



Inheritance Pattern of Fruit Color and Shape in Multi-Pistil and Purple Tomato Crossing

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ABSTRACT

Purple tomato is the only cultivated tomato containing anthocyanin inside the fruit, while multi-pistil tomato has a unique shape and the ability to be split into smaller parts without damaging the whole fruit. Purple tomato breeding is a new direction of agriculture research to enrich antioxidant fruit, which nowadays is increasingly in demand. The objective of this research was to obtain multi-pistil tomato fruit containing anthocyanin (purple colored), also to discover the inheritance patterns and heritability of qualitative traits related to fruit color and shape obtained from multi-pistil and purple tomato crossing. This research was conducted using seven populations consisted of 2 parental populations (Multi-pistil Tomato and Purple Tomato), 2 first progeny populations (F_1 and F_1 Reciprocal), 2 backcross populations ($BC_{1,1}$ and $BC_{1,2}$), and second progeny population (F_2). The result showed that pistil type, unripe fruit color, ripe fruit color, fruit shape and fruit type were inherited autosomally. The inheritance pattern of the traits followed the epistasis gene interaction with moderate to high heritability value.

INTRODUCTION

Fruit color and shape are two important factors in tomato for consumers. Consumers will pay more attention to fruit color and shape when choosing tomatoes for consumption (Fardhani, Ambarwati, Trisnowati, & Murti, 2013). Fruit color is a simple indicator of antioxidants content, such as purple as anthocyanin indicator (Gonzali, Mazzucato, & Perata, 2009). Meanwhile, fruit shape is closely related to fruit shelf life. Oblong-shaped fruits tend to have a longer shelf life than round and flattened fruits (Rachmatika, Murti, & Basunanda, 2017).

Nowadays, there is an increasing demand for anthocyanin-rich foods. The reason for this demand is related to anthocyanin effect in reducing the risk of chronic diseases in humans (Hassan & Abdel-Aziz, 2010). Anthocyanin is a flavonoid subcategory with the highest antioxidant activity (de Pascual-Teresa & Sanchez-Ballesta, 2008). Purple tomato breeding has become one of the recent works for anthocyanin-rich food production, given the higher consumption level compared to other anthocyanin-rich fruits such as berries.

The purple pigment of tomato fruit is an

expression of anthocyanin. Unfortunately, at the beginning, anthocyanin was not present in the fruit of cultivated tomato, which only produce anthocyanin in vegetative tissues (Mes, Boches, Myers, & Durst, 2008). Only small amounts of other flavonoids, such as naringenin chalcone and flavonols, can be found in the fruit (Muir et al., 2001; Torres, Davies, Yañez, & Andrews, 2005). The presence of anthocyanin in cultivated tomato is a result of anthocyanin-coding genes, *Aft* (anthocyanin fruit), *Abg* (aubergine), and *atv* (atroviolaceum). The dominant gene *Aft* (Anthocyanin fruit) was introgressed into domesticated tomato plants by a cross with *Solanum chilense* (Jones, Mes, & Myers, 2003), *atv* (atroviolacea) gene was derived from the interspecific cross with *Solanum cheesmanii*, and *Abg* (aubergine) gene was introgressed from *Solanum lycopersicoides* (Mes, Boches, Myers, & Durst, 2008).

In this study, purple tomato and multi-pistil tomato which have a unique fruit shape are crossed. Multi-pistil tomato looks like a few cherry tomatoes that merge. This tomato could be split into smaller parts (like cloves in garlic) without damaging the

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whole fruit (Grant, 2016). This allows the fruit to be stored again after being consumed partly.

Tomato fruit shape diversity is controlled by several genes, including *sun*, *ovate*, *Fasciated* (*Fas*), and *Locule number* (*Lc*) (Rodríguez et al., 2011). The locus *ovate* and *sun* regulate the fruit length. *Sun* encodes the fruit lengthening in a positive direction, while the *ovate* encodes the opposite direction (Liu, Van Eck, Cong, & Tanksley, 2002; Xiao, Jiang, Schaffner, Stockinger, & van der Knaap, 2008). *Fas* and *Lc* locus regulate the number of locules (fruit cavities), which have pleiotropic effects on the fruit shape. *Fas* mutations increase the number of sepals, petals, and carpels during flower development (Cong, Barrero, & Tanksley, 2008). Meanwhile, the *Lc* mutation produces paprika-shaped tomato (Rodríguez et al., 2011). The gene regulating the irregular shape of multi-pistil tomato is not known yet. However, there is a correlation to the *Eno* gene as a form of *Fas* mutation (Fernández-Lozano et al., 2015).

Until this research was conducted, there is no purple multi-pistil tomato has been found. Multi-pistil and purple tomato crossing is carried out to obtain purple multi-pistil tomato. However, before the breeding process advances to selection and further stages, it is important to know how the purple color and the unique shape of multi-pistil tomato are inherited to the next generation.

Several studies on fruit purple color inheritance have previously been reported. Jones, Mes, & Myers (2003) found that fruit purple color is controlled by a single dominant gene based on purple tomato (LA1996) and red tomato (UC82B) crossing. Li et al. (2018) used the crossing result between purple tomato (Zi Ying) and green tomato (Lv Ying) and reported a 1:3 (green: purple) distribution ratio with a possibility of major + polygene gene model interaction. Meanwhile, fruit shape inheritance is controlled by two loci with two alleles per locus where the gene follow dominant epistasis gene interaction. Several studies concluded that flattened tomato dominant over elliptic, circular, ovate, and pear-shaped tomato (Lindstorm, 1927; Murti, Ambarwati, & Supriyanta, 2000).

The objective of this research is to discover the inheritance pattern of fruit color and fruit shape from multi-pistil and purple tomato crossing. Knowledge of inheritance is important considering every trait has a different pattern. Traits inheritance information

has great impact and direction on developing and conducting plant breeding strategies (Hallauer, 2011). The number of genes involved can be estimated based on the frequency distribution of F_2 segregation and the narrow sense heritability can be estimated based on F_2 and backcross populations. Therefore, understanding the inheritance pattern and heritability value becomes very important to determine the next breeding stage, so the variety development program will run more effectively and efficiently.

MATERIALS AND METHODS

This study was conducted at the Center for Development of Food Crops and Horticulture Seedling Yogyakarta and Plant Breeding Laboratory UGM, in February-August 2019. Two tomato cultivars were used as crossbreeding parents, namely multi-pistil tomato (P_1) and purple tomato (P_2). From the crosses, five genetic populations were obtained, namely 2 first progeny populations (F_1 and F_1 reciprocal), second progeny population (F_2), and 2 backcross populations ($BC_{1.1}$ and $BC_{1.2}$). The number of individuals for P_1 , P_2 , F_1 , and F_{1R} were 80 plants each, F_2 was 640 plants, and 160 plants for each of $BC_{1.1}$ and $BC_{1.2}$.

Observations were made on 5 traits: pistil type, unripe fruit color, ripe fruit color, fruit shape, and fruit type.

Pistil Type

In each population group, 3 mature flowers were taken from each sample plant. Flower organs were examined using a magnifier. The flowers are observed to see the character of the pistil, whether the flower considered as single-pistil or multi-pistil.

Unripe and Ripe Fruit Color

Skin fruit color was observed visually in three fruits taken from the 2nd or 3rd fruit bunch which exposed to maximum sunlight, because anthocyanin requires direct sunlight exposure to be expressed (Jones, Mes, & Myers, 2003). Fruit colors were observed respectively under the unripe and ripe conditions. This observation is carried out to see the presence or absence of anthocyanin expression.

Fruit Shape

Fruit shape was observed in 3 mature fruits from each plant, which were taken from the 2nd or 3rd fruit bunch. This observation was based on the

categories of tomato shape released by UPOV (2001), which are flattened, slightly flattened, circular, rectangular, cylindrical, elliptic, heart-shaped, obovate, ovate, and pear-shaped.

Fruit Type

Fruit type observation was done by splitting 3 mature fruits from each sample plant, whether they are included in a single fruit (cannot be separated into smaller parts) or compound (easily separated into smaller parts).

Types of inheritance, inheritance patterns, and heritability were analyzed in three different ways. Type of inheritance aimed to determine that a trait is inherited chromosomally or extra-chromosomally. The comparing phenotypes of F_1 and F_1 reciprocal populations were done. Inheritance pattern was aimed to determine the number of genes control a trait. The test is carried out using the chi-square (χ^2) test on the F_2 population data. And, estimation of narrow-sense heritability is done by the Backcross-Warner method.

$$h^2 = \frac{2\sigma_{F_2}^2 - (\sigma_{BC1}^2 + \sigma_{BC2}^2)}{\sigma_{F_2}^2} \dots\dots\dots 1)$$

If the value of heritability (h^2) is < 0.2 , the inheritance potency is classified as low, if $0.2 < h^2 < 0.5$, then the heritability is moderate, and the h^2 value > 0.5 means high heritability.

RESULTS AND DISCUSSION

Types of Inheritance

A trait is inherited to the offspring in two ways, chromosomally (the genetic materials are located inside the chromosome) or extra-chromosomally (the genetic materials are located outside the cell nucleus, such as in the mitochondria or chloroplast). The type of inheritance is detected by comparing the F_1 phenotype with its reciprocity (F_{1R}). If there is no difference between F_1 and F_{1R} phenotype, it

means the trait is inherited chromosomally (Lönnig & Saedler, 2001).

The crossing parents have different characters in pistil type, unripe fruit color, ripe fruit color, fruit shape, and fruit type. Multi-pistil tomato has many pistils in one flower. Each pistil has its own ovule which develops into a whole fruit. Multi-pistil flowers produce many fruits in one petal (compound fruit), caused an irregular shape of the fruit. Multi-pistil fruit color is green in unripe condition and red when it's ripe. On the other parent, the purple tomato flower only has one pistil. The fruit is single-type and has a round shape. Unripe fruit color is purple and red-black when it's ripe as an anthocyanin expression.

The population phenotypes of F_1 and F_{1R} did not show any difference in the number of pistils, fruit color, fruit shape, and fruit type (Table 1). F_1 and F_{1R} populations have single-pistil flower and circular-single type fruit. The fruit color is green and red in unripe and ripe conditions, respectively. It shows that the genetic material regulating these traits (pistil type, fruit color, fruit shape, and fruit type) is located in the chromosome. This result corresponds to several previous gene mapping studies in tomato. The gene- regulating purple color (anthocyanin) in fruit is mapped on chromosome number 7 and number 10 in cultivated tomatoes (Boches & Myers, 2007). Other tomato fruit pigment genes have also been mapped: The *R* (red-lycopene) gene was found in chromosome number 3 (Fray & Grierson, 1993), *B* (β -carotene) gene in chromosome number 6 (Zhang & Stommel, 2000), and *gf* (green flesh) gene in chromosome number 8 (Akhtar et al., 1999). Studies on anthocyanin inheritance in vegetative organs of tomatoes (hypocotyl) conducted by Mustafa, Syukur, Sutjahjo, & Sobir (2016) also concludes that there is no difference between F_1 and F_{1R} phenotype.

Table 1. P_1 , P_2 , F_1 , and F_{1R} Phenotype

No	Characters	Generation			
		P_1	P_2	F_1	F_{1R}
1	Type of Pistil	Multi-pistil	Single-pistil	Single-pistil	Single-pistil
2	Unripe fruit color	Green	Purple	Green	Green
3	Ripe fruit color	Red	Red-Black	Red	Red
4	Fruit shape	Irregular	Circular	Circular	Circular
5	Fruit type	Compound	Single	Single	Single

Remarks: P_1 = multi-pistil tomato, P_2 = purple tomato, $F_1 = P_1 \times P_2$, and $F_{1R} = P_2 \times P_1$

In addition, the genes regulating fruit shape expressions (*sun*, *ovate*, *Fas*, and *Lc*) are also found in chromosomes. Based on the previous gene mapping studies, *sun* and *ovate* are located in chromosomes number 7 and chromosomes number 2, respectively (Liu, Van Eck, Cong, & Tanksley, 2002; Xiao, Jiang, Schaffner, Stockinger, & van der Knaap, 2008). Meanwhile, *Fas* and *Lc* are located in chromosome number 11 (Cong, Barrero, & Tanksley, 2008) and chromosome number 2 (Mayer et al., 1998; Rodríguez et al., 2011) on cultivated tomatoes.

Pattern of Inheritance

The phenotype of a trait is influenced by two main factors, genetic and environment. From the genetic side, the correlation between genes and the phenotype does not always appear directly. Different combinations of alleles of a gene may give rise to different manifestations (phenotypes). A dominant allele can suppress a recessive allele expression in the same locus. At the transcriptional level, dominant alleles show increased transcription and recessive alleles show decreased transcription, compared with the wild type (Wilkie, 2006). On the other hand, allele interactions at different loci

also can change the gene expressions, which often referred as epistasis effect. Most epistasis interactions are additive-additive models, although dominance-dominance and dominance-additive interactions may play a major role (Vitezica, Reverter, Herring, & Legarra, 2018).

Pistil Type

There are two pistil type phenotypes in the F_2 population, single-pistil, and multi-pistil (Fig. 1). The segregation of pistil type follows the double recessive epistasis gene interaction with a ratio of 9:7 (single-pistil:multi-pistil) (Table 2). Double recessive epistasis is a gene interaction where the dominant functional alleles at both loci are required for the expression of the phenotype. Presence of homozygous recessive alleles at either locus masks the phenotype (Pal, 2017). This means that the expression of multi-pistil flowers is controlled by two genes at two different loci. Multi-pistil flower type arises due to the presence of recessive homozygous allele pairs. Thus if both loci are heterozygous or homozygous dominant, the appeared phenotype will be single-pistil flowers. This finding was different from other crops.



Fig. 1. Pistil type variability in F_2 population

Table 2. Pistil type segregation

Inheritance Pattern	Ratio	Observed (O)		Expected (E)		χ^2 (3.841)**
		SP	MP	SP	MP	
Complete Dominance	3:1	309	254	422.25	140.75	121.497 *
Lethal Gene	2:1	309	254	375.33	187.67	35.170 *
Dominant-Recessive Epistasis	13:3	309	254	457.43	105.57	256.894 *
Double Dominant Epistasis	15:1	309	254	527.81	35.19	1451.391 *
Double Recessive Epistasis	9:7	309	254	316.69	246.31	0.426 ns

Remarks: ns = no significant, * = significantly differences between observed and expected value based on χ^2 test; ** = χ^2 table; SP = Single-pistil, MP = Multi-pistil

Studies on the inheritance of a multi-pistil trait in tomatoes have not been conducted a lot. Multi-pistil inheritance research has been mostly done on wheat and rice. Recent studies on wheat reported that multi-pistil flowers are controlled by a single recessive gene (Ma, Zhang, Liu, Wang, & Wang, 2000), a single semi-dominant gene (Zhu et al., 2019), and a single dominant gene (Wang et al., 2009). Meanwhile, research on rice shows that multi-pistil trait is controlled by a single recessive gene (Sahu, Sarawgi, & Tiwari, 2017).

Unripe Fruit Color (Anthocyanin Expression in Unripe Fruit)

The color segregation on unripe fruit in the F_2 population produced three-color phenotypes, green, shoulder-purple (purple only appears on the shoulder of the fruit), and purple (Fig. 2). The appearance of the phenotypes follows recessive epistasis gene interaction with a ratio of 9:3:4 (Table 3). Recessive epistasis is gene interaction where the presence of two recessive alleles at one locus

masks the phenotype of both alleles at the other loci (Pal, 2017). It can be concluded that the color of the unripe fruit is controlled by two loci with two alleles at each locus. The dominant genes at both locus whether it is homozygous or heterozygous raise the green color. Purple appears when there is a recessive homozygous allele pair at the second locus, while shoulder purple appears when there is a recessive homozygous allele pair at the first locus.

In previous studies, the inheritance of purple fruit color follows complete dominance gene interaction, although it was possible to be controlled by a pair of major genes that followed the major+polygene gene model (Li et al., 2018). The results of this study show a quite distinct difference from the results of the previous researches. It's due to the inheritance of the anthocyanin character is still not really understood because it is so complex (Kniewel, Abdel-Aal, Rabalski, Nakamura, & Hucl, 2009), both fruit and vegetative organs.

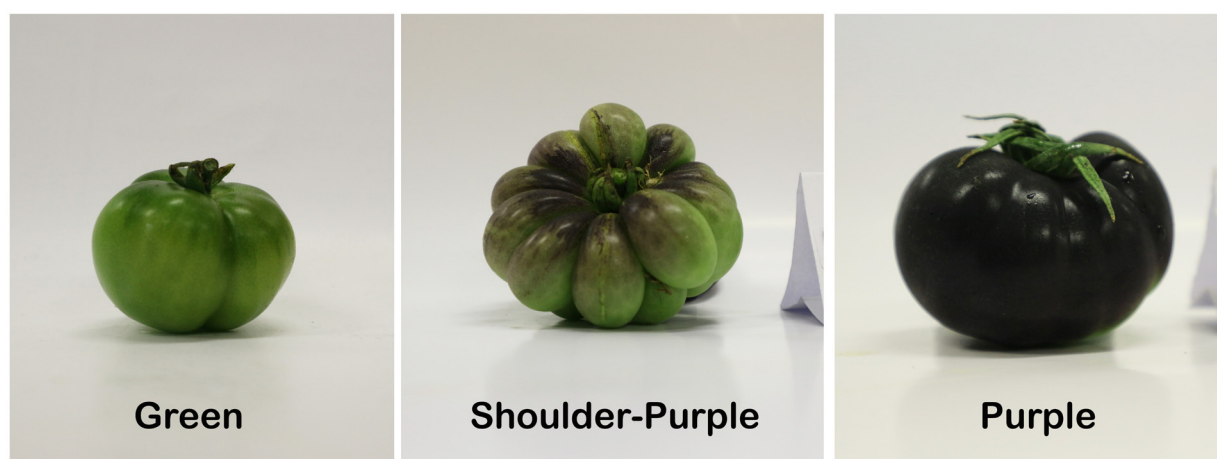


Fig. 2. Unripe fruit color variability in F_2 population

Table 3. Unripe fruit color segregation

Inheritance Pattern	Ratio	Observed (O)			Expected (E)			χ^2 (5.991)**
		G	P	SP	G	P	SP	
Partial Dominance	1:2:1	291	119	153	140.75	281.50	140.75	255.263 *
Dominant Epistasis	12:3:1	291	119	153	422.25	105.56	35.19	436.960 *
Recessive Epistasis	9:3:4	291	119	153	316.69	105.56	140.75	4.860 ns
Partial Epistasis	9:6:1	291	119	153	316.69	211.12	35.19	436.735 *

Remarks: ns = no significant, * = significantly differences between observed and expected value based on χ^2 test; ** = χ^2 table; G = green, P = purple, SG = shoulder-purple

Ripe Fruit Color (Expression of Anthocyanin in Ripe Fruit)

The ripe fruit color segregation in the F_2 population produced two different phenotypes, fruits that express anthocyanin (red-black) and those that do not express anthocyanin (full red). Unlike the expression on unripe fruits, there is no ripe fruit that expresses anthocyanin only on the shoulder of the fruit (Fig. 3). Purple expression tends to fade when the fruit ripens. The shoulder-purple fruit color is degraded when the fruit enters the ripening phase (Li et al., 2018). The segregation of phenotypes appearance on F_2 follows the pattern of dominant-recessive epistasis gene interaction with a ratio of 13:3 (Table 4). In case of dominant-recessive epistasis, the dominant allele at one locus suppresses the dominant allele phenotype at the other locus (Pal, 2017). This shows that the expression of anthocyanin in ripe fruit is controlled by

two loci with two alleles at each locus. Anthocyanin will only be expressed if there are homozygous allele pairs at the one locus and dominant alleles at the other locus.

In previous studies, the inheritance of ripe fruit color has been widely reported. Murti, Kurniawati, & Nasrullah (2004) reported that the color inheritance of ripe fruit was controlled by two loci with two alleles at each locus with dominant epistasis and partial epistasis genes interaction. Meanwhile, the purple color is controlled by a single dominant gene (Jones, Mes, & Myers, 2003). The results of this study differ from previous reports. This result actually resembles the expression of anthocyanin in hypocotyl as reported by Mustafa, Syukur, Sutjahjo, & Sobir (2016). These differences can be caused by the difference of pigment type in ripe fruit or even the type of anthocyanin gene that controls the expression of each tomato.



Fig. 3. Ripe fruit color variability in F_2 population

Table 4. Ripe fruit color segregation

Inheritance Pattern	Ratio	Observed (O)		Expected (E)		χ^2 (3.841)**
		R	R-B	R	R-B	
Complete Dominance	3:1	447	116	422.25	140.75	5.803 *
Lethal Gene	2:1	447	116	375.33	187.67	41.052 *
Dominant-Recessive Epistasis	13:3	447	116	457.43	105.57	1.270 ns
Double Dominant Epistasis	15:1	447	116	527.81	35.19	197.969 *
Double Recessive Epistasis	9:7	447	116	316.69	246.31	122.564 *

Remarks: ns = no significant, * = significantly differences between observed and expected value based on χ^2 test; ** = χ^2 table; R = red, R-B = red-black

Fruit Shapes

The fruit shape segregation in F_2 produced three phenotypes, circular, flattened, and irregular shape (Fig. 4). Fruit shape expression follows the dominant epistasis genes in a ratio of 12:3:1 (Table 5). In dominant epistasis, the dominant allele at one locus masks the phenotype of both alleles at the second loci (Pal, 2017). To conclude, the shape of the fruit is controlled by two alleles at two different loci.

The circular shape will be expressed when the dominant allele emerges at the one locus. The flat shape appears when the recessive homozygous allele pair at one locus interacts with the heterozygote allele pair at the other locus. Meanwhile, the irregular shape appears when genes at both loci is recessive homozygous. Murti, Ambarwati, & Supriyanta (2000) also reported the same results. The fruit shape was controlled by two loci with two alleles per locus with dominant epistasis gene interaction.

Fruit Type

One important trait that needs more attention as one of the main purposes of this plant breeding program is the production of compound fruits with the ability to be broken down into smaller pieces. In the F_2 population, there are two phenotypes related to this trait, single fruit (cannot be split into smaller parts) and compound fruit (can be split into smaller parts) (Fig. 5). This inheritance is controlled by double dominant epistasis genes interaction with a ratio of 15:1 (single fruit: compound fruit) (Table 6).

In double dominant epistasis case, dominant alleles at both loci have the same function. Hence, the presence of functional dominant allele at either locus is sufficient to give rise to the resultant phenotype (Pal, 2017). So, that the type of fruit is controlled by two different loci. Compound fruit will only appear in the recessive homozygous genotype at both loci. Compound fruit is also indirectly related to other traits, fruit shape, and the number of ribbing. The irregular shape and a high number of ribbings tend to have the ability to be split.



Fig. 4. Fruit shape variability in F_2 population

Table 5. Fruit shape segregation

Inheritance Pattern	Ratio	Observed (O)			Expected (E)			χ^2 (5.991)**
		C	F	I	C	F	I	
Partial Dominance	1:2:1	443	96	24	140.75	281.50	140.75	868.140 *
Dominant Epistasis	12:3:1	443	96	24	422.25	105.56	35.19	5.443 ns
Recessive Epistasis	9:3:4	443	96	24	316.69	105.56	140.75	148.089 *
Partial Epistasis	9:6:1	443	96	24	316.69	211.12	35.19	116.714 *

Remarks: ns = no significant, * = significantly differences between observed and expected value based on χ^2 test; ** = χ^2 table; C = circular, F = flattened, I = irregular

**Fig. 5.** Fruit type variability in F_2 population**Table 6.** Fruit type segregation

Inheritance Pattern	Ratio	Observed (O)		Expected (E)		χ^2 (3.841)**
		S	C	S	C	
Complete Dominance	3:1	539	24	422.25	140.75	129.12 *
Lethal Gene	2:1	539	24	375.33	187.67	214.10 *
Dominant-Recessive Epistasis	13:3	539	24	457.43	105.57	200.65 *
Double Dominant Epistasis	15:1	539	24	527.81	35.19	3.79 ns
Double Recessive Epistasis	9:7	539	24	316.69	246.31	77.56 *

Remarks: ns = no significant, * = significantly differences between observed and expected value based on χ^2 test; ** = χ^2 table; S = single fruit, C = Compound fruit

Heritability

The role of genetic factors in phenotypes is conveyed in a value called heritability. Heritability values range from 0 to 1. The higher the heritability value, the greater the role of genetic factors in determining the phenotype appearance of a trait (Mangoendidjojo, 2007). In this study, the observed trait has moderate to high heritability values (0.47-0.73) (Table 7). This shows that the phenotypic expression of these traits is influenced more by genetic factors than environmental factors, so the selection of these traits can be carried out more effectively.

Table 7. Heritability value

No	Trait	Heritability	
1	Pistil type	0.47	Moderate
2	Unripe fruit color	0.56	High
3	Ripe fruit color	0.47	Moderate
4	Fruit shape	0.73	High
5	Fruit type	0.69	Moderate

These traits have moderate to high heritability because they are qualitative traits. Qualitative traits are monogenic (controlled by one gene) or oligogenic (controlled by a few genes) with little environmental influence. Several previous studies of qualitative trait heritability on cultivated tomato showed relatively similar results, fruit shape heritability value is 0.43 (Del Medico, Cabodevila, Vitelleschi, & Pratta, 2019), lycopene and β -carotene are 0.92 and 0.98, respectively (Dar & Sharma, 2011), plant height is 0.97 (Mohamed, Ali, & Mohamed, 2012), caterpillars fruit resistance, fruit breaking resistance, and irregularities shape resistance are 0.69, 0.73, and 0.63, respectively (Iqbal et al., 2013). Heritability indicates how much genetic factor effect the variation in a trait. High heritability implies a strong resemblance between parents and offspring. Heritability is a key parameter in quantitative genetics because it determines the response to selection (Piepho & Möhring, 2007). If a trait is estimated to have high heritability value, then the

pedigree selection method is more recommended for self-pollinating plants (Iqbal et al., 2013).

Diversity of Tomatoes in F_2 and Backcross Populations

Based on the two main traits, fruit shape and unripe fruit color when the maximum level of anthocyanin is expressed, there are 9 variations in the F_2 population (Fig. 6). The variation of irregularly shaped fruit indicates an uneven color emergence (the purple color is not expressed in the fruit grooves). It happens because anthocyanin requires direct sunlight exposure to be expressed

maximally (Jones, Mes, & Myers, 2003). Light is difficult to reach the curve of the fruit, so that part remains green. In the BC_1 population ($F_1 \times$ multi-pistil tomato), there are 3 fruit variations. Variations appear in the fruit shape side, which is a circular, flattened, and irregular shape. Meanwhile, the color of the fruit is uniform, which is green. On the other hand, more variations appeared in the BC_2 population ($F_1 \times$ purple tomatoes). In this generation, 6 variations appear. They are two variations in fruit shape (round and flat) and three variations in color (green, shoulder purple, and purple).

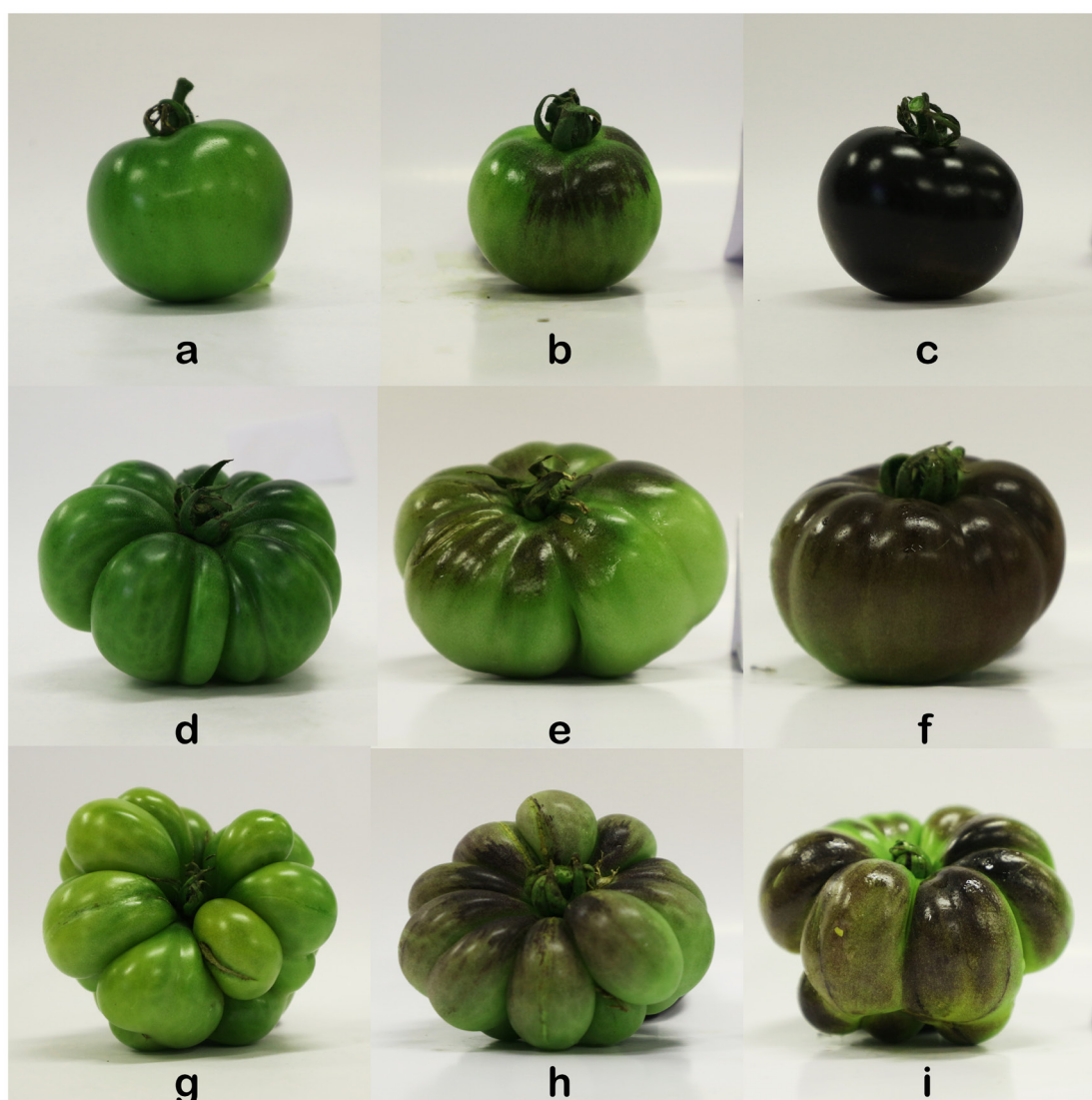


Fig. 6. Fruit phenotype variability in F_2 population; (a) circular green, (b) circular shoulder-purple, (c) circular purple, (d) flattened green, (e) flattened shoulder-purple, (f) flattened purple, (g) irregular green, (h) irregular shoulder-purple, and (i) irregular purple.

CONCLUSION

Fruit color and fruit shape are two important qualitative traits in cultivated tomato. In trait inheritance, fruit color, fruit shape, and other traits associated with the two main traits are inherited chromosomally with moderate to high heritability. In bringing out their expressions, these traits are controlled by two alleles at two different loci (inter-locus interaction).

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