



Research article

## Metaxenia effects on fruit quality attributes in diverse passion fruit (*Passiflora edulis*) crosses

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### Abstract

**Importance of the work:** Metaxenia as a result of cross-pollination in passion fruit affects the quality of the fruit produced.

**Objectives:** To investigate the effect of metaxenia on fruit quality produced from crosses of different types of passion fruit.

**Materials and Methods:** A completely randomized design was used, with crossing parental and crosses between passion fruit types as treatments, namely red-skinned with an oval-shape (ML), red-skinned with a round-shape (MB), yellow-skinned with yellow-pulp (KK), yellow-skinned with orange-pulp (KO) from *Passiflora edulis* f. *edulis* and yellow-skinned from *Passiflora edulis* f. *flavicarpa* (FF).

**Results:** Crossing various types of passion fruit produced metaxenia effects on the characteristics of fruit length, fruit shape, fruit pulp color, total soluble solid value and sweetness of passion fruit. However, the characteristics of fruit width, fruit weight, number of seeds, total titratable acid and edible portion percentage were not influenced by the source of pollen used in the cross. The cross combination between the KO and ML passion fruit types produced superior fruit from both parents in terms of fruit length (up to 8.62 cm), total soluble solids (reaching 17.2°Brix) and fruit sweetness (score of up to 3.40). However, the metaxenia effect from the other cross combinations tended to reduce fruit quality.

**Main finding:** The effect of metaxenia on passion fruit tended to reduce fruit quality. Therefore, it is advisable to avoid the co-cultivation of multiple passion fruit types within the same growing area, to maintain superior fruit quality, especially in fruit sweetness.

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## Introduction

Passion fruit (*Passiflora edulis* Sims.) is a tropical fruit often referred to as the “King of Fruit Juices” because of its unique aroma and refreshing flavor (He et al., 2020). It is enjoyed in fresh and processed forms, particularly as juice, rich in essential nutrients and beneficial compounds (Zhang et al., 2023). Besides juice, passion fruit is commonly incorporated into various food products such as cakes, ice cream, fruit vinegar and cocktails (He et al., 2020; Lamsis, 2025). In addition, its seeds and peel are valuable by-products, as they contain bioactive compounds and oils high in polyunsaturated fatty acids, which contribute to the nutritional quality of foods and act as natural preservatives (Moia et al., 2019; Dos Santos et al., 2021). Beyond its culinary uses, passion fruit is recognized for its wide range of pharmacological effects, including antidiabetic, anti-anxiety, antitumor, antioxidant, pain-relieving and anti-inflammatory properties (Dos Santos et al., 2021; Rai et al., 2022).

The growing importance of passion fruit in the food and pharmaceutical sectors has resulted in it becoming a focal point of cultivation research (especially in the technical aspects) to increase production and fruit quality (Arshad et al., 2025). Passion fruit production in Indonesia has fluctuated and has tended to decline, from 113,130 t in 2015 to only 53,319 t in 2020 (Central Bureau of Statistics, 2020). This downward trend reflects production constraints, including limited availability of high-quality cultivars and vulnerability to pests and diseases (Chepkoech et al., 2023). In addition, consumer preferences are shifting toward sweeter, more aromatic fruits with attractive appearance (Stiletto and Trestini, 2021), driving the need for fruit quality improvement alongside yield enhancement. Therefore, breeding strategy and agronomic approaches to enhancing yield and fruit quality have become increasingly critical. Key attributes that define fruit quality include color, shape, size and taste (Callahan, 2003; Kumar et al., 2023). Generally, references related to passion fruit *P. edulis* f. *edulis* report that this form of passion fruit has a sour fruit flavor. Based on the evaluation results of dos Reis et al. (2018) on purple-colored *P. edulis* f. *edulis*, this passion fruit had a sour taste with a total soluble solid value of 11.6°Brix. However, Sutoyo et al. (2023) reported that red and yellow-skinned variants of *P. edulis* f. *edulis* grown in Padang City, Indonesia, at 163 m above mean sea level produced fruit with a noticeably sweeter flavor, reaching a total soluble solid value of 19.5°Brix.

The sweet passion fruit is distinguished by its yellow-skin and pale yellow pulp, with its flavor being similar to that of *P. ligularis*, which has adapted to high altitudes in Indonesia around 1,450 m above mean sea level in Bukit Batabuah, Agam Regency and Alahan Panjang, Solok Regency (Hayati, 2021). However, passion fruit is self-incompatible and thus depends on cross-pollination for reproduction (Bruckner et al., 1995; Do Rêgo et al., 1999). As a cross-pollinated (allogamous) species, it exhibits considerable genetic variation among its progeny, making it difficult to maintain uniform fruit quality (Deng et al., 2022). Additionally, cross-pollination can lead to metaxenia, a phenomenon where the pollen donor affects the taste and overall quality of the fruit (Militaru et al., 2015; Saini et al., 2022).

Xenia refers to the direct influence of pollen on the tissues derived from fertilization, specifically the embryo and endosperm. In contrast, metaxenia describes the effect of pollen on fruit characteristics such as shape, pericarp color and chemical composition (Saini et al., 2022). These effects have been documented in several crops, including alterations in fruit weight, seed size and oil content in tung trees (Qin et al., 2020), cob diameter, seed number, seed weight, seed color, seed shape, protein content and oil content in maize (Kahrman et al., 2017; Trihatmojo et al., 2017), fruit weight, fruit color, fruit size, fruit flavor and storability of strawberry fruit (Tuohimetsä et al., 2014; Dung et al., 2023), fruit set, fruit retention, fruit weight, fruit size and number of seeds in grapes (Sabir, 2015; Dhakad et al., 2024).

Despite evidence of metaxenia effects in crops including maize, grapes and strawberries, limited scientific information exists regarding its role in passion fruit, particularly concerning fruit quality attributes in different cross combinations. The lack of studies on the impact of metaxenia is an obstacle in efforts to market passion fruit with consistent quality, especially in lowland passion fruit types that show potential for sweetness and good adaptation to tropical environments. Therefore, this study aimed to evaluate the effect on fruit quality of the pollen source from different types of *P. edulis*. The results of this study should provide a scientific basis for the development of passion fruit cultivation and breeding techniques to improve fruit quality.

## Materials and Methods

### Experimental design and cultural practices

The research was conducted from October 2023 to March 2024 at the Research Station (0°55'22.72"S, 100°27'17.60"E, 163 m above mean sea level) and the Plant Physiology Laboratory of the Faculty of Agriculture, Universitas Andalas, Padang City, Indonesia. The study involved several passion fruit types: red-skinned passion fruit with an oval-shape (ML), red-skinned passion fruit with a round-shape (MB), yellow-skinned passion fruit with yellow-pulp (KK), yellow-skinned passion fruit with orange-pulp (KO) from *P. edulis* f. *edulis* and yellow-skinned passion fruit from *P. edulis* f. *flavicarpa* (FF). The passion fruit plants used were the result of natural crosses having diverse fruit characteristics and high adaptability in the lowlands. This diversity of fruit characteristics allows for a better evaluation of the effects of metaxenia, which subsequently could be used to inform the production of superior quality passion fruit from the lowlands.

The experiment was designed using a completely randomized design, with crossing parental and crosses between the passion fruit types consisting of 14 cross combinations as treatments, with parents presented as female × male, namely: ML × KK, KK × ML, MB × ML, ML × MB, KK × MB, MB × KK, KO × ML, ML × KO, KO × MB, MB × KO, KK × KO, KO × KK, KK × FF and FF × KK. In total, 8–30 of each cross were performed, depending on the availability of flowers during the crossing period. Fruit characteristic data were collected from three separate crosses. Additionally, the characteristics of crossed fruits were compared to those of their respective parental plants obtained from crosses between plants of the same type.

All plants were cultivated under optimal agronomic conditions, including pruning, weeding, pest and disease control and manuring. The pruning done during the study was secondary pruning to multiply tertiary branches. Further pruning was done to remove unproductive branches. Weeding was done once a month to remove weeds growing around the plantation area. Diseases that appeared on the passion fruit plants were fusarium wilt and stem base rot; they were controlled by spraying fungicides according to established practice containing *Bacillus amyloliquefaciens*, *Bacillus pumilus* and *Bacillus licheniformis*. Fruit fly pest control was carried out by applying insecticides containing methyl eugenol (800 g/L). Furthermore, plant manuring was carried

out according to the type and dosage recommended by Silalahi et al. (2010), namely urea, 117 g/plant, SP-36, 75 g/plant and KCl, 45 g/plant, applied at intervals of once every 3 mo.

### Controlled pollination

Flowers designated as female parents underwent emasculation in the late afternoon before the scheduled crossing. The only flower buds selected were in the advanced developmental stage and were expected to bloom the following day. These selected flowers were isolated in paper bags to prevent unwanted pollination. Pollen donors were selected from the fully bloomed flowers of the male parents. The pollination process involved transferring pollen from the male parent anther to the stigma of the pre-isolated female flower. The pollination was conducted during 1200–1400 hours to optimize pollination success. Following pollination, the flowers were re-isolated in paper bags and labelled with the parental cross information and the crossing date.

### Data collection

Successful crossing was determined by monitoring flower retention 5–7 d after pollination (DAP). The resulting fruits were evaluated upon reaching full maturity, which occurred around 60–65 DAP, marked by a color transition to red in the red-skinned types and to yellow in the yellow-skinned types.

The study recorded various parameters: crossing success rate, fruit set, fruit length, fruit width, fruit weight, fruit skin thickness, the number of seeds, fruit shape, fruit skin color, fruit pulp color, total soluble solids (TSS), total titratable acid (TTA), fruit sweetness and edible portion percentage. The rate of crossing success was calculated using Equation (1):

$$\text{Crossing success rate (\%)} = \frac{\text{Number of successful crosses}}{\text{Total crosses}} \times 100 \quad (1)$$

Fruit set was calculated using Equation (2):

$$\text{Fruit set (\%)} = \frac{\text{Crosses surviving until harvest}}{\text{Total crosses}} \times 100 \quad (2)$$

Morphological parameters and fruit flavor were observed from three fruits. Fruit weight was measured using a digital balance, while fruit length and width were monitored based on measuring the transverse and longitudinal diameters of the fruit using calipers.

Fruit skin thickness was measured by cutting the fruit transversely and measuring three sides of the fruit skin using calipers and the mean value of fruit skin thickness was recorded. Any fruit that had been cut open to collect data on fruit skin thickness was subsequently counted for the number of seeds.

TSS were measured using a hand-held refractometer, while five panelists who had undergone preparatory training assessed fruit sweetness organoleptically. The assessed fruit flavor was assigned to one of five categories: 1) very sour; 2) sour; 3) sweet-sour; 4) sweet; and 5) very sweet. The TTA analysis followed the procedure outlined by Tadele et al. (2022), where 10 g of fruit juice was diluted with 250 mL water. The solution was titrated with 0.1 N NaOH using 2–3 drops of 1% phenolphthalein as an indicator solution. Then, the amount of NaOH used was recorded. Finally, the TTA percentage was calculated based on the recorded data using Equation (3):

$$\text{TTA (\%)} = \left( \frac{\text{Volume titre} \times \text{Normality NaOH} \times \text{Meq of citric acid}}{\text{Volume of sampel taken}} \right) \times 100 \quad (3)$$

where Meq (milliequivalent) is the correction factor for anhydrous citric acid (0.064) and volumes are in milliliters.

The edible portion was determined by separating the fruit peel from the pulp, then weighing the pulp and calculating the edible portion percentage using Equation (4):

$$\text{Edible portion (\%)} = \left( \frac{\text{Weight of fruit pulp}}{\text{Weight of whole fruit}} \right) \times 100 \quad (4)$$

where all weights were measured in grams.

### Statistical analysis

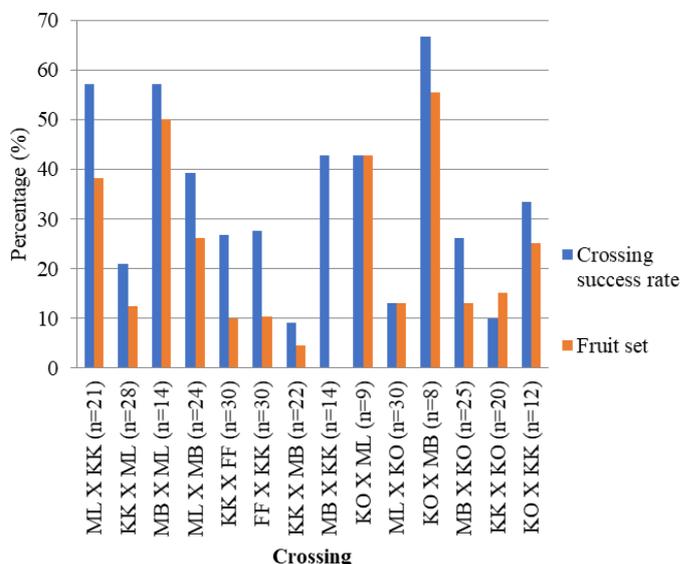
The quantitative data on fruit quality attributes were analyzed to determine significant differences between the crossed fruits and their parental lines. A *t*-test at the 5% significance level ( $p < 0.05$ ) was used to compare the mean values of each trait. All quantitative data were processed using STAR software (STAR 2.0.1; IRRRI, Philippines) and Microsoft Excel (Microsoft Corp.; USA).

## Results and Discussion

### Crossing success and fruit formation

The cross-pollination and fruit formation success rates varied considerably among the different types of passion fruit

crossings (Fig. 1). The KO × MB cross produced the highest percentages of crossing success and fruit formation of all the tested crosses (66% and 55%, respectively). The cross MB × KK had a cross success percentage of 42%; however, all developing fruits aborted before reaching maturity. Likewise, the reciprocal cross had a minimal fruit formation success rate of only 5%, rendering further analysis of fruit characteristics from the cross MB × KK infeasible.

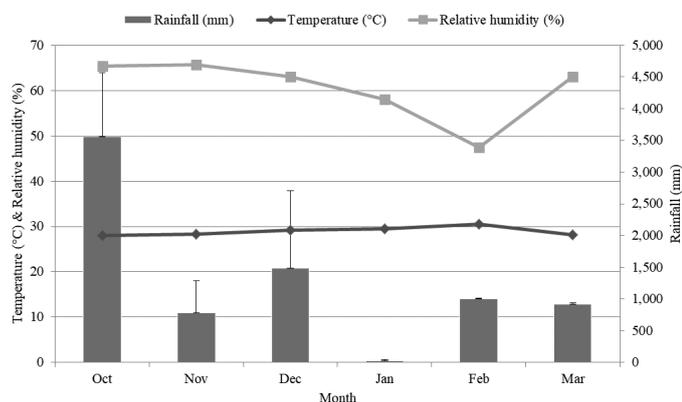


**Fig. 1** Percentage crossing success and fruit set from cross combinations of various passion fruit types, where n= number of crosses, ML = red-skinned with an oval-shape; MB = red-skinned with a round-shape; KK = yellow-skinned with yellow-pulp, KO = yellow-skinned with orange-pulp (from *Passiflora edulis* f. *edulis*) and FF = yellow-skinned (from *Passiflora edulis* f. *flavicarpa*).

The percentages of crossing success and fruit formation differed significantly among the 14 crossing combinations evaluated. Key factors influencing these outcomes were the pollen source, stigma receptivity and environmental conditions such as temperature (Din et al., 2019). However, the findings from the different passion fruit crosses revealed no consistent pattern of successful pollination or fruit formation linked to any specific passion fruit type. None of the passion fruit types had consistently high compatibility when used as either male or female parents in the crosses.

In addition to genetic compatibility between parent plants, environmental conditions such as temperature, humidity and rainfall played a crucial role in determining the success of pollination and fruit set. During the study, notable variations in climate were observed, with temperatures in the range 28–31°C, relative humidity in the range 78–94% and

monthly rainfall levels in the range 29.4–3,556.9 mm (Fig. 2). These environmental conditions did not align with the optimal climate parameters for yellow passion fruit (*P. edulis* f. *flavicarpa*), which prefers temperatures of 22–25°C, relative humidity of 70% and annual rainfall in the range 800–1,500 mm (Fischer and Miranda, 2021).



**Fig. 2** Temperature (Temp), relative humidity (RH) and rainfall conditions during study period (October 2023–March 2024), where error bars =  $\pm$  SD

Unfavorable environmental conditions significantly impacted the success of crossing and subsequent fruit set in passion fruit. When average temperatures exceed 28°C, vegetative growth is enhanced, but fruit production declines due to stigma dehydration, which hampers fertilization

(Fischer et al., 2009). Furthermore, the fertilization process was disrupted by large variations in moisture from drought to heavy rainfall. Notably, rainfall patterns affected pollen availability, with levels below 5 mm/hr reducing pollen presence. This reduction is further influenced by environmental factors such as temperature, humidity and day length (Kluska et al., 2020).

### Morphological characteristics of fruit from crosses

The fruit morphology from the different crossing combinations showed notable variation (Table 1). Specifically, the KO  $\times$  ML cross produced significantly longer fruits than both parent plants. Of the 12 hybrid combinations evaluated, only one, accounting for 8%, showed a clear metaxenia effect on fruit length. This finding aligned with other studies that reported the influence of pollen source on fruit length in crops such as Mandarin Clementine orange (Jahromi et al., 2019), edible fig (Koşar et al., 2022) and Japanese plum (Deng et al., 2022). However, the metaxenia effect on fruit length was not consistent across all hybrid combinations, likely because such effects only manifested in specific cultivars. According to Shahsavar and Shahhosseini, (2022), certain genotypes contain higher concentrations of gibberellic acid and indole-3-acetic acid hormones in the reproductive organs, which can trigger metaxenia effects during various stages of fruit development.

**Table 1** Fruit length, fruit width, fruit weight, skin thickness and seed number of 12 cross combinations of various passion fruit types

Types and their cross	Fruit length (cm) (mean $\pm$ SD)	Fruit width (cm) (mean $\pm$ SD)	Fruit weight (g) (mean $\pm$ SD)	Fruit skin thickness (cm) (mean $\pm$ SD)	Seed number (mean $\pm$ SD)
ML	6.67 $\pm$ 0.63 <sup>ns</sup>	6.07 $\pm$ 0.52 <sup>ns</sup>	93 $\pm$ 6.65 <sup>ns</sup>	0.45 $\pm$ 0.08 <sup>ns</sup>	263 $\pm$ 9.18 <sup>ns</sup>
KK	7.56 $\pm$ 0.44 <sup>ns</sup>	6.69 $\pm$ 0.12 <sup>ns</sup>	108 $\pm$ 3.86 <sup>ns</sup>	0.47 $\pm$ 0.03 <sup>ns</sup>	207 $\pm$ 14.84 <sup>ns</sup>
ML $\times$ KK	7.03 $\pm$ 0.76	6.07 $\pm$ 0.75	96.67 $\pm$ 28.01	0.50 $\pm$ 0.10	211 $\pm$ 50.90
KK	7.56 $\pm$ 0.44 <sup>ns</sup>	6.69 $\pm$ 0.12 <sup>ns</sup>	108 $\pm$ 3.86 <sup>ns</sup>	0.47 $\pm$ 0.03 <sup>ns</sup>	207 $\pm$ 14.84 <sup>ns</sup>
ML	6.67 $\pm$ 0.63 <sup>ns</sup>	6.07 $\pm$ 0.52 <sup>ns</sup>	93 $\pm$ 6.65 <sup>ns</sup>	0.45 $\pm$ 0.08 <sup>ns</sup>	263 $\pm$ 9.18 <sup>ns</sup>
KK $\times$ ML	8.13 $\pm$ 0.62	7.12 $\pm$ 0.43	101.5 $\pm$ 20.51	0.34 $\pm$ 0.00	204 $\pm$ 84.85
MB	7.08 $\pm$ 0.40 <sup>ns</sup>	6.84 $\pm$ 0.43 <sup>ns</sup>	115 $\pm$ 5.72 <sup>ns</sup>	0.51 $\pm$ 0.09 <sup>ns</sup>	260 $\pm$ 17.91 <sup>ns</sup>
ML	6.67 $\pm$ 0.63 <sup>ns</sup>	6.07 $\pm$ 0.52 <sup>ns</sup>	93 $\pm$ 6.65 <sup>ns</sup>	0.45 $\pm$ 0.08 <sup>ns</sup>	263 $\pm$ 9.18 <sup>ns</sup>
MB $\times$ ML	7.28 $\pm$ 0.65	6.80 $\pm$ 0.42	120.7 $\pm$ 33.23	0.36 $\pm$ 0.06	233 $\pm$ 44.91
ML	6.67 $\pm$ 0.63 <sup>ns</sup>	6.07 $\pm$ 0.52 <sup>ns</sup>	93 $\pm$ 6.65 <sup>ns</sup>	0.45 $\pm$ 0.08 <sup>ns</sup>	263 $\pm$ 9.18 <sup>ns</sup>
MB	7.08 $\pm$ 0.40 <sup>ns</sup>	6.84 $\pm$ 0.43 <sup>ns</sup>	115 $\pm$ 5.72 <sup>ns</sup>	0.51 $\pm$ 0.09 <sup>ns</sup>	260 $\pm$ 17.91 <sup>ns</sup>
ML $\times$ MB	7.21 $\pm$ 0.63	6.40 $\pm$ 0.76	109 $\pm$ 37.51	0.45 $\pm$ 0.14	222 $\pm$ 91.01
KO	7.82 $\pm$ 0.07 <sup>*</sup>	6.85 $\pm$ 0.11 <sup>ns</sup>	95 $\pm$ 6.13 <sup>ns</sup>	0.72 $\pm$ 0.17 <sup>ns</sup>	268 $\pm$ 6.60 <sup>ns</sup>
ML	6.67 $\pm$ 0.63 <sup>*</sup>	6.07 $\pm$ 0.52 <sup>ns</sup>	93 $\pm$ 6.65 <sup>ns</sup>	0.45 $\pm$ 0.08 <sup>ns</sup>	263 $\pm$ 9.18 <sup>ns</sup>
KO $\times$ ML	8.62 $\pm$ 0.43	7.19 $\pm$ 0.50	115 $\pm$ 14.14	0.74 $\pm$ 0.70	239 $\pm$ 36.77
ML	6.67 $\pm$ 0.63 <sup>ns</sup>	6.07 $\pm$ 0.52 <sup>ns</sup>	93 $\pm$ 6.65 <sup>ns</sup>	0.45 $\pm$ 0.08 <sup>ns</sup>	263 $\pm$ 9.18 <sup>ns</sup>
KO	7.82 $\pm$ 0.07 <sup>ns</sup>	6.85 $\pm$ 0.11 <sup>ns</sup>	95 $\pm$ 6.13 <sup>ns</sup>	0.72 $\pm$ 0.17 <sup>ns</sup>	268 $\pm$ 6.60 <sup>ns</sup>
ML $\times$ KO	6.13 $\pm$ 0.45	6.00 $\pm$ 0.30	82.5 $\pm$ 9.19	0.37 $\pm$ 0.07	128 $\pm$ 49.50
KO	7.82 $\pm$ 0.07 <sup>ns</sup>	6.85 $\pm$ 0.11 <sup>ns</sup>	95 $\pm$ 6.13 <sup>ns</sup>	0.72 $\pm$ 0.17 <sup>ns</sup>	268 $\pm$ 6.60 <sup>ns</sup>
MB	7.08 $\pm$ 0.40 <sup>ns</sup>	6.84 $\pm$ 0.43 <sup>ns</sup>	115 $\pm$ 5.72 <sup>ns</sup>	0.51 $\pm$ 0.09 <sup>ns</sup>	260 $\pm$ 17.91 <sup>ns</sup>
KO $\times$ MB	7.40 $\pm$ 0.78	6.38 $\pm$ 0.24	63 $\pm$ 11.31	0.36 $\pm$ 0.08	79 $\pm$ 42.43

**Table 1** Continued

Types and their cross	Fruit length (cm) (mean±SD)	Fruit width (cm) (mean±SD)	Fruit weight (g) (mean±SD)	Fruit skin thickness (cm) (mean±SD)	Seed number (mean±SD)
MB	7.08±0.40 <sup>ns</sup>	6.84±0.43 <sup>ns</sup>	115±5.72 <sup>ns</sup>	0.51±0.09 <sup>ns</sup>	260±17.91 <sup>ns</sup>
KO	7.82±0.07 <sup>ns</sup>	6.85±0.11 <sup>ns</sup>	95±6.13 <sup>ns</sup>	0.72±0.17 <sup>ns</sup>	268±6.60 <sup>ns</sup>
MB × KO	7.24±0.04	6.78±0.44	105±14.14	0.37±0.08	240±56.57
KK	7.56±0.44 <sup>ns</sup>	6.69±0.12 <sup>ns</sup>	108±3.86 <sup>ns</sup>	0.47±0.03 <sup>ns</sup>	207±14.84 <sup>ns</sup>
KO	7.82±0.07 <sup>ns</sup>	6.85±0.11 <sup>ns</sup>	95±6.13 <sup>ns</sup>	0.72±0.17 <sup>ns</sup>	268±6.60 <sup>ns</sup>
KK × KO	7.57±0.12	6.82±0.56	108.5±53.03	0.29±0.06	154±57.98
KO	7.82±0.07 <sup>ns</sup>	6.85±0.11 <sup>ns</sup>	95±6.13 <sup>ns</sup>	0.72±0.17 <sup>ns</sup>	268±6.60 <sup>ns</sup>
KK	7.56±0.44 <sup>ns</sup>	6.69±0.12 <sup>ns</sup>	108±3.86 <sup>ns</sup>	0.47±0.03 <sup>ns</sup>	207±14.84 <sup>ns</sup>
KO × KK	7.52±0.01	6.31±0.16	85±16.97	0.32±0.01	179±74.25
KK	7.56±0.44 <sup>ns</sup>	6.69±0.12 <sup>ns</sup>	108±3.86 <sup>ns</sup>	0.47±0.03 <sup>ns</sup>	207±14.84 <sup>ns</sup>
FF	8.21±0.20 <sup>ns</sup>	7.44±0.40 <sup>ns</sup>	153±7.48 <sup>ns</sup>	1.21±0.38 <sup>ns</sup>	330±14.84 <sup>ns</sup>
KK × FF	8.06±0.72	7.08±0.36	117.3±9.45	0.36±0.08	273±75.64
FF	8.21±0.20 <sup>ns</sup>	7.44±0.40 <sup>ns</sup>	153±7.48 <sup>ns</sup>	1.21±0.38 <sup>ns</sup>	330±14.84 <sup>ns</sup>
KK	7.56±0.44 <sup>ns</sup>	6.69±0.12 <sup>ns</sup>	108±3.86 <sup>ns</sup>	0.47±0.03 <sup>*</sup>	207±14.84 <sup>ns</sup>
FF × KK	7.93±0.00	7.43±0.25	145±1.41	0.78±0.16	279±7.78

Abbreviations for passion fruit types are provided in Fig. 1 caption.

\* = significantly ( $p < 0.05$ ) different from cross; ns = not significantly ( $p \geq 0.05$ ) different from cross, based on  $t$ -tests.

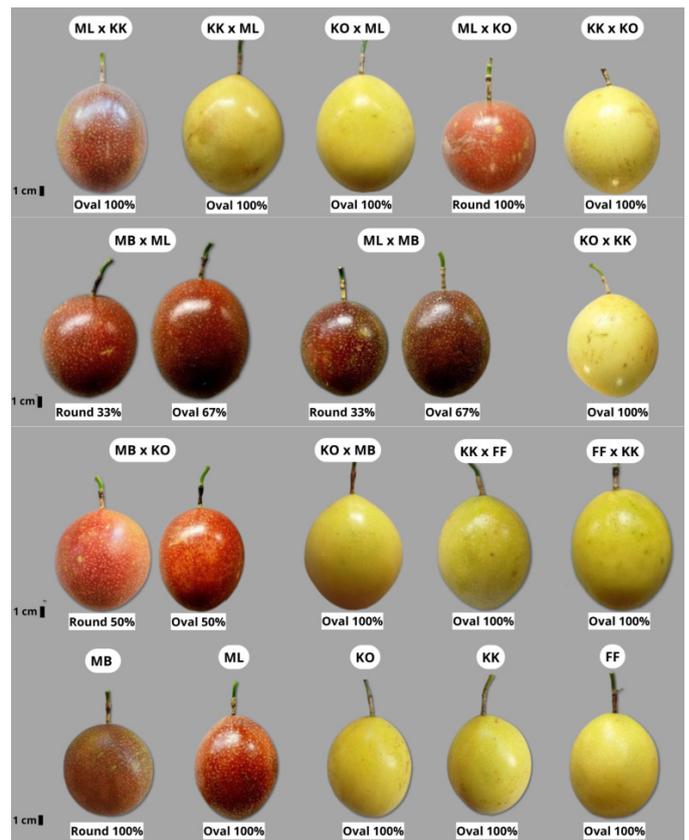
In contrast, no metaxenia effect was observed regarding fruit skin thickness among the passion fruit crosses. The FF × KK hybrid produced fruit with significantly thicker skin than the KK parent, but it did not differ significantly from the FF parent, suggesting that fruit skin thickness was largely influenced by the maternal parent, with limited impact from the pollen source.

Likewise, traits, such as fruit width, weight and seed number, did not show significant differences from either parent in any hybrid combination. In these cases, the offspring closely resembled their parental lines. Based on these results, among the traits evaluated, fruit length, width, weight, skin thickness and seed number, only fruit length produced an apparent metaxenia effect. This was particularly noticeable in crosses between yellow-skinned orange-pulp passion fruit and oval-shaped red passion fruit. These findings differed from those in grapevine studies, where metaxenia significantly affected multiple fruit traits, including length, width, size, weight and seed number (Sabir, 2015; Dhakad et al., 2024)

The metaxenia effect, where pollen from a different plant influences fruit traits, did not appear consistently across all passion fruit crosses. Typically, this effect occurs when there is genetic compatibility between the male and female parents for specific traits. As a result, not all cross combinations or fruit characteristics exhibited signs of metaxenia.

There were two primary forms of fruit shape among the hybrids: oval and round (Fig. 3). The crosses MB × ML, ML × MB and MB × KO produced fruits with variable shapes, showing both oval and round types. The ML × KO cross resulted in round fruits, even though both parent plants produced oval fruits, suggesting that metaxenia may have played a role in

influencing fruit shape in specific crosses, although its presence was not consistent across all combinations.



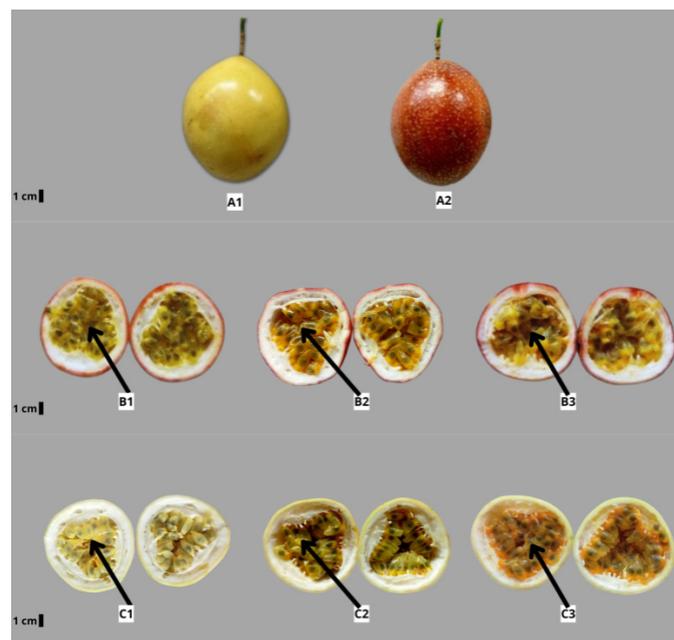
**Fig. 3** Fruit-shaped characteristics in crosses of various passion fruit types, where abbreviations for passion fruit types are provided in Fig. 1 caption and crosses MB × KK and KK × MB not included because they had no fruit set

The effect of metaxenia on fruit shape has been reported in apples (Bodor et al., 2008) and cucumbers (Olfati et al., 2010). The effect of metaxenia on fruit shape may occur because pollen from male parents carries genetic factors or physiological signals that can influence the development of fruit tissue from female plants. This begins with the initial interaction between the pollen and female tissue that affects the rate of cell division and expansion, followed by the transmission of signals from the pollen that affect metabolic pathways and hormone synthesis in female parent tissues, thus affecting the appearance of fruit shape (Widyasmara et al., 2018; Huang et al., 2020). This was consistent with Hu et al. (2011) and Nakata et al. (2012), whose studies on pumpkins indicated that fruit shape and size were determined by the dynamics of cell proliferation and expansion that external influences, including pollen, could modulate. Wang et al. (2022) added that regulatory genes, protein interactions and the balance of hormones, such as auxin and cytokinin, played important roles in shaping fruit morphology and could be affected by signals from foreign pollen through the mechanism of metaxenia.

Crossing different passion fruit types did not affect the fruit skin color, as all hybrids retained the same skin color as their female parent (Table 2). This observation differed from other studies on apples (Militaru et al., 2015) and pears (Cheng et al., 2020; Li et al., 2023), where changes in skin color were reported following cross-pollination.

In contrast, there was considerable variation in the color of the fruit pulp (Table 2 and Fig. 4). Crosses, such as KO × MB, MB × KO, KK × KO and FF × KK, produced diverse pulp colors, with

some hybrids resembling the male parent and others the female. Additionally, combinations, such as ML × MB, MB × ML, KK × FF and FF × KK, resulted in pulp colors that differed from both parents, including shades of pale yellow and orange-yellow.



**Fig. 4** Fruit skin color and fruit pulp color of crosses of different types of passion fruit, where abbreviations for passion fruit types are provided in Fig. 1 caption and A1= yellow-skinned, A2= red skinned, B1= red-skinned and yellow fruit pulp, B2= red skinned and orange fruit pulp, B3= red skinned and orange-yellow fruit pulp, C1= yellow skinned and pale yellow fruit pulp, C2= yellow skinned and yellow fruit pulp and C3= yellow skinned and orange fruit pulp

**Table 2** Characteristics of fruit skin and fruit pulp color from crosses of various types of passion fruit

Cross	Fruit skin color (n/Number of fruit)			Fruit pulp color (n/Number of fruit)		
	Red	Yellow	Yellow	Orange	Pale yellow	Orange yellow
ML × KK	3/3	-	3/3	-	-	-
KK × ML	-	3/3	3/3	-	-	-
MB × ML	3/3	-	-	1/3	-	2/3
ML × MB	3/3	-	1/3	1/3	-	1/3
KO × ML	-	3/3	3/3	-	-	-
ML × KO	3/3	-	3/3	-	-	-
KO × MB	-	3/3	1/2	1/2	-	-
MB × KO	3/3	-	1/2	1/2	-	-
KK × KO	-	3/3	1/2	1/2	-	-
KO × KK	-	3/3	-	3/3	-	-
KK × FF	-	3/3	1/3	-	2/3	-
FF × KK	-	3/3	2/3	-	-	1/3
MB	3/3	-	3/3	-	-	-
ML	3/3	-	3/3	-	-	-
KO	-	3/3	-	3/3	-	-
KK	-	3/3	3/3	-	-	-
FF	-	3/3	3/3	-	-	-

Abbreviations for passion fruit types are provided in Fig. 1 caption.

One notable example was the KO × ML cross, which exhibited a strong effect of metaxenia on pulp color. Although KO (female parent) has orange pulp and ML (male parent) has yellow pulp, all resulting fruits from this cross displayed yellow pulp. A similar metaxenia effect on pulp color has been observed in pomegranates (Gharaghani et al., 2017). The mechanisms behind xenia and metaxenia involve hormonal activity from the embryo or endosperm that diffuses into surrounding fruit tissues, influencing their development, with genetic factors, such as transposons and genomic imprinting, perhaps also playing a role in these phenomena (Saini et al., 2022).

### Flavor characteristics of fruit from crosses

There were notable differences in fruit flavor characteristics, particularly TSS, among the various parental crosses (Table 3). The KO × MB and KO × KK hybrids had significantly higher TSS levels than their female parents, though not significantly different from their male parents. Notably, the KO × ML cross-produced fruits with a TSS value of 17.2°Brix, exceeding both parent plants. In crosses where the female parent was a yellow-skinned, orange-pulp passion fruit, the TSS levels in the resulting hybrids were influenced by the male parent, indicating a metaxenia effect.

**Table 3** Fruit flavor characteristics and edible portion of crossed fruit

Cross	TSS (°Brix) (mean±SD)	TTA (%) (mean±SD)	Fruit sweetness (1–5) (mean±SD)	Edible portion (%) (mean±SD)
ML	14.7±0.5 <sup>ns</sup>	0.21±0.02 <sup>ns</sup>	2.67±0.09 <sup>ns</sup>	58.48±0.93 <sup>ns</sup>
KK	19.8±0.5 <sup>ns</sup>	0.12±0.01*	4.13±0.34 <sup>ns</sup>	54.66±0.94 <sup>ns</sup>
ML × KK	14±3.0	0.23±0.07	2.60±0.20	58.13±2.21
KK	19.8±0.5 <sup>ns</sup>	0.12±0.01 <sup>ns</sup>	4.13±0.34 <sup>ns</sup>	54.66±0.94 <sup>ns</sup>
ML	14.7±0.5*	0.21±0.02 <sup>ns</sup>	2.67±0.09*	58.48±0.93 <sup>ns</sup>
KK × ML	17±1.0	0.15±0.05	3.40±0.00	51.72±4.88
MB	16.3±0.9 <sup>ns</sup>	0.22±0.03 <sup>ns</sup>	2.60±0.16 <sup>ns</sup>	59.99±1.83 <sup>ns</sup>
ML	14.7±0.5 <sup>ns</sup>	0.21±0.02 <sup>ns</sup>	2.67±0.09 <sup>ns</sup>	58.48±0.93 <sup>ns</sup>
MB × ML	16±1.0	0.17±0.02	2.20±1.04	60.08±1.78
ML	14.7±0.5 <sup>ns</sup>	0.21±0.02 <sup>ns</sup>	2.67±0.09 <sup>ns</sup>	58.48±0.93 <sup>ns</sup>
MB	16.3±0.9 <sup>ns</sup>	0.22±0.03 <sup>ns</sup>	2.60±0.16 <sup>ns</sup>	59.99±1.83 <sup>ns</sup>
ML × MB	14±2.0	0.14±0.04	2.00±0.69	59.73±3.82
KO	15.3±0.2*	0.27±0.01 <sup>ns</sup>	2.47±0.09*	53.37±1.58 <sup>ns</sup>
ML	14.7±0.5*	0.21±0.02 <sup>ns</sup>	2.67±0.09*	58.48±0.93 <sup>ns</sup>
KO × ML	17.2±1.2	0.15±0.03	3.40±0.00	54.34±0.08
ML	14.7±0.5 <sup>ns</sup>	0.21±0.02 <sup>ns</sup>	2.67±0.09 <sup>ns</sup>	58.48±0.93 <sup>ns</sup>
KO	15.3±0.2 <sup>ns</sup>	0.27±0.01 <sup>ns</sup>	2.47±0.09 <sup>ns</sup>	53.37±1.58 <sup>ns</sup>
ML × KO	14.7±3.3	0.29±0.09	2.70±0.42	53.09±4.37
KO	15.3±0.2*	0.27±0.01 <sup>ns</sup>	2.47±0.09 <sup>ns</sup>	53.37±1.58 <sup>ns</sup>
MB	16.3±0.9 <sup>ns</sup>	0.22±0.03 <sup>ns</sup>	2.60±0.16 <sup>ns</sup>	59.99±1.83 <sup>ns</sup>
KO × MB	16±1.0	0.25±0.17	2.60±1.70	38.69±11.01
MB	16.3±0.9 <sup>ns</sup>	0.22±0.03 <sup>ns</sup>	2.60±0.16 <sup>ns</sup>	59.99±1.83 <sup>ns</sup>
KO	15.3±0.2 <sup>ns</sup>	0.27±0.01 <sup>ns</sup>	2.47±0.09 <sup>ns</sup>	53.37±1.58 <sup>ns</sup>
MB × KO	15±1.0	0.22±0.02	2.10±1.27	58.23±3.73
KK	19.8±0.5 <sup>ns</sup>	0.12±0.01 <sup>ns</sup>	4.13±0.34 <sup>ns</sup>	54.66±0.94 <sup>ns</sup>
KO	15.3±0.2 <sup>ns</sup>	0.27±0.01 <sup>ns</sup>	2.47±0.09 <sup>ns</sup>	53.37±1.58 <sup>ns</sup>
KK × KO	14±4.0	0.20±0.06	2.30±0.99	51.61±13.23
KO	15.3±0.2*	0.27±0.01*	2.47±0.09 <sup>ns</sup>	53.37±1.58 <sup>ns</sup>
KK	19.8±0.5 <sup>ns</sup>	0.12±0.01*	4.13±0.34 <sup>ns</sup>	54.66±0.94 <sup>ns</sup>
KO × KK	15.8±0.4	0.29±0.09	1.70±0.14	53.52±5.95
KK	19.8±0.5 <sup>ns</sup>	0.12±0.01 <sup>ns</sup>	4.13±0.34 <sup>ns</sup>	54.66±0.94 <sup>ns</sup>
FF	10.4±0.9*	0.38±0.01 <sup>ns</sup>	1.20±0.16*	47.95±0.81 <sup>ns</sup>
KK × FF	17±2.0	0.14±0.09	3.40±1.25	53.37±4.88
FF	10.4±0.9 <sup>ns</sup>	0.38±0.01 <sup>ns</sup>	1.20±0.16 <sup>ns</sup>	47.95±0.81 <sup>ns</sup>
KK	19.8±0.5 <sup>ns</sup>	0.12±0.01*	4.13±0.34 <sup>ns</sup>	54.66±0.94 <sup>ns</sup>
FF × KK	13±2.0	0.34±0.02	1.10±0.14	48.27±0.50

TSS = total soluble solids; TTA = total titratable acidity.

Fruit sweetness: 1) very sour, 2) sour, 3) sweet-sour, 4) sweet, and 5) very sweet.

\* = significantly ( $p < 0.05$ ) different from cross; ns = not significantly ( $p \geq 0.05$ ) different from cross, based on  $t$ -tests.

Conversely, no such effect was observed in other combinations, such as KK × ML and KK × FF, where the TSS values remained similar to those of the female parent, suggesting no influence from the pollen donor. In general, TSS patterns corresponded with the observed levels of fruit sweetness, although some inconsistencies were noted. For example, the KO × MB hybrid, despite having a higher TSS, did not differ significantly from either parent. However, its sweetness level matched that of the male parent (2.60) and was higher than the female parent's value (2.47). Importantly, none of the hybrids exceeded the highest recorded TSS (19.8°Brix) or sweetness level (4.13) found in the yellow passion fruit with yellow pulp, suggesting that metaxenia effects in the passion fruit crosses may lead to a reduction in both TSS and sweetness. Comparable influences of metaxenia on TSS have also been documented in other fruits such as papaya (Sharma and Singh, 2008), guava (Usman et al., 2013) and date palm (Maryam et al., 2023).

The passion fruit crosses showed relatively limited variation in TTA values (Table 3). Among all the tested combinations, only the KO × KK cross produced a TTA level significantly higher than both parent plants. In other hybrid combinations, the pollen donor had little to no influence on this trait. For example, the ML × KK and FF × KK crosses had TTA values significantly higher than the male parent, but not different from the female parent, indicating that acidity levels were primarily inherited from the maternal line.

The notable increase in TTA observed in the KO × KK cross was likely due to the combined metaxenia effect of both parent plants. Such a cumulative influence can occur when male and female parents contribute to the metaxenia effect on the resulting fruit. TTA represents the overall organic acid content in passion fruit, which is primarily made up of six acids: citric, malic, lactic, tartaric, ascorbic and acetic (Zhang et al., 2021). Among these, citric acid is the most abundant in *P. edulis* fruits.

Alterations in fruit flavor resulting from cross-pollination are driven by a combination of biochemical and genetic processes. For example, pollen from specific male parents can trigger metabolic shifts in the tissues of the female fruit, particularly affecting the synthesis of the sugars, organic acids and volatile compounds that determine flavor, involving changes in metabolite composition, genetic diversity and epigenetic modifications (Shahsavari and Shahhosseini, 2022; Chai et al., 2023). Genetic studies have shown that the perception of sweetness is controlled by particular genes, with differences in taste receptor function influencing sweetness levels (Kennedy et al., 1997). Additionally, epigenetic mechanisms (such as DNA methylation) can cause disruptions and imbalances in

allelic expression, thereby impacting the activity of genes related to flavor development in fruit crops (Zhou et al., 2023). As such, metaxenia affects fruit flavor stemming from inherited genetic traits and complex interactions between pollen-derived signals and the metabolic responses of the maternal plant.

The proportion of edible fruit in the hybrids did not differ significantly from the proportions of either the male or female parent (Table 3). This outcome may be attributed to maternal inheritance, where the trait is largely influenced by the female parent. A comparable maternal influence on the inheritance of edible portion traits has been reported in durian (Indriyani et al., 2012).

The effects of metaxenia can either increase or decrease fruit quality, with their effectiveness varying depending on the species involved and the specific conditions during pollination. For example, crossing *Vanilla planifolia* using pollen from *V. pompona* resulted in larger and heavier fruits, while the opposite cross produced smaller fruits (Barreda-Castillo et al., 2023). Likewise, based on the results of the current study, the effect of metaxenia on passion fruit plants could affect fruit quality, which generally tended to reduce fruit quality in crosses between passion fruit species, except for the ML × KO cross. This cross showed that the crossed fruits were superior to both parents, especially in the length (up to 8.62 cm), TSS (reaching 17.2°Brix) and fruit sweetness (scoring up to 3.40). However, reciprocal crosses of the ML and KO combination still showed a decrease in fruit quality.

In conclusion, these results could be applied in the passion fruit cultivation system, especially in regulating the varieties or types of passion fruit planted. To produce good fruit quality, it is recommended that various kinds of passion fruit not be grown on nearby land. However, further biochemical and molecular studies are still needed to identify the changes in the metabolites or gene expression that are involved in the decline in fruit quality due to metaxenia.

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### Conflict of Interest

The authors declare that there are no conflicts of interest.

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