (Hasnunnahar et al. 2012), respectively. The former two CMS lines are pollen nonrelease types. These lines exhibited functional male sterility, characterized by indehiscent anthers, resulting in the nonrelease of pollen grains (Isshiki and Kawajiri 2002; Khan and Isshiki 2009). The latter three CMS lines exhibited pollen nonformation type male sterility, characterized by the absence of pollen grains in the anthers. Each of these CMS systems has the male fertile line, which carries the restorer of fertility (RF) genes against pollen nonformation type sterility (Khan and Isshiki 2010; 2011, Hasnunnahar et al. 2012). Two independent dominant RF genes restore fertility in each pollen nonformation type CMS systems. Therefore, all five CMS lines are expected to contribute significantly to the production of F1 hybrid seed and seedless eggplant fruit.

For the commercial use of CMS lines, it is necessary to compare the fertility traits of each line; however, to date, only one report has been published by us (Khan et al. 2023). In the present study, we compared and evaluated the pollen and seed fertility traits of the CMS lines of *S. kurzii*, *S. violaceum*, *S. aethiopicum*, *S. anguivi*, and *S. grandifolium* and the three restorers of fertility (RF) lines of CMS of *S. aethiopicum*, *S. anguivi*, and *S. grandifolium* to determine which CMS lines are effective as seed parents for hybrid and seedless eggplant cultivars.

2 | Materials and Methods

2.1 | Plant Materials

The CMS lines were developed previously by cytoplasmic substitution through interspecific crosses in which wild *Solanum* species were used as female parents, followed by repeated backcrossing with the recurrent pollen parent *S. melongena* ‘Uttara,’ a Bangladeshi variety of cultivated eggplant. The *S. melongena* cytoplasm was substituted with cytoplasm from each of the five wild species *S. violaceum* (Isshiki and Kawajiri 2002), *S. kurzii* (Khan and Isshiki 2009), *S. aethiopicum*, (Khan and Isshiki 2010), *S. anguivi* (Khan and Isshiki 2010), and *S. grandifolium* (*S. integrifolium*) (Hasnunnahar et al. 2012) by the backcross method. The first two, *S. kurzii* and *S. violaceum*, are closely related wild species of Asian origin like *S. melongena*, and they are likely to have relatively high hybrid compatibility with *S. melongena* (Isshiki and Kawajiri 2002; Khan and Isshiki

2009; Tegally et al. 2019; Aubriot et al. 2018; Sewa 2020; Mansa et al. 2021; Weese and Bohs 2010). The other three, *S. aethiopicum*, *S. anguivi*, and *S. grandifolium* (*S. integrifolium*), are closely related and have been referred to as the scalet eggplant of Africa (Weese and Bohs 2010; Taher et al. 2017). The hybrid compatibility with eggplant is likely to be low. (Lester 1986; Lester and Daunay 2003; Lester and Thitai 1989).

The backcrossed generations of the CMS lines used in the present study were the BC₅ lines of *S. kurzii*, the BC₁₄ lines of *S. violaceum*, the BC₁₄ lines of *S. aethiopicum* Aculeatum Group, the BC₉ lines of *S. anguivi*, and the BC₇ lines of *S. grandifolium*. For convenience, these lines are referred to as CMS KUR, CMS VIO, CMS AET, CMS ANG, and CMS GRA. In addition, the fertility restored lines of the CMS AET, CMS ANG, and CMS GRA by the *Rf* genes were also used for the analyses, and are referred to as RF AET, RF ANG, and RF GRA for convenience. *Solanum melongena* ‘Uttara’ was used as a control. A minimum of three plants from each line were used as plant materials.

The cultivation was carried out in unglazed pots (width 25 cm × height 20 cm) in a glasshouse at the University of the Ryukyus field. The soil composition was a mixture of 0.1 l of chicken manure, 20 g of oil dregs of Camellia, 0.5 l of magnesium lime, 0.01 l of organic compound fertilizer (N: P₂O₅: K₂O = 8:8:8), 2.4 l of cattle manure and 2.4 l of red clay, with a total volume of about 5 l used per plant in the unglazed pot. The plants were grown in a glasshouse with OK-F-1 (N: P₂O₅: K₂O = 15:8:17, OAT Agrio Co., Ltd.) applied twice a week, with no heating and ventilation set at 30°C. The study was conducted from August to October 2022. Seedlings were sown on 15 March, potted in 9 cm-diameter black plastic pots on April 15, and repotted into unglazed pots on May 15.

2.2 | Pollen Release Ability

The anther tips were observed under a stereo microscope to assess pollen release ability. Anthers from 15 flowers were examined for each plant.

2.3 | Pollen Fertility

Pollen staining ability and in vitro germination of pollen were examined to assess pollen fertility (Figures 1 and 2). Pollen grains from freshly opened flowers were extracted from the anthers by dissection

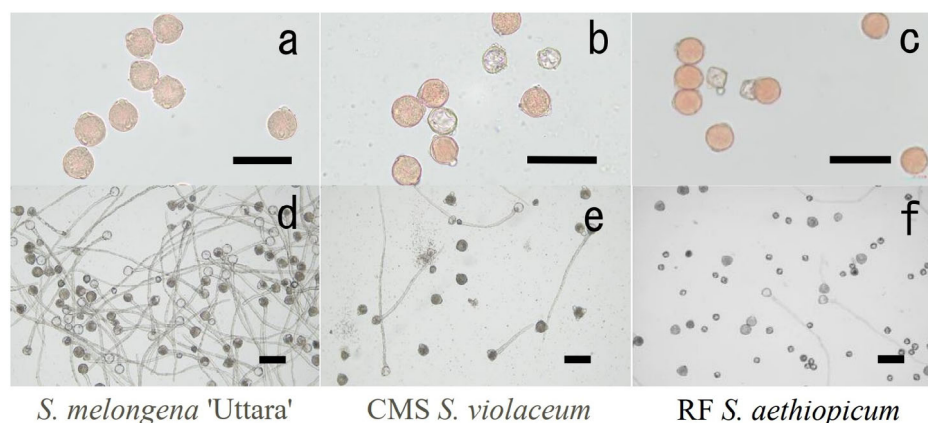


FIGURE 1 | (a,d) Pollen stainability and germination ability of *S. melongena* “Uttara,” (b,e) the CMS VIO, and (c,f) the RF AET. The scale bar of a, b, and c = 50 μm, while that of d, e, and f = 100 μm.

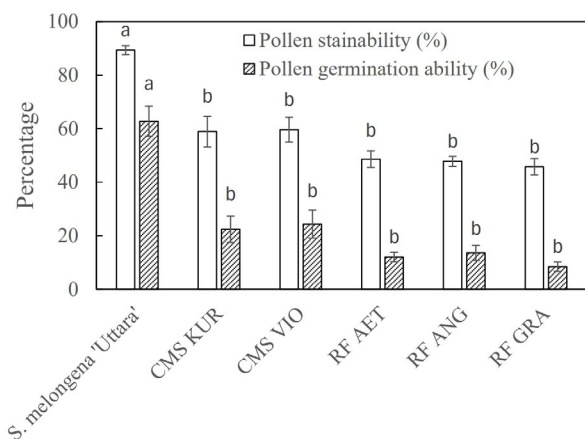


FIGURE 2 | Pollen stainability and germination ability of *S. melongena* "Uttara," the CMS KUR, VIO and the RF AET, ANG, GRA. Different letters indicate significant differences at $p < 0.05$ by the Tukey–Kramer test.

and then smeared in 1% (w/v) acetic carmine to assess their staining ability using the method described by Singh (2002). The in vitro germination ability of pollen was assessed according to Singh (2002) with a slight modification using a germination medium consisting of 1% (w/v) agar, 5% (w/v) sucrose, and 50 mg/l boric acid. The experiments were carried out in early September.

2.4 | Seed Fertility

Fruit set percentages and number of seeds per fruit were counted to evaluate seed fertility (Figures 3 and 5). For this study, the five CMS lines and three RF lines were pollinated by *S. melongena* 'Uttara.' As a control, *S. melongena* 'Uttara' was self-pollinated. Selfing was also carried out on the CMS KUR, VIO and RF AET, ANG, and GRA (Table 1). For the evaluation of fruit set and number of seeds per fruit, three individuals were used in each line, and crosses were made with at least five flowers per plant. The observations were carried out from September to October.

2.5 | Statistical Analysis

The significance of differences between means ($p \leq 0.05$) was assessed by the Tukey–Kramer test.

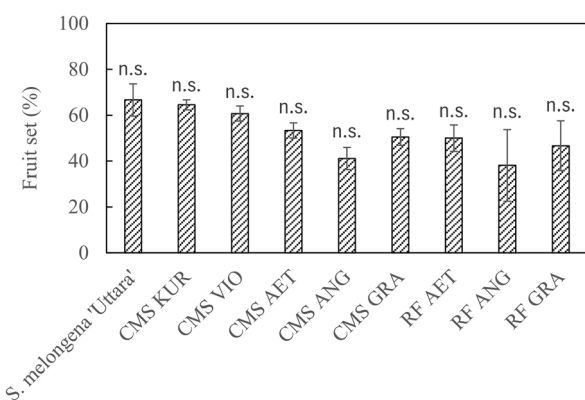


FIGURE 3 | Fruit set of *S. melongena* "Uttara," the five CMS lines and three RF lines after pollination by "Uttara." The letters "n.s." indicate not significant at $p > 0.05$ by the Tukey–Kramer test.

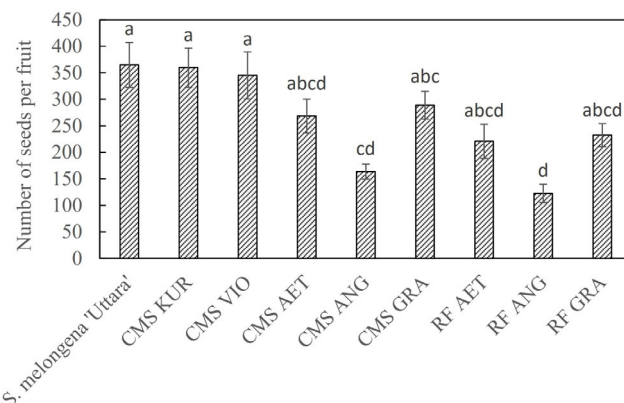


FIGURE 4 | Number of seeds per fruit of *S. melongena* "Uttara," the five CMS lines and three RF lines after pollination by "Uttara." Different letters indicate significant differences at $p < 0.05$ by the Tukey–Kramer test.

3 | Results

3.1 | Pollen Release Ability

The anthers of the control *S. melongena* 'Uttara' and the RF AET, ANG, and GRA were dehiscent, resulting in the natural release of pollen grains. On the other hand, the anthers of CMS KUR and VIO did not release pollen grains. The anthers of CMS AET, ANG, and GRA had no pollen grains at all.

3.2 | Pollen Fertility

The pollen stainability of CMS KUR, VIO and the RF AET, ANG, and GRA was statistically significantly lower than that of *S. melongena* 'Uttara' (Figures 1 and 2). There is no significant difference in pollen stainability between the CMS and RF lines.

The pollen germination ability of CMS KUR, VIO and the RF AET, ANG, and GRA was also statistically significantly lower than that of *S. melongena* 'Uttara' (Figures 1 and 2). There is no significant difference in pollen germination ability between the CMS and RF lines.

3.3 | Seed Fertility

The fruit set of CMS and RF lines is shown in Figures 3 and 5. The fruit set of CMS and RF lines was not significantly different than that of *S. melongena* 'Uttara.'

The number of seeds per fruit of CMS and RF lines is shown in Figure 4. The number of seeds per fruit of CMS ANG and RF ANG was significantly lower than that of *S. melongena* 'Uttara,' while those of the other CMS and RF lines were not. The number of seeds per fruit of CMS AET, ANG, and GRA was statistically similar to that of their own RF line.

3.4 | Seed Fertility After Self-Pollination

The fruit set and number of seeds per fruit of *S. melongena* 'Uttara,' the CMS KUR, VIO and the RF AET, ANG, and GRA after self-pollination are shown in Table 1. The CMS

TABLE 1 | Fruit set and number of seeds per fruit of *S. melongena* “Uttara,” the CMS KUR, VIO and the RF AET, ANG, GRA after self-pollination.

	Number of cross	Number of fruits	Fruit set, %	Number of seeds per fruit
<i>S. melongena</i> “Uttara”	32	20	66.3 ± 7.0	364.9 ± 42.2
CMS KUR	10	0	0	–
CMS VIO	13	1	7.7	65
RF AET	17	1	5.9	75
RF ANG	20	0	0	–
RF GRA	15	1	6.7	91

Values are expressed as mean ± S.D.
Statistical processing was not possible due to the small number of fruits obtained.



S. melongena ‘Uttara’ CMS *S. violaceum*

FIGURE 5 | Fruiting of *S. melongena* “Uttara” and a CMS *S. violaceum*.

VIO and the RF AET and GRA each produced one fruit and several dozen seeds.

4 | Discussion

We have developed five eggplant cytoplasmic substitution lines by interspecific crosses in which wild *Solanum* species were used as female parents (cytoplasm donors), followed by repeated backcrossing with recurrent pollen parent *S. melongena* ‘Uttara,’ and further, we have demonstrated that these are the CMS lines of eggplant (Isshiki and Kawajiri 2002; Khan and Isshiki 2009, 2010, 2011; Hasnunnahar et al. 2012). These CMS lines are considered effective for breeding eggplant F₁ hybrids and seedless varieties; however, the next step is to determine which of these CMS lines are most suitable for use. Therefore, in this study, the five CMS lines were cultivated under the same conditions, and an analysis was attempted of the basic characteristics related to fruit formation, such as fruit set, pollen, and seed fertility. Additionally, the possibility of using the RF lines, which restore the fertility of the CMS lines, was investigated.

First, the ability of the CMS lines to release pollen was investigated. Pollen was released in *S. melongena* ‘Uttara,’ but none of

the five CMS lines released pollen. The CMS KUR and VIO are types of functional male sterility, in which pollen is produced in the anthers but not released from the anthers (Isshiki and Kawajiri 2002; Khan and Isshiki 2009). The results of this study also showed that both CMS lines expressed functional male sterility, which was maintained in subsequent generations. On the other hand, the CMS AET, ANG, and GRA are types of male sterility in which no pollen is formed (Khan and Isshiki 2010, 2011; Hasnunnahar et al. 2012). The results of this study also showed the same expression of male sterility, characterized by the absence of pollen formation, and, like functional male sterility, it is evident that these male sterilities are maintained over successive generations. In these pollen nonformation type male sterility, pollen formation is controlled by the dominant Rf genes (Khan and Isshiki 2010, 2011; Hasnunnahar et al. 2012). The RF AET, ANG, and GRA all showed normal pollen release, and fertility was restored, confirming that the *Rf* was working in the present study.

The next step was to determine the fertility of the pollen grains extracted from the anthers (Figures 1 and 2). The CMS KUR and VIO contained pollen in their anthers, so their fertility was analyzed. The CMS AET, ANG, and GRA could not be analyzed for pollen fertility because no pollen was present in their anthers, so

the pollen grains from the RF AET, ANG, and GRA were analyzed instead. Pollen fertility was assessed by examining pollen staining with acetocarmine and the in vitro germination ability of pollen extracted from the anthers on the day of anthesis.

The results showed that the CMS KUR and VIO and the RF AET, ANG, and GRA had significantly lower staining and germination rates than that of the eggplant 'Uttara' (Figures 1 and 2). This could be an effect caused by the introduction of heterologous cytoplasm into the eggplant. This is a common phenomenon; for example, when the cytoplasm of *Brassica juncea* was replaced in *Enarthrocarpus lyratus*, pollen fertility was reduced (Banga et al. 2003). The results of this study are almost identical to the pollen staining and germination rates shown in the papers that generated these male sterile lines (Isshiki and Kawajiri 2002; Khan and Isshiki 2009, 2010, 2011; Hasnunnahar et al. 2012), indicating that pollen fertility is stably low from generation to generation.

The seed fertility of the CMS lines is described next (Figures 3 and 5). There were no significant differences in fruit set among all tested lines when pollinated with 'Uttara' pollen (Figure 3). This suggests that there is no adverse effect of cytoplasmic substitution on the rate of fruit set. Khan et al. (2023) compared the fruit set of 'Uttara' with that of CMS KUR and VIO and found that 'Uttara' had a statistically significantly higher fruit set rate than CMS KUR and VIO. The reason for the difference between the current and previous surveys may seem purely coincidental. In any case, the fruit set of 'Uttara' tends to be higher than that of the CMS KUR and VIO (Figure 3).

The number of seeds per fruit pollinated by 'Uttara' pollen was about 350 for 'Uttara,' the CMS KUR and VIO, and there was no statistically significant difference between them. Despite having heterologous cytoplasm, the CMS KUR and VIO had almost the same number of seeds per fruit as eggplant 'Uttara,' indicating that they did not have these negative effects. *Solanum kurzii* and *S. violaceum* are native to India, as is eggplant (Tegally et al. 2019; Aubriot et al. 2018; Sewa 2020; Mansa et al. 2021; Weese and Bohs 2010). They have also been taxonomically classified as belonging to the same group by inter-simple sequence repeat (ISSR) analysis (Isshiki et al. 2008). The relatively high F₁ fertility of *S. kurzii* and *S. violaceum* with eggplant (Isshiki and Kawajiri 2002; Khan and Isshiki 2009) suggests that hybridization compatibility is not low. The same result was obtained during a study of the number of seeds per fruit when pollinated with 'Uttara' pollen (Khan et al. 2023). Therefore, eggplant and these two species are considered to be very closely related, which may explain why the number of seeds per fruit has not changed much.

On the other hand, the number of seeds per fruit pollinated by 'Uttara' pollen was about 268 for CMS AET, 220 for RF AET, 163 for CMS ANG, 122 for RF ANG, 288 for CMS GRA, and 232 for RF GRA, which were lower than that of *S. melongena* 'Uttara.' This may be due to the fact that all of the cytoplasmic parents are African species (Weese and Bohs 2010; Taher et al. 2017), which have low hybrid compatibility with eggplant (Lester 1986; Lester and Daunay 2003; Lester and Niakan 1986; Lester and Thitai 1989).

Fruit set and number of seeds per fruit of cytoplasmic male sterility and fertility restoration lines, i.e., the CMS AET and the RF AET, the CMS ANG and the RF ANG, and the CMS GRA and the

RF GRA, were not significantly different from each other. It is assumed that the *Rf* gene is not associated with the formation of seeds. The *Rf* has been reported not to affect seed fertility in many plants (McVetty 1997).

The number of seeds per fruit averaged 163 for the CMS ANG and 122 for the RF ANG, statistically significantly lower than *S. melongena* 'Uttara' (Figure 4). This could be attributed to the extreme hybrid incompatibility of the cytoplasm of *S. anguivi* with the nucleus of the *S. melongena* 'Uttara.' It has been demonstrated cytogenetically that the genome of *S. anguivi* is highly homogeneous and likely represents a pure ancestral species among the African indigenous groups (Anaso 1991). The heterogeneity between this cytoplasmic genome and the nuclear genome in *S. melongena* may be the reason for the extremely low hybrid incompatibility with *S. melongena*.

Self-pollination of the CMS VIO, RF AET, and RF GRA lines resulted in only one fruit, with each fruit producing only a few dozen seeds. However, the seeds obtained germinated normally (data not shown). Although the pollen germination capacity of these three lines was low (8% to 24%), it can be assumed that fertilizable pollen grains are present. The other two lines, the CMS KUR and the RF ANG, are expected to produce progeny as the number of crosses increases. Therefore, these pollen grains from the two CMS lines and the three RF lines could be used for further crosses, anther culture, and other breeding experiments.

When incorporating CMS into seed parent lines for producing F₁ hybrids or for developing parthenocarpic varieties that produce seedless fruit, it is advisable to use the four lines that have consistently yielded a relatively high number of seeds per fruit: CMS KUR, VIO, AET, and GRA. The CMS AET and GRA have a slightly lower number of seeds per fruit, but still yielded over 220 seeds, which is considered sufficient for seed production. *Solanum anguivi* appears to be an unsuitable seed parent for the CMS due to its genomic heterogeneity, as described in the preceding section.

In conclusion, this study represents the first comprehensive report on the comparative analysis of fertility traits using a large number of CMS lines in eggplant. This groundbreaking research offers valuable insights into the genetic and phenotypic variations that influence fertility traits in eggplant, with significant implications for breeding programs and agricultural practices worldwide. We are currently conducting extensive field trials of the CMS lines in collaboration with several leading seed companies. These trials are designed to evaluate the performance and stability of the CMS lines under different environmental conditions and to assess their potential for commercial use. Working with seed companies ensures that the results of our research are directly applicable to real-world agricultural scenarios, facilitating the development of seedless eggplant varieties. In the future, we plan to expand our research by analyzing the results of this study alongside those from seedless lines developed through parthenocarpy.

Funding

This study was supported by the Japan Society for the Promotion of Science KAKENHI (Grant 21K05566).

Conflicts of Interest

No potential conflict of interest was reported by the author(s).

References

- Anaso, H. U. 1991. "Comparative Cytological Study of *Solanum aethiopicum*, Gilo Group, *Solanum aethiopicum* Shum Group and *Solanum anguivi*." *Euphytica* 53: 81–85.
- Aubriot, X., S. Knapp, M. M. Syfert, P. Poczaï, and S. Buerki. 2018. "Shedding New Light on the Origin and Spread of the Brinjal Eggplant (*Solanum melongena* L.) and its Wild Relatives." *The American Journal of Botany* 105: 1175–1187.
- Banga, S. S., J. S. Deol, and S. K. Banga. 2003. "Alloplasmic Male-Sterile *Brassica juncea* with *Enarthrocarpus lyratus* Cytoplasm and the Introgression of Gene(s) for Fertility Restoration from Cytoplasm Donor Species." *Theoretical and Applied Genetics* 106: 1390–1395.
- Donzella, G., A. Spena, and G. L. Rotino. 2000. "Transgenic Parthenocarpic Eggplants: Superior Germplasm for Increased Winter Production." *Molecular Breeding* 6: 79–86.
- Hasnunnahar, M., M. M. R. Khan, and S. Isshiki. 2012. "Inheritance of Male Fertility Restoration of a Male Sterility System in Eggplant with the Cytoplasm of *S. grandifolium*." *Australian Journal of Crop Science* 6: 475–479.
- Isshiki, S., N. Iwata, and M. M. R. Khan. 2008. "ISSR Variations in Eggplant (*Solanum melongena* L.) and Related *Solanum* Species." *Scientia Horticulturae* 117: 186–190.
- Isshiki, S., and N. Kawajiri. 2002. "Effect of Cytoplasm of *Solanum violaceum*, Ort. On Fertility of Eggplant (*S. melongena* L.)." *Scientia Horticulturae* 93: 9–18.
- Kakizaki, Y. 1931. "Hybrid Vigor in Eggplant and Its Practical Utilization." *Genetics* 16: 1–25.
- Khan, M. M. R., and S. Isshiki. 2009. "Functional Male Sterility Expressed in Eggplant (*Solanum melongena* L.) Containing the Cytoplasm of *S. Kurzii* Brace & Prain." *The Journal of Horticultural Science and Biotechnology* 84: 92–96.
- Khan, M. M. R., and S. Isshiki. 2010. "Development of the Male-Sterile Line of Eggplant Utilizing the Cytoplasm of *Solanum aethiopicum* L. Aculeatum Group." *The Japanese Society for Horticultural Science* 79: 348–353.
- Khan, M. M. R., T. Arita, M. Iwayoshi, Y. Ogura-Tsujita, and S. Isshiki. 2023. "Seed Productivity of the CMS Eggplants Carrying *Solanum kurzii* and *S. violaceum* Cytoplasm in the Temperate and Subtropical Areas." *Journal of the Japanese Society of Agricultural Technology Management* 30: 77–80. (In Japanese with English summary).
- Khan, M. M. R., and S. Isshiki. 2011. "Development of a Cytoplasmic Male-Sterile Line of Eggplant (*Solanum melongena* L.) with the Cytoplasm of *Solanum anguivi*." *Plant Breeding* 130: 256–260.
- Lester, R. N. 1986. "Taxonomy of Scarlet Eggplants, *Solanum aethiopicum* L." *Acta Horticulturae* 182: 125–132.
- Lester, R. N., and L. Niakan. 1986. *Origin and Domestication of the Scarlet Eggplant, Solanum aethiopicum, from S. anguivi in Africa*. Solanaceae: Biology and systematics, 433–456.
- Lester, R. N., and M. C. Daunay. 2003. "Diversity of African vegetable *Solanum* species and its implications for a better understanding of plant domestication." *Schriften zu Genetischen Ressourcen* 22: 137–152.
- Lester, R. N., and G. N. W. Thitaiz. 1989. "Inheritance in *Solanum aethiopicum*, the Scarlet Eggplant." *Euphytica* 40: 67–74.
- Manasa, A. P., S. Moutusi, D. C. Mendez, P. Kiranmayee, and M. K. Prasannakumar. 2021. "Phytochemical Distribution, Antimicrobial Activity, Enzyme Production of Phylogenetically Differentiated Endophytes from, *Solanum violaceum* Ortega Fruits." *Current Research in Environmental & Applied Mycology (Journal of Fungal Biology)* 11: 210–229.
- McVetty, P. B. E. 1997. "Cytoplasmic Male Sterility." In *Pollen Biotechnology for Crop Production and Improvement*, edited by K. R. Shivanna and V. K. Sawhney, 155–182. Cambridge University Press.
- Saito, T., K. Miyatake, Y. Shinmura, and H. Matsunaga. 2019. *Development of the Parthenocarpic Eggplant Cultivars* 54: 151–155. (In Japanese with English summary).
- Sambandum, C. N. 1962. "Heterosis in Eggplant (*Solanum melongena* Linn.) Prospects and Problems in Commercial Production of Hybrid Seeds." *Economic Botany* 16: 71–76.
- Sewa, N. K., A. Bora, J. Das, and S. K. Dwivedi. 2020. "Ethnobotanicals of Senapati District of Manipur in North East India." *World Journal of Pharmaceutical Sciences* 8: 96–101.
- Singh, R. J. 2002. *Plant Cytogenetics*. 2nd ed., CRC Press Inc.
- Taher, D., S. Ø. Solberg, J. Prohens, Y. Chou, M. Rakha, and T. Wu. 2017. "World Vegetable Center Eggplant Collection: Origin, Composition, Seed Dissemination and Utilization in Breeding." *Frontiers in Plant Science* 8: 1484. <https://doi.org/10.3389/fpls.2017.01484>.
- Tegally, A., Y. Jaufeerally-Fakim, and M. E. Dulloo. 2019. "Molecular Characterization of *Solanum melongena* L. and the Crop Wild Relatives, *S. violaceum* Ortega and *S. torvum* Sw., Using Phylogenetic/DNA Barcoding Markers." *Genetic Resources and Crop Evolution* 66: 1625–1634.
- Weese, T. L., L. Bohs, 2010. "Eggplant Origins: Out of Africa, into the Orient." *Taxon* 59: 49–56.
- Yamaguchi, M. 1983. "Eggplant, Aubergine, Guinea Squash, Brinjal, Berenjena: *Solanum melongena*." In *World Vegetables*, edited by M. Yamaguchi, 298–303. AVI.