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Genetic control of fruit shelf-life in a cross between *Sletr1-2* mutant and some Indonesian tropical tomatoes

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Abstract. *Wiguna G, Damayanti F, Mubarok S, Ezura H, Anas. 2021. Genetic control of fruit shelf-life in a cross between Sletr1-2 mutant and some Indonesian tropical tomatoes. Biodiversitas 22: 4671-4675.* Postharvest losses are a primary concern for tomato breeders that is associated with a short fruit shelf-life. *Sletr1-2* is a novel ethylene insensitive mutant with significantly longer shelf-life compared to its commercial cultivars. The objective of this study was to estimate the combining ability of *Sletr1-2* mutant and also to determine the appropriate selection method for longer fruit shelf-life tomato breeding. Four lines of tropical tomato, 'Intan,' 'Mirah,' 'Ratna,' and 'Mutiara,' were crossed both with the wild type Micro-Tom (WT-MT) and *Sletr1-2* mutant tomato using a line × tester mating design. A randomized complete block design with four replications was arranged to evaluate eight F1 hybrids and their parents. The line × tester showed no significance for fruit shelf-life. Thus, fruit shelf-life depends on tropical tomato parent and the tester. 'Intan' and *Sletr1-2* mutants tended the high GCA for shelf-life. Predominant additive gene action was considered for fruit shelf-life traits. Therefore, the number and generation of progenies should be considered for a successful fruit shelf-life breeding program.

Keywords: GCA, shelf-life, *Sletr1-2*, tomato

INTRODUCTION

The main obstacle in tomato (*Solanum lycopersicum*) production is postharvest losses caused by the short shelf-life of the fruit (Narasimhamurthy and Gowda 2013). Tomatoes are perishable, and their quality degrades quickly after harvest (Arah et al. 2015). The percentage of damaged fruit had the most significant impact on the decrease in tomato fruit yield. Especially in some tropical countries, high temperatures and humidity throughout the year can shorten the shelf-life of fruit quickly. Shelf-life is a factor that affects the quality of tomato fruit (Veena et al. 2019). Shelf-life is one of the essential characteristics considered by consumers before purchasing a produce (Ambarwati et al. 2015). Early harvest and manipulation of postharvest storage environments are amongst the most common practice employed by farmers and traders to delay tomato ripening (Matas et al. 2009). This is because, after harvest fruit quality cannot be improved but only maintained. Therefore, postharvest control is vital in extending fruit storage time and delaying its ripening. Various technologies, such as cold storage, gas storage, wax coating, and ethylene treatment, are commonly used today to preserve fruit quality (Deepika and Rex 2020).

Shelf life of fruit can be extended through a breeding program (Panthee and Gardner 2011). Breeders have experimented with various innovative methods to address fruit shelf-life and quality issues. Breeders use genetic approaches to develop late-ripening cultivars (Matas et al. 2009). Tomatoes shelf-life can be increased by crossing new cultivars with mutated lines that are insensitive to ethylene. Fruits from heterozygous mutant plants have a much longer fruit shelf-life than wild varieties, and they have good color and flavor (Garg et al. 2008). However, not all studies showed the same results. Some breeders use tomato ripening mutants as breeding materials to prolong tomato shelf-life, however it resulted in a tomato fruit that has a bland flavor, colorless, and low in nutritional content (Uluisik et al. 2016). Through mutations using ethyl methanesulfonate (EMS), the *Sletr1-2* mutant allele has recently been discovered in Micro-Tom tomatoes (Okabe et al. 2011). The allele extends the shelf-life of tomato fruits through a mechanism of reduced ethylene sensitivity. Unlike other mutant genes like Nr and *Sletr1-1*, hybridization of the *Sletr1-2* gene did not significantly degrade fruit quality (Mubarok et al. 2015).

In reality, F1 hybrids cannot always show whether the parent is a better or inferior combiner. On the other hand, phenotypically superior or equally promising parents do not always produce the desired cross combination and produce superior offspring in different generations (Bhalala and Acharya 2019). Therefore, breeders need preliminary information to decide which parents and crosses to use in their breeding program. Consequently, it is crucial to evaluate the impact of combining ability of the desired parent's genotype (Anand and Sankari 2015; Memon et al. 2015). Genetic component analysis and combining ability analysis are powerful tools to distinguish whether the parent is a good or lousy combiner so that the desired parent can be selected for future breeding programs (Veena et al. 2019). Line × Tester is one of the most effective

methods for determining a parent's general and specific combining ability. Simultaneously, it aids in estimating a variety of gene effects (Bocianowski et al. 2015). This research was performed to determine the potential of *Sletr1-2* mutants to combine with tropical tomatoes, with the aim of extending tropical tomatoes shelf-life.

MATERIALS AND METHODS

Experimental material

Four tropical tomato cultivars, namely, 'Intan,' 'Mirah,' 'Ratna,' and 'Mutiara,' each was crossed with the wild type 'Micro-Tom' (WT-MT) and *Sletr1-2* as male parents in the line × tester mating system design from April until July 2017 (Table 1). Seed multiplication and homogeneity evaluation were conducted prior to the main experiment to ensure the homozygosity of the genetic materials.

The evaluation of all crosses and their parental genotypes was conducted from August to December 2017. The cultivation took place in a screen house at the Indonesian Vegetable Research Institute in Lembang, 1250 meters above sea level. The minimum/maximum temperature and humidity were 20.6/33.3°C and 51.6/79.7%, respectively. Each plant was grown in a 40 cm diameter plastic bag using a soil and manure (1:1/v:v) mixture as the plant growing medium. A synthetic fertilizer of 600 kg ha^{-1} NPK (15:15:15) was applied in three split doses, a half dose at field preparation before transplanting, a one-fourth dose after first weeding, and a one-fourth dose after the second weeding. Irrigation, weeding, monitoring, and pest and disease control were all part of the plant management process.

Traits evaluation

Agronomic data for various quantitative traits were collected from 10 plants of each genotype. Plant height (PH) was measured at 45 DAP. PH was calculated from the soil surface to the highest growing point of the plant. The number of flowers per cluster (NFC), number of fruits per cluster (NFrC), and percentage of fruit set (FS) were calculated using the average data from the four observed clusters/plant. Days to first harvest (DFH) are recorded when the first fruit is harvested from each plant. All fruit produced by a single plant is calculated as fruit weight per plant (FWP) or yield. Fruits were harvested six days after reaching the breaking stage (Br + 6), indicated by 60% to 90% of the fruit's surface turning red or reaching the bright red stage (Mubarok et al. 2015).

Table 1. Line × tester schematic crosses of tropical tomato cultivars with 'Micro-Tom' and *Sletr1-2* mutant

	Male (Testers)	
Female (Lines)	**'Micro-Tom' (Tester 1)**	***Sletr1-2* (Tester 2)**
'Intan'	'Intan' × 'Micro-Tom'	'Intan' × *Sletr1-2*
'Ratna'	'Ratna' × 'Micro-Tom'	'Ratna' × *Sletr1-2*
'Mirah'	'Mirah' × 'Micro-Tom'	'Mirah' × *Sletr1-2*
'Mutiara'	'Mutiara' × 'Micro-Tom'	'Mutiara' × *Sletr1-2*

The same maturity level (Br + 6) was determined as 0 days after storage (DPS). Five fruits from each plant were measured for their fruit appearances, such as the number of locules (NL), weight per fruit (WF), and pericarp thickness (PT). The other five fruits from each plant were measured for fruit quality characteristics such as total soluble solids (TSS), fruit shelf-life (SL), and fruit firmness (FF) in the laboratory at a temperature of ± 22°C and humidity of ± 77%. TSS in the fruit flesh was measured using a hand refractometer (Atago, Tokyo, Japan). The refractometer reading stated the percentage of TSS. SL was calculated as the total days since the first storage (0 DPS) until the appearance of wrinkles on the fruit surface. Fruit firmness was measured using a penetrometer (Precision Scientific Inc., Chicago, IL, USA).

Statistical data analysis

This experiment used a four-replication randomized complete block design. Combining ability analysis was performed using the application software AGD-R (Analysis of Genetic Designs with R for Windows) Version 5.0 released by CIMMYT (Rodríguez et al. 2015). Estimation of general combining ability used the following formulas (Singh and Chaudhary 1979):

GCA line = $\bar{X}$i../tr - $\bar{X}$.../ltr
GCA tester = $\bar{X}$.j./lr - $\bar{X}$.../ltr
SCA tester = $\bar{X}$ij./r - $\bar{X}$i../tr - $\bar{X}$.j./lr + $\bar{X}$.../ltr

Where; $\bar{X}$i..: total of the i^{th} line, $\bar{X}$.j.: total of the j^{th} tester, $\bar{X}$... = grand total, r, l, and t: number of replications, lines, and testers, respectively, SE: Standard Error of the estimate and *Me*: Error mean square.

GCA and SCA effects were checked for significance by comparing with their critical difference.

For computing the additive and dominance components of variances following formulae:

$\sigma^2GCA = [(1 + F) / 4] \sigma^2A = ½ \sigma^2A$
so $\sigma^2A = 2 \sigma^2GCA$
$\sigma^2SCA = [(1+F) / 2]^2 \sigma^2D = \sigma^2D$
so $\sigma^2D = \sigma^2SCA$

Where, F: Inbreeding coefficient (F = 1.0 in self-pollinated crops), σ^2A: additive variance, and σ^2D: dominance variance.

Per cent contribution of lines, testers and their interactions were computed as the formulae: (i) Per cent contribution of lines = [SS (lines)/SS (crosses)] x 100, (ii) Per cent contribution to testers = [SS (testers)/SS (crosses)] x 100, (iii) Per cent contribution of lines x testers = [SS (lines x testers)/SS (crosses)] x 100.

RESULTS AND DISCUSSION

Phenotypic diversity of fruit shelf-life, agronomic traits, and yield

Analysis of variance for combining ability in Table 2 revealed that the variance due to line and tester was

significant on fruit shelf-life (days). These results suggest substantial genetic diversity in parents for this trait. Combination ability analysis was carried out to evaluate whether the parents used in hybridization could be used as genetic material in a breeding program to increase the shelf-life of tropical tomatoes. In addition, combining ability analysis can better understand the nature of gene action involved in the inheritance of the desired trait (Meena et al. 2020). The variance due to the line × tester interaction, which represents specific combining ability, was not significant for fruit shelf-life and all other trait studied. This study revealed that no specific combination has a better shelf-life than any other cross combination. The increase in shelf-life in F1 plants depends on the genetic background of the parents.

Mean squares due to lines (female parents) were significant for some agronomic traits (PH, NFC, NFrC, and DFH), yield trait (FWP), and fruit quality traits (SL and TSS). Meanwhile, significant differences between the testers (male parents) were observed in several traits such as FS, NFrC, DFH, NL, SL, and FF. The combining ability analysis will only be carried out on the line, tester, and traits with significant variance. The significant differences among the genotypes for various traits suggested extensive genetic diversity (Ravikesavan et al. 2020). Breeders require this variability to choose the most relevant parent to develop new varieties (Abrha et al. 2013; Elmyhun et al. 2020; Memon et al. 2015). Sizeable genetic diversity between genotypes provides excellent potential for selecting suitable genetic material for plant improvement. The genetic diversity of the parental lines observed in this study is sufficient to allow their use in breeding programs to improve shelf-life traits in the future.

‘Intan’ and *Sletr1-2* exhibits good general combining ability (GCA) for fruit shelf-life

The estimation of GCA in Table 3 reveals that ‘Intan’ showed a high-positive GCA value for SL among the lines. On the other hand, 'Mutiara' showed a high positive value for FWP, which means that 'Mutiara' had the best GCA effect for yield per plant. Estimating the GCA value is essential for optimizing the genetic potential of parents to create superior lines (Saeed et al. 2014). Genotypes that exhibit the desired GCA values have a high possibility to transfer the desired gene to their cross-breeds (Abrha et al. 2013) and may be recommended for genetic improvement through varietal breeding (Katkar et al. 2012). In addition, ‘Intan’ showed a high-negative GCA of DFH, indicated that ‘Intan’ has the potential desirable trait of earliness. Developing new tomato genotypes with early harvestable fruits is one of the mechanisms to avoid abiotic and biotic stresses during the plant life cycle.

‘Mutiara' has desired GCA values for PH, FS, NFrC, DFH, FWP, TSS traits. This study shows that 'Mutiara' has a high potential in transmitting genes controlling these traits to their offspring. This study also reveals that 'Mutiara' has the potential to be selected as a female parent in improving these traits and can produce superior offspring. General combining ability indicates how well the genotypes combine to develop viable and superior offspring. Combining ability analysis can select the best parents for a successful breeding program (Aminu and Kingimi 2015; Narasimhamurthy and Gowda 2013). The term general combining ability refers to the average performance of individual lines in a series of cross combinations and is caused by additive gene action (Kumar and Gowda 2016; Shankar et al. 2014).

Table 2. Analysis of variance for combining ability on fruit self-life, agronomic traits, and yield

	Mean squares			
Trait	**Line**	**Tester**	**Line × tester**	**Error**
(df)	**3**	**1**	**3**	**21**
SL (days)	94.70*	215.63*	33.81	29.65
FF (mm/s/50 g)	0.35	9.70**	2.09	0.95
TSS (°Brix)	0.64**	0.11	0.08	0.07
PH (cm)	5341.04**	108.00	51.60	106.41
NFC	1.19*	0.37	0.38	0.30
FS (%)	140.03	715.28**	63.84	47.87
NFrC	0.83**	5.00**	0.09	0.12
DFH (days)	48.60**	76.26**	21.53	5.79
FWP (g)	165131.09*	29853.46	83982.58	52778.92
NL	0.34	1.04**	0.24	0.12
PT (mm)	0.14	0.04	0.17	0.06

Note: *: significant according to the F-test at the level of $\alpha = 5\%$; **: significant according to the F-test at the level of $\alpha = 1\%$. Note: SL: Fruit shelf-life, FF: fruit firmness, TSS: total soluble solids, PH: plant height, NFC: number of flowers per cluster, FS: percentage of fruit set, NFrC: number of fruits per cluster, DFH: days to first harvest, FWP: fruit weight per plant, NL: number of locules, PT: pericarp thickness

Table 3. GCA effects of line and testers on fruit shelf-life, agronomic traits, and yield

Parents	**SL (days)**	**FF (mm/s/50 g)**	**TSS (°Brix)**	**PH (cm)**	**NFC**	**FS (%)**	**NFrC**	**DFH (days)**	**FWP (g)**	**NL**
Line										
‘Intan’	4.81	0.03	-0.08	-17.97	-0.37	-1.36	-0.36	-3.04	-108.62	-0.087
‘Ratna’	-0.63	0.29	-0.24	-14.35	0.53	-3.13	0.16	0.48	41.28	0.301
‘Mirah’	-0.82	-0.13	-0.09	-5.66	0.02	-1.68	-0.16	-0.37	-118.24	-0.047
‘Mutiara’	-3.37	-0.18	0.41	37.98	-0.18	6.17	0.36	2.93	185.58	-0.168
Tester										
Micro tom	-2.60	0.55	-0.06	-1.84	-0.11	-4.73	-0.40	-1.54	-30.54	-0.180
Sletr1-2	2.60	-0.55	0.06	1.84	0.11	4.73	0.40	1.54	30.54	0.180

Note: SL: Fruit shelf-life, FF: fruit firmness, TSS: total soluble solids, PH: plant height, NFC: number of flowers per cluster, FS: percentage of fruit set, NFrC: number of fruits per cluster, DFH: days to first harvest, FWP: fruit weight per plant, NL: number of locules

Meanwhile, the *Sletr1-2* was an excellent general combiner for shelf-life, as it exhibits a mutation that causes reduced ethylene sensitivity which leads to longer shelf-life (Mubarok et al. 2015). *Sletr1-2* has also shown desirable GCA effects for most of the traits observed, except for DFH and FF. This result reflected the potential of this genotype to transfer desirable genes into their hybrids. Using the parental genotype with high GCA values in breeding for shelf-life traits will increase the possibility of creating varieties with extended fruit shelf-life.

Additive gene action mainly controls the fruit shelf-life and agronomic traits

After determining the combining ability of the tested lines, the next step is to select the appropriate breeding technique to achieve the desired results. This step is related to the action of the genes that control these traits. According to Table 4, the additive genetic variance had a larger estimate than the non-additive genetic variance for some of the traits studied. The ratio of additive and non-additive genetic variance for these traits is greater than one. These results indicate that additive gene action is dominant in controlling the trait. When additive gene action predominates in self-pollinating species, such as tomatoes, breeders should consider using pure-line selection methods (Dixit and Pandey 2017), simple phenotypic selection (Jadav et al. 2017; Shankar 2013), mass selection, offspring selection, and hybridization (Acquaah 2012).

In addition, the results of the variance analysis showed that the additive gene action mainly controls all observable traits since the variance of the line × tester is not significant. However, it can be seen in Table 4 that four traits, namely DFH, FWP, NL, and FF, showed predominantly dominant variance than additive variance. This means that the genes action of additive and non-additive are involved in controlling the four traits. Bharathkumar et al. (2017) reported the same result, stating that additive and non-additive gene action was involved in trait inheritance of days to 50% flowering, fruit firmness, and yield per hectare. Dharva et al. (2018) described the same result for the number of locules per fruit. The presence of non-additive gene action in controlling a trait, emphasizes the importance of heterosis for its breeding strategy (Aditika et al. 2020). Therefore, population heterozygosity is required for FWP, DFH, NL, and FF traits (Table 4). According to Figueiredo et al. (2016), a breeding method investigating the effects of dominance and epistasis is the best choice when non-additive gene action dominates the trait.

The proportional contribution of lines, testers, and their interaction

The lines (females) and testers (males) contributed more to total variance than their interaction in all traits (Table 5). According to the findings, the line's contribution to total variance was higher for almost all traits studied. The line showed a higher contribution than the tester for fruit shelf-life and for almost all understudied traits, such as PH, NFC, DFH, FWP, and TSS. These results indicate that the genetic background of the female parent plays an important role in increasing shelf-life of tomatoes. Studies have shown that proportional contributions of line, tester, and line × tester vary among different traits, as have been stated by Shams et al. (2010) and Sultan et al. (2016). The tester showed a higher total variance contribution in this study on several traits such as FF, FS, and NFrC. These results revealed the importance of lines and testers, as the degree of additive variation was relatively strong for all traits of interest.

In conclusion, 'Intan' and *Sletr1-2* could be the key to develop tomato varieties with longer fruit shelf-life in future breeding programs. Fruit shelf-life and most of the traits observed in this experiment are controlled by additive gene action. Thus, pure line selection, simple phenotypic selection, mass selection, offspring selection, and hybridization from selected crosses in advanced generations would be preferable to improve the fruit shelf-life in tomatoes.

Table 5. The contribution of lines, testers, and their interaction to fruit shelf-life, agronomic traits, and hybrids yield

Source	Due to lines (%)	Due to testers (%)	Due to lines x testers (%)
SL	47.26	35.87	16.87
FF	6.19	56.96	36.85
TSS	84.16	4.79	11.05
PH	98.37	0.66	0.95
NFC	70.19	7.32	22.49
FS	31.66	53.91	14.44
NFrC	32.08	64.38	3.54
DFH	50.87	26.61	22.53
FWP	63.74	3.84	32.42
NL	36.67	37.15	26.18

Note: Fruit shelf-life (SL), and fruit firmness (FF), total soluble solids (TSS), plant height (PH), number of flowers per cluster (NFC), percentage of fruit set (FS), number of fruits per cluster (NFrC), days to first harvest (DFH), fruit weight per plant (FWP), and number of locules (NL).

Table 4. Estimates of variance components

Variance components	PH	NFC	FS	NFrC	DFH	FWP	NL	SL	FF	TSS
σ^2A	1592.44	0.24	88.00	0.71	0.85	18.931.64	0.11	36.45	0.24	0.17
σ^2D	0.00	0.09	16.00	0.00	4.50	31.203.65	0.13	4.16	1.15	0.02
σ^2A/σ^2D	-	2.75	5.50	-	0.19	0.61	0.86	8.76	0.21	11.21

Fruit shelf-life (SL), and fruit firmness (FF), total soluble solids (TSS), plant height (PH), number of flowers per cluster (NFC), percentage of fruit set (FS), number of fruits per cluster (NFrC), days to first harvest (DFH), fruit weight per plant (FWP), and number of locules (NL).

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