



Yield and yield components of tomato (*Solanum lycopersicum*) selected through pedigree method in the lowlands, Bogor-Indonesia*

Rendimiento y componentes del rendimiento del tomate (*Solanum lycopersicum*) seleccionados mediante el método de pedigrí en las tierras bajas, Bogor-Indonesia

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Abstract

Introduction. Segregated populations can exhibit fluctuating yields from one generation to the next. This can sometimes perplex plant breeders when interpreting observed phenomena and determining which selection methods to choose. **Objective.** To analyze the performance and yield components of several tomato (*Solanum lycopersicum*) populations selected through the pedigree method in lowland environments in Bogor, West Java, Indonesia. **Materials and methods.** This study was conducted from December 2018 to April 2019 at the Experimental Garden of Bogor Agricultural University, Tajur II (207 meters above sea level), Bogor, West Java, Indonesia. Four generations were utilized, derived from 99D×Tora, i.e., 200 plants from the F₂ generation and 100 plants each from the F₃, F₅, and F₆ generations, respectively. **Results.** Population variance in terms of yield and yield components, as well as heritability, were lower in later generations compared to earlier generations. An increase in mean value was observed in the F₃ generation, but decreased in the F₅ and F₆ generations across all observed traits. This could be attributed to fixation resulting from the elimination of epistatic genes that played a role in environmental stress. **Conclusion.** Pedigree selection in early generation was not suitable in lowland. It is suggested to evaluate mass selection methods or single seed descent, as these methods were able to maintain population variance into later generations.

Keywords: gene fixation, genetic improvement, selection progress, transgressive segregation.

Resumen

Introducción. Las poblaciones segregadas pueden mostrar un rendimiento fluctuante de una generación a otra. Esto a veces puede confundir a los mejoradores de plantas al interpretar los fenómenos observados y determinar los métodos de selección que deben elegirse. **Objetivo.** Analizar el rendimiento y los componentes de rendimiento de



varias poblaciones de tomate (*Solanum lycopersicum*), mediante el método de pedigrí en entornos de tierras bajas, Bogor, Java Occidental, Indonesia. **Materiales y métodos.** Este estudio se llevó a cabo de diciembre de 2018 a abril de 2019 en el Jardín Experimental de la Universidad Agrícola de Bogor, Tajur II (207 metros sobre el nivel del mar), Bogor, Java Occidental, Indonesia. Se utilizaron cuatro generaciones, obtenidas a partir de 99D×Tora, es decir, 200 plantas de la generación F_2 y 100 plantas de cada una de las generaciones F_3 , F_5 y F_6 , respectivamente. **Resultados.** La varianza de la población en cuanto al rendimiento y los componentes de rendimiento y la heredabilidad fueron menores en las generaciones posteriores en comparación con las generaciones anteriores. Se observó un aumento en el valor medio en la generación F_3 , pero disminuyó en las generaciones F_5 y F_6 en todos los caracteres observados. Esto podría ser causado por la fijación como resultado de la eliminación de genes de epistasia que desempeñaron un papel en el estrés ambiental. **Conclusión.** La selección de pedigrí en las primeras generaciones no fue adecuada en las tierras bajas. Se sugiere evaluar métodos masales o descendencia de una sola semilla, ya que esos métodos fueron capaces de mantener la varianza de la población hasta las generaciones posteriores.

Palabras clave: fijación de genes, mejora genética, progreso de selección, segregación transgresora.

Introduction

Tomato (*Solanum lycopersicum*) is known as a self-pollinating plant (Lin et al., 2014). Similar to other self-pollinating plants, selection and progeny testing are generally conducted in the early generations (Acharya et al., 2018; Cappetta et al., 2020; Kahani & Hittalmani, 2016). This early generation testing helps improve breeding efficiency by selecting superior genotypes and eliminating inferior ones from the segregating populations (Abdelmoghny, 2021; Crossa et al., 2017; Dama et al., 2022; Limbongan et al., 2021; Ramos Guimarães et al., 2021; Wibisono et al., 2022). However, due to environmental effects, sometimes the selected genotypes do not exhibit optimal performance in later generations, especially regarding yield characteristics (Avdikos et al., 2021; Collard et al., 2017; Wibisono et al., 2019; Wibisono et al., 2021).

In plant breeding, the F_2 to F_6 generations are critical phases for selection and evaluation (Ahmad et al., 2017; Pontes Júnior et al., 2016; Yadav et al., 2021). Variance and heritability are mostly assessed in F_2 to F_6 generations to predict the response of the selected population (Hakim & Suyamto, 2017; Oliveira Silva et al., 2021). Selection conducted over several generations with the same intensity has been reported to reduce the values of heritability, phenotypic variance, and selection response (Asrat, 2021; Sinha et al., 2021).

Several studies related to the selection response of yield component traits in self-pollinated plants have show different patterns for each species (de Paula et al., 2020; Purnamasari et al., 2019; Ritonga, Chozin et al., 2018). In *Capsicum annum* L., the selection response observed from the F_2 to F_6 generations exhibited a decreasing pattern in each generation (Ritonga, Syukur et al., 2018). However, in different crossbred populations, it progressed in an increasing pattern (Rosminah et al., 2019). Selection responses within the same generation range for yield component traits of *Vigna unguiculata* L. showed an irregular pattern but a lower mean value in F_6 compared to its F_4 generation (Varghese et al., 2021).

The selection response that tends to decrease in later generations is not only caused by genetic factors from the parental lines but also external factors such as environmental influences and selection methods (Wanga et al., 2021). In self-pollinated crops such as rice (Collard et al., 2017; Rini et al., 2018), tomato (Hernández-Leal et al., 2019), and chili pepper (Massot Padilha & Barbieri, 2016), pedigree selection from early generations have been carried out to improve generative traits (Hamam, 2014; Sarutayophat & Nualsri, 2010) as well as resistance to biotic stress (Presello et al., 2005).

Pedigree selection from early generations aims to maintain superior segregation and leverage the natural potential of self-pollinating plants in assembling pure breeds (Avdikos et al., 2021; Thien Tran et al., 2021). However, when performance in early generations is controlled by epistatic genes, pedigree selection is not recommended (Khalaf et al., 2021). In this case, the superiority of the segregants is due to non-allelic interactions (epistasis), while there is no such interaction in the subsequent generations in self-pollinated plants (Fisher, 1919; Khalaf et al., 2021). This study was conducted to analyze the performance and yield components of several tomato populations using the pedigree method in lowland environments, Bogor, West Java, Indonesia.

Materials and methods

Study area

This study was conducted from December 2018 to April 2019, encompassing the selection and development of F_2 to F_6 populations at the Experimental Garden of Bogor Agricultural University, Tajur II (207 meters above sea level), Bogor, West Java, Indonesia. The average environmental temperature average at Tajur II during December 2018-April 2019 was 26.03 °C, based on the data from West Java Climatology Station, Bogor, Indonesia.

Plant materials

Seeds of tomato (*Solanum lycopersicum*) were obtained from the Plant Breeding Laboratory, Department of Agronomy and Horticulture, Bogor Agricultural University. Four generations resulting from the 99D×Tora cross were utilized in the study, comprising 200 plants of the F_2 generation and 100 plants of each of the F_3 , F_5 , and F_6 generations, respectively. The 99D variety is a pure line of tomato with large fruit size, developed in highland areas, (>600 meters above sea level). Tora, on the other hand, is an open-pollinated (OP) variety with medium-sized fruit suitable for cultivation in medium (300 – 600 m a.s.l.) to lowland (0 – 300 m a.s.l.) areas. The crossbreeding was aimed at obtaining recombinants or lines with large fruit size while being adaptable to lowland areas. Intan and Ratna varieties (open-pollinated (OP) varieties or non-hybrids) served as control varieties, which are commercially available varieties. The use of commercial varieties adheres to the regulations for variety testing and release in Indonesia. The reason for not using 99D and Tora directly is that they are proprietary pure lines owned by the company (PT BISI) and are not permitted for planting outside the company. Additionally, Tajur is not owned by PT BISI.

Procedures

The entire experimental population was planted in the same season and field. Planting took place in open fields using a double-row system with two rows per single bed. Rows were spaced 0.5×0.6 m apart, and beds were 1 m apart. Each bed measured 20×1 m, accommodating 80 plants per bed. Seven days before planting, each bed received 15 kg of manure, 2 kg of urea and KCl, 3 kg of SP-36 (a phosphate and sulfate fertilizer containing 36 % phosphorus as P_2O_5), and 4 kg of dolomite. Black silver mulch was applied to cover each bed.

Plant maintenance included irrigation, fertilizer application, as well as pest and disease control. A NPK (16:16:16) fertilizer solution at a concentration of 15 g L⁻¹ was applied at 2, 3, 4, and 5 weeks after planting (wap). Supplementary fertilizer was applied by pouring 250 mL of solution for each plant into a hole located 8-10 cm from the base of the plant stem. Gandasil D and Gandasil B fertilizers, foliar fertilizers, were applied once a week along with spesticide praying according to the plant growth phase, with a concentration of 2 g L⁻¹ from 2 to 5 weeks after planting. Gandasil D contains 14 % nitrogen, 12 % phosphate, 14 % potassium, 1 % magnesium and

other micronutrients to promote vegetative growth. Gandasil B contains 16 % nitrogen, 20 %, phosphorus, 30 % potassium, and 3 % magnesium to promote fruiting or flowering. Weed control was performed manually.

Observations were made on quantitative yield components traits of all individual plants (Mawasid et al., 2019). The observed traits included flowering time (days after planting, dap), harvest time (dap), fruit length (cm), fruit diameter (cm), fruit weight (g), fruit weight per plant (g), and number of fruits. Ten fruit samples were measured, based on the mean measurement. Typically, the samples used for measurement were obtained from the early stages of harvest.

Data analysis

The analysis aimed to understand the pattern of selection responses across several generations. It included two main components: 1) genetic advance to determine the difference in the mean value between selected population and the base population, as described by Syukur et al. (2015) (equation 1), and 2) estimation of narrow-sense heritability using offspring-parent regression with two segregated populations (F_3 and F_2 , etc), following Falconer & Mackay (1996) (equation 2).

$$G = \bar{x}F_n - \bar{x}F_{n-1} \quad (1)$$

Where G represents the genetic advance, $\bar{x}F_n$ is the mean of F_n population, and $\bar{x}F_{n-1}$ is the mean of F_{n-1} population.

$$h^2_{ns} = bOP = \frac{Cov_{OP}}{\sigma_p^2} \quad (2)$$

Where h^2_{ns} denotes the narrow-sense heritability, bOP is the offspring-parent regression, Cov_{OP} represents the variance between offspring and parent, and σ_p^2 is the variance of the F_2 population. Heritability is classified as low (< 20 %), moderate (20 % \geq h^2_{ns} \geq 50 %), and high (> 50 %), according to Syukur et al. (2015).

Results

Selection response of several generations

The mean values of each generation and the comparison for each observed trait are presented in Table 1. A distinct selection was observed for each trait. Flowering time increased from the F_2 to F_3 generations but decreased from the F_5 to F_6 generations. Similarly, harvest time exhibited a similar trend. Flowering (Figure 1a) and harvest time (Figure 1b) shifted towards the left side of the graph, indicating improved traits for both flowering and harvest time, as they are correlated with early maturity.

Fruit length, fruit diameter, fruit weight, and number of fruits also showed a positive selection response in F_2 to F_3 generations, and a decreased in F_5 and F_6 generations. Fruit weight per plant showed a genetic advancement in the mean value from F_2 to F_3 generation, and in F_5 generation, the mean fruit weight was still higher compared with the F_3 population. The decrease in fruit weight per plant was only seen in the F_6 generation. Although the F_6 generation had a lower mean value than F_2 for each character, its fruit weight and fruit weight per plant characters were still higher than those of the Intan and Ratna varieties. Fruit weight and fruit weight per plant are the main yield component characters.

Table 1. Mean \pm standard deviation of tomato (*Solanum lycopersicum*) yield components in F₂ – F₆ generations of 99D×Tora compared to Intan and Ratna varieties. Bogor Agricultural University, Bogor, Indonesia. 2018-2019.

Cuadro 1. Media \pm desviación estándar de los componentes del rendimiento del tomate (*Solanum lycopersicum*) en las generaciones F₂ – F₆ de 99D×Tora en comparación con las variedades Intan y Ratna. Universidad Agrícola de Bogor, Bogor, Indonesia. 2018-2019.

Ch	Mean					
	F ₂	F ₃	F ₅	F ₆	Intan	Ratna
FT	30.74±2.41 ^{bc}	29.27±2.72 ^b	29.39±2.07 ^b	31.53±3.40 ^c	27.82±3.42 ^a	30.13±4.05 ^{bc}
HT	70.69±3.14 ^b	70.43±3.57 ^b	71.33±4.11 ^b	75.22±3.42 ^c	68.18±3.21 ^a	70.00±3.54 ^b
FL	6.56±0.70 ^c	6.77±0.68 ^c	6.15±0.63 ^b	5.90±0.47 ^b	4.44±0.65 ^a	4.50±0.55 ^a
FD	4.79±0.62 ^a	4.87±0.56 ^a	4.85±0.48 ^a	4.68±0.42 ^a	4.88±0.58 ^a	5.48±0.85 ^b
FW	75.13±19.80 ^b	79.88±20.40 ^b	76.16±17.16 ^b	58.37±17.07 ^b	58.37±15.93 ^a	52.36±17.23 ^a
FWP	1627.27±824.04 ^b	1697.80±691.50 ^b	1745.39±746.89 ^b	1156.45±541.64 ^b	1156.45±446.23 ^a	1168.25±468.37 ^a
NF	40.01±16.45 ^{bc}	44.45±18.09 ^c	38.92±12.60 ^{bc}	32.78±9.39 ^{ab}	31.45±9.60 ^a	35.13±12.93 ^{ab}

Remarks: values marked with different letters in the same row show significant differences based on Duncan Multiple Range Test at $p < 0.05$. Ch: characters, FT: flowering time (days after planting, dap), HT: harvest time (days after planting, dap), FL: fruit length (cm), FD: fruit diameter (cm), FW: fruit weight (g), FWP: fruit weight per plant (g), NF: number of fruits. / Observaciones: los valores marcados con letras diferentes en la misma fila muestran diferencias significativas basadas en la Prueba de Rango Múltiple de Duncan en $p < 0,05$. Ch: caracteres, FT: época de floración (días después de la siembra, ddp), HT: época de cosecha (días después de la siembra, ddp), FL: longitud del fruto (cm), FD: diámetro del fruto (cm), FW: peso del fruto (g), FWP: peso de frutos por planta (g), NF: número de frutos.

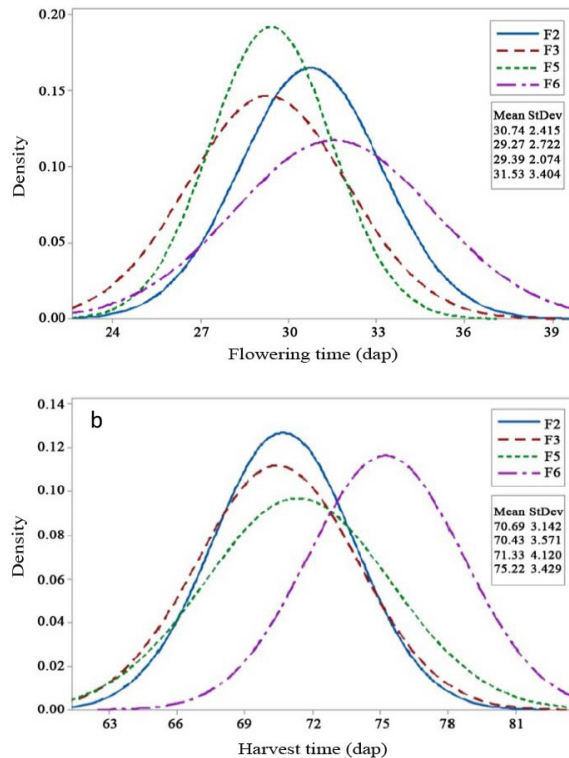


Figure 1. Selection response in F₂ – F₆ generations of 99D×Tora tomato (*Solanum lycopersicum*). a. Flowering time (days after planting, dap); b. Harvest time (days after planting, dap). Bogor Agricultural University, Bogor, Indonesia. 2018-2019.

Figura 1. Respuesta de selección en generaciones F₂ – F₆ de tomate (*Solanum lycopersicum*) 99D×Tora. a. Época de floración (días después de la siembra, dap); b. Tiempo de cosecha (días después de la siembra, dap). Universidad Agrícola de Bogor, Bogor, Indonesia. 2018-2019.

The mean and variance of flowering time fluctuated among generations (Figure 1a), as did harvest time (Figure 1b). The mean value of flowering time increased the F_3 generation but gradually decreased in F_5 to F_6 generations. As for variance (Table 2), its value showed an increase in F_3 compared with the F_2 generation, a decrease in F_5 , and followed by another increase in the F_6 generation. The mean value of harvest time showed similar advancement to the flowering time character, but not its variance. For traits with positive values on the left side (Table 1), such as flowering time, a lower value indicates an improvement. In other words, when the value is low, it is considered to have increased. Similarly, the opposite applies. The harvest time's variance increased gradually in the F_3 and F_5 generations but decreased in the F_6 . The changes of the mean value among generations can be inferred from the curve's peak position to the X-axis, while the value of variance can be seen from the curve's peak position to the Y-axis. A higher peak reflects lower variance.

Table 2. Variance of tomato (*Solanum lycopersicum*) yield components in $F_2 - F_6$ generations of 99D×Tora compared to Intan and Ratna varieties. Bogor Agricultural University, Bogor, Indonesia. 2018-2019.

Cuadro 2. Varianza de los componentes del rendimiento del tomate (*Solanum lycopersicum*) en las generaciones $F_2 - F_6$ de 99D×Tora en comparación con las variedades Intan y Ratna. Universidad Agrícola de Bogor, Bogor, Indonesia. 2018-2019.

Ch	Variance					
	F_2	F_3	F_5	F_6	Intan	Ratna
FT	5.83	7.41	4.30	11.59	11.76	16.41
HT	9.87	12.75	16.97	11.76	10.36	12.57
FL	0.57	0.47	0.40	0.22	0.43	0.31
FD	0.39	0.32	0.24	0.18	0.34	0.73
FW	392.04	415.96	294.33	291.50	253.85	296.78
FWP	679038.13	478174.67	557838.02	293371.40	199122.27	219371.64
NF	270.62	327.13	158.65	88.22	92.07	167.27

Remarks: values marked with different letters in the same row show significant differences based on Duncan Multiple Range Test at $p < 0.05$. Ch: characters, FT: flowering time (days after planting, dap), HT: harvest time (days after planting, dap), FL: fruit length (cm), FD: fruit diameter (cm), FW: fruit weight (g), FWP: fruit weight per plant (g), NF: number of fruits. / Observaciones: los valores marcados con letras diferentes en la misma fila muestran diferencias significativas basadas en la Prueba de Rango Múltiple de Duncan en $p < 0.05$. Ch: caracteres, FT: época de floración (días después de la siembra, ddp), HT: época de cosecha (días después de la siembra, ddp), FL: longitud del fruto (cm), FD: diámetro del fruto (cm), FW: peso del fruto (g), FWP: peso de frutos por planta (g), NF: número de frutos.

Selection responses of fruit length and fruit diameter (Figures 2a and 2b, respectively) showed an increase in the mean value in the F_3 generation and subsequent decrease in F_5 to F_6 . Similarly, fruit weight and the number of fruits (Figures 3a and 3b) exhibited an increase in the mean value in the F_3 generation, followed by a decrease from F_3 to F_6 . Variances of fruit length and fruit diameter decreased gradually from F_3 to F_6 , while variances of fruit weight and the number of fruits increased in F_3 but gradually decreased from F_5 to F_6 generations.

Selection response of fruit weight per plant was shown in Figure 4. The mean value of this character increased in F_3 to F_5 , and decreased in F_6 generation. On the other hand, variance of fruit weight per plant showed a gradual decrease from F_3 to F_6 generation.

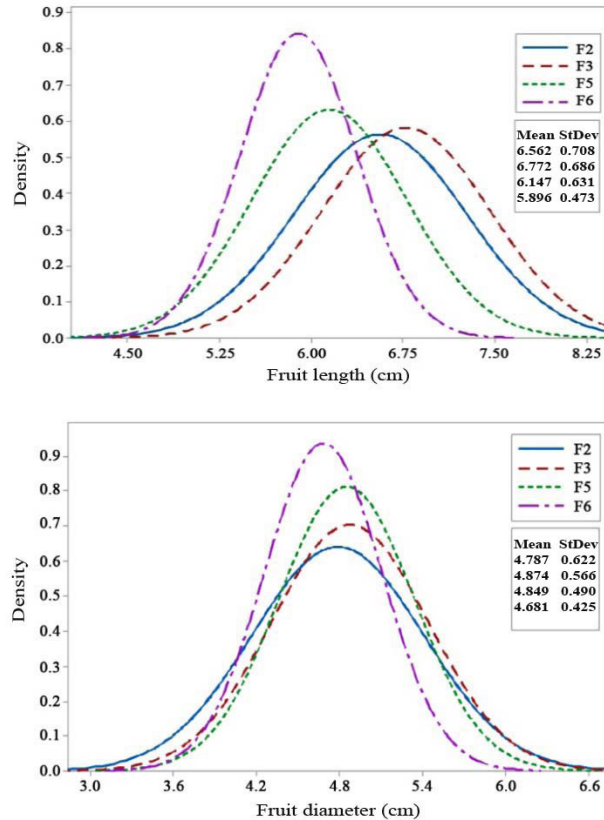


Figure 2. Selection response in F_2 – F_6 generations of 99D×Tora tomato (*Solanum lycopersicum*). a. Fruit length (cm); b. Fruit diameter (cm). Bogor Agricultural University, Bogor, Indonesia. 2018-2019.

Figura 2. Respuesta de selección en generaciones F_2 – F_6 de tomate (*Solanum lycopersicum*) 99D×Tora. a. Longitud del fruto (cm); b. diámetro del fruto (cm). Universidad Agrícola de Bogor, Bogor, Indonesia. 2018-2019.

Heritability

The narrow-sense heritability values between early (F_2 - F_3) and later (F_5 - F_6) generations are shown in Table 3. Heritability in the early generation was greater than in the following generations, suggesting a decrease in heritability along with the fixation process.

The highest heritability in the early generation was observed in the number of fruits (13.12 %) character, while the lowest was found in harvest time (-20.61 %). The character with the highest heritability in the next generation was number of fruits (11.33 %), and the lowest was flowering time (-23.47 %).

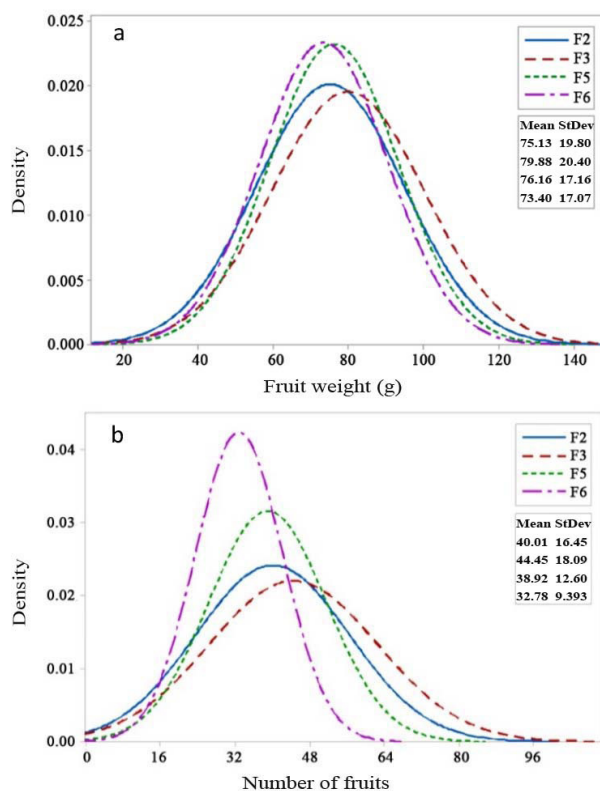


Figure 3. Selection response in $F_2 - F_6$ generations of 99D x Tora tomato (*Solanum lycopersicum*). a. Fruit weight (g); b. Number of fruits. Bogor Agricultural University, Bogor, Indonesia. 2018-2019.

Figura 3. Respuesta de selección en varias generaciones $F_2 - F_6$ de tomate (*Solanum lycopersicum*) 99D x Tora. a. Peso del fruto (g); b. Número de frutos. Universidad Agrícola de Bogor, Bogor, Indonesia. 2018-2019.

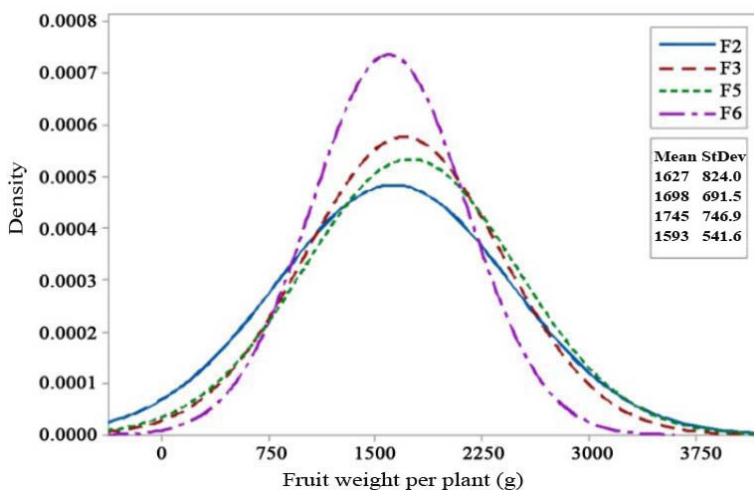


Figure 4. Selection response in $F_2 - F_6$ generations of 99D x Tora tomato (*Solanum lycopersicum*) on the character of fruit weight per plant (g). Bogor Agricultural University, Bogor, Indonesia. 2018-2019.

Figura 4. Respuesta de selección en generaciones $F_2 - F_6$ de tomate (*Solanum lycopersicum*) 99D x Tora sobre el carácter del peso del fruto por planta (g). Universidad Agrícola de Bogor, Bogor, Indonesia. 2018-2019.

Table 3. Narrow-sense heritability values between $F_2 - F_3$ and $F_5 - F_6$ generations of 99D×Tora tomato (*Solanum lycopersicum*). Bogor Agricultural University, Bogor, Indonesia. 2018-2019.

Cuadro 3. Valores de heredabilidad en sentido estricto entre $F_2 - F_3$ y $F_5 - F_6$ generaciones de tomate (*Solanum lycopersicum*) 99D×Tora. Universidad Agrícola de Bogor, Bogor, Indonesia. 2018-2019.

No	Characters	h^2_{ns} (%)	
		F2 - F3	F5 - F6
1	Flowering time (dap)	-16.07 (low)	-23.47 (low)
2	Harvest time (dap)	-20.61 (low)	-10.33 (low)
3	Fruit length (cm)	1.43 (low)	1.29 (low)
4	Fruit diameter (cm)	2.63 (low)	1.64 (low)
5	Fruit weight (g)	-1.82 (low)	-11.52 (low)
6	Fruit weight per plant (g)	8.62 (low)	5.57 (low)
7	Number of fruits	13.12 (low)	11.33 (low)

Remarks: h^2_{ns} : narrow-sense heritability. / Observaciones: h^2_{ns} : heredabilidad en sentido estricto.

Discussion

The selection response was observed by comparing the mean of one generation (F_n) with the subsequent generation (F_{n+1}). There was a difference in the selection method used in this experiment between F_2 and F_3 populations, as well as the F_4 to F_6 populations. The F_2 and F_3 populations were selected using a weighted index selection method from the previous study (Mawasid et al., 2019), while the F_4 to F_6 populations were selected based on visual observations (eyeballing) of different lineages, and the genotype with the best performance was chosen. The F_5 and F_6 populations reflected the selection response of the later generations derived from pedigree selection of the F_3 population from the previous experiments (Mawasid et al., 2019).

The F_4 population was not included in the planting due to a decrease in its seed vigor. The F_5 and F_6 populations could be used as simulators since both were obtained from the 99D×Tora cross (parental) and selected using the pedigree method. The genetic constitutions of the F_5 and F_6 generations would be similar to those of the F_2 and F_3 populations. Intan and Ratna varieties were used as comparisons. These two varieties were of pure breed, registered, and commercialized.

In general, there was a positive selection response in the early generations but a negative response in the later generations. The same response to tomato yield components was also reported by Ahmad et al. (2017) and Ahmad et al. (2018). This could be due to differences in the inheritance pathways used or the dominance of epistasis gene action due to the existing environmental stress (Mawasid et al., 2019). Epistasis genes seemed to be the main cause, considering that the F_2 to F_3 and F_4 to F_6 generations were obtained from pedigree selection, where only the best genotypes would be continued. There is a decrease in the variance in each generation because pedigree selection leads to the formation of a homozygous homogeneous population (Acquaah, 2012; Syukur et al., 2015).

The value of variance changed in each observed generation. A pedigree-derived generation did not always have a lower value than its previous generation (Table 2). This happened because selection was carried out on several characters at once through index selection. There was a possibility of uneven fixation on all characters. Selection carried out on a character will encourage fixation on its controlling genes, but when selected individuals have higher heterozygosity, segregation will occur which causes the variance of the later generation to increase. Inaccuracy in selection can occur when the proportion of non-additive genes (dominant and epistatic) in a character

are greater than the additive genes. A smaller variance reflects the fixation of its genotypes and an increase in its homozygosity. If the variance is already low and the phenotype is good (yield, etc.), then it is worthy of multi-location testing to be released as an open-pollinated variety.

In general, selection responses of flowering time and harvest time from F_2 to F_6 moved to the right. Fruit length, fruit diameter, fruit weight, fruit weight per plant, and number of fruits moved to the left, which meant a negative selection response, especially in the later generation. Pedigree selection in this study resulted in the lowest mean and variance in F_6 generation. This indicated that the gene fixation process in the early generations eliminated superior traits. As previously explained, in an environmentally stressed condition, the action of non-allelic genes (epistasis) plays a major role. In the later generations, the action of these genes will be eliminated because they are not fixed (Mather & Jinks, 1982), so that the superiority of the genotype in the early generations will disappear.

Based on the data presented in this paper, pedigree selection was not suitable for selection in a stressed condition, especially in the lowland. This was due to the possibility of inaccuracy selection in early generations. Selection using bulk or single seed descent is more recommended (Mistry et al., 2016; Said, 2014), considering that variance among generations is still controlled until later generations. Selection will be more convincing because performance and variance within a population are controlled by the genotype which has been fixed.

Narrow-sense heritability is defined as the fraction of phenotypic variance that can be attributed to variation in the additive effects of genes. A negative heritability value indicated that variances in these characters were not statistically inherited in the next generations, or in other words, $h^2_{ns} = 0$. The low heritability of each character can be caused by environmental factor and non-additive genes (Mawasid et al., 2019). The selection process applied to each generation will cause changes in gene frequency so that it will affect the heritability values of the next generation. Heritability values decreased in the next generations due to gene fixation and increased homozygosity. A decrease in heritability value in F_3 to F_5 generations was also reported by Ahmad (2016) for the yield component of *Vicia faba* L.

Conclusions

Selection across multiple generations tends to decrease the variance and heritability of characters. This reduction in value occurs due to fixation, which alters gene frequency and increases homozygosity. While the mean value tends to increase in the early generations, it often decreases in later ones due to the fixation process, which eliminates the influence of epistatic genes. Therefore, pedigree selection in the early generation may not be suitable for selection in the lowland conditions. Instead, the bulk or single seed descent method are recommended because they were capable of maintaining variance in later generation.

References

- Abdelmoghny, A. M. (2021). Prediction of new genetic recombination in two Egyptian cotton crosses. *Egyptian Journal of Agronomy*, 43(1), 83–96. <https://doi.org/10.21608/agro.2021.65016.1251>
- Acharya, B., Dutta, S., Dutta, S., & Chattopadhyay, A. (2018). Breeding tomato for simultaneous improvement of processing quality, fruit yield, and dual disease tolerance. *International Journal of Vegetable Science*, 24(5), 407–423. <https://doi.org/10.1080/19315260.2018.1427648>
- Acquaah, G. (2012). *Principles of plant genetics and breeding*. John Wiley & Sons, Inc.

- Ahmad, M. S. H. (2016). Studies on genetic variability, heritability and genetic advance in segregating generations of faba bean (*Vicia faba* L.). *Middle East Journal of Agriculture*, 5(1), 82–89. <https://www.curreweb.com/mejar/mejar/2016/82-89.pdf>
- Ahmad, M., Iqbal, M., Ahmed Khan, B., Ullah Khan, Z., Akbar, K., Ullah, I., Shahid, M., & Rehman, A. (2017). Tomato, F2, F3, range, mean, selection response, heritability, variability, genetic advance. *International Journal of Plant Research*, 7(1), 1–4. <http://article.sapub.org/10.5923.j.plant.20170701.01.html>
- Ahmad, M., Ahmed Khan, B., Iqbal, M., Saleem, M., Ahmad, F., Shahid, M., Rehman, A., Ullah, I., & Nawaz, A. (2018). Comparison of response of F4 and F3 generations of tomato from year to year selection. *Asian Journal of Agriculture & Biology*, 6(2), 245–250. https://www.asianjab.com/wp-content/uploads/2018/06/19.-OK_Response-of-F4-and-F3-generations-of-tomato-from-year-to-year-selection1.pdf
- Asrat, Z. (2021). The improvement of maize (*Zea mays* L.) for drought stress tolerance. *International Journal of Advanced Research in Biological Sciences*, 8(7), 90–102. <https://ijarbs.com/pdfcopy/2021/july2021/ijarbs10.pdf>
- Avdikos, I. D., Tagiakas, R., Tsouvaltzis, P., Mylonas, I., Xynias, I. N., & Mavromatis, A. G. (2021). Comparative evaluation of tomato hybrids and inbred lines for fruit quality traits. *Agronomy*, 11(3), Article 609. <https://doi.org/10.3390/agronomy11030609>
- Cappetta, E., Andolfo, G., Di Matteo, A., Barone, A., Frusciante, L., & Ercolano, M. R. (2020). Accelerating tomato breeding by exploiting genomic selection approaches. *Plants*, 9(9), Article 1236. <https://doi.org/10.3390/plants9091236>
- Collard, B. C. Y., Beredo, J. C., Lenaerts, B., Mendoza, R., Santelices, R., Lopena, V., Verdeprado, H., Raghavan, C., Gregorio, G. B., Vial, L., Demont, M., Biswas, P. S., Iftekharrudaula, K. M., Akhlaqur Rahman, M., Cobb, J. N., & Rafiqul Islam, M. (2017). Revisiting rice breeding methods – evaluating the use of rapid generation advance (RGA) for routine rice breeding. *Plant Production Science*, 20(4), 337–352. <https://doi.org/10.1080/1343943X.2017.1391705>
- Crossa, J., Pérez-Rodríguez, P., Cuevas, J., Montesinos-López, O., Jarquín, D., de los Campos, G., Burgueño, J., González-Camacho, J. M., Pérez-Elizalde, S., Beyene, Y., Dreisigacker, S., Singh, R., Zhang, X., Gowda, M., Roorkiwal, M., Rutkoski, J., & Varshney, R. K. (2017). Genomic Selection in plant breeding: Methods, models, and perspectives. *Trends in Plant Science*, 22(11), 961–975. <https://doi.org/10.1016/j.tplants.2017.08.011>
- Dama, H., Aisyah, S. I., Sudarsono, S., Dewi, A. K., & Wibisono, K. (2022). Identification, selection, and response of radiation induced towuti mutant rice (*Oryza sativa* L.) in drought stress conditions. *Atom Indonesia*, 48(2), 107–114. <https://doi.org/10.17146/aij.2022.1198>
- de Paula, R. G., Pereira, G. S., de Paula, I. G., Carneiro, A. L. N., Carneiro, P. C. S., dos Anjos, R. S. R., & Carneiro, J. E. S. (2020). Multipopulation recurrent selection: An approach with generation and population effects in selection of self-pollinated progenies. *Agronomy Journal*, 112(6), 4602–4612. <https://doi.org/10.1002/agj2.20422>
- Falconer, D. S., & Mackay, T. F. C. (1996). *Introduction to quantitative genetics* (4th ed.). Addison Wesley Longman, Inc.
- Fisher, R. A. (1919). XV.—The correlation between relatives on the supposition of mendelian inheritance. *Transactions of the Royal Society of Edinburgh*, 52(2), 399–433. <https://doi.org/10.1017/S0080456800012163>
- Hakim, L., & Suyanto, S. (2017). Gene action and heritability estimates of quantitative characters among lines derived from varietal crosses of soybean. *Indonesian Journal of Agricultural Science*, 18(1), 25–32. <https://media.neliti.com/media/publications/178192-none-88528313.pdf>
- Hamam, K. A. (2014). Late and early pedigree selection for grain yield with three selection criteria in two populations in bread wheat. *Journal of Plant Production*, 5(11), 1831–1847. <https://doi.org/10.21608/jpp.2014.64730>

- Hernández-Leal, E., Lobato-Ortiz, R., García-Zavala, J. J., Hernández-Bautista, A., Reyes-López, D., & Bonilla-Barrientos, O. (2019). Stability and breeding potential of tomato hybrids. *Chilean Journal of Agricultural Research*, 79(2), 181–189. <https://doi.org/10.4067/S0718-58392019000200181>
- Kahani, F., & Hittalmani, S. (2016). Identification of F2 and F3 segregants of fifteen rice crosses suitable for cultivation under aerobic situation. *SABRAO Journal of Breeding and Genetics*, 48(2), 219–229. <https://sabraojournal.org/wp-content/uploads/2018/01/SABRAO-J-Breed-Genet-48-2-219-229-Kahani-1.pdf>
- Khalaf, A. E. A., Eid, M. A. M., Ghallab, K. H., El-Areed, S. R. M., Yassein, A. A. M., Rady, M. M., Ali, E. F., & Majrashi, A. (2021). Development of a five-parameter model to facilitate the estimation of additive, dominance, and epistatic effects with a mediating using bootstrapping in advanced generations of wheat (*Triticum aestivum* L.). *Agronomy*, 11(7), Article 1325. <https://doi.org/10.3390/agronomy11071325>
- Limbongan, Y. L., Driyunita, D., Sjahril, R., Riadi, Muh., Jamaluddin, I., Okasa, A. M., & Panga, N. J. (2021). Heritability and genetic advancement on agronomic characters of Toraja red rice x Inpari-4 white rice genotypes. *Biodiversitas Journal of Biological Diversity*, 22(8), 3446–3451. <https://doi.org/10.13057/biodiv/d220842>
- Lin, T., Zhu, G., Zhang, J., Xu, X., Yu, Q., Zheng, Z., Zhang, Z., Lun, Y., Li, S., Wang, X., Huang, Z., Li, J., Zhang, C., Wang, T., Zhang, Y., Wang, A., Zhang, Y., Lin, K., Li, C., ... Huang, S. (2014). Genomic analyses provide insights into the history of tomato breeding. *Nature Genetics*, 46(11), 1220–1226. <https://doi.org/10.1038/ng.3117>
- Massot Padilha, H. K., & Barbieri, R. L. (2016). Plant breeding of chili peppers (*Capsicum*, Solanaceae) – A review. *Australian Journal of Basic and Applied Sciences*, 10(15), 148–154.
- Mather, S. K., & Jinks, J. L. (1982). *Biometrical Genetics* (3rd ed.). Springer Nature. <https://doi.org/10.1007/978-1-4899-3406-2>
- Mawasid, F. P., Syukur, M., & Trikoesoemaningtyas. (2019). Epistatic gene control on the yield of tomato at medium elevation in the tropical agroecosystem. *Biodiversitas Journal of Biological Diversity*, 20(7), 1880–1886. <https://doi.org/10.13057/biodiv/d200713>
- Mistry, C., Kathiria, K. B., Sabolu, S., & Kumar, S. (2016). Heritability and gene effects for yield related quantitative traits in eggplant. *Annals of Agricultural Sciences*, 61(2), 237–246. <https://doi.org/10.1016/j.aoas.2016.07.001>
- Oliveira Silva, C., Toshiyuki Hamawaki, O., Oliveira Nogueira, A. P., Ramos Campos de Almeida, M., Goulart Castro, D., Marques, F. S., Lemes Hamawaki, R., Lemes Hamawaki, C. D., Marques Cardoso, G., & Rodrigues Diniz, V. H. (2021). Genetic parameters and selection indexes in F2 and F2:3 soybean populations. *Agronomy Journal*, 113(4), 2991–3004. <https://doi.org/10.1002/agj2.20692>
- Pontes Júnior, V. A., Melo, P. G. S., Pereira, H. S., & Melo, L. C. (2016). Genetic potential of common bean progenies obtained by different breeding methods evaluated in various environments. *Genetics and Molecular Research*, 15(3), Article gmr.15038622. <https://doi.org/10.4238/gmr.15038622>
- Presello, D. A., Reid, L. M., Butler, G., & Mather, D. E. (2005). Pedigree selection for Gibberella ear rot resistance in maize. *Euphytica*, 143(1–2), 1–8. <https://doi.org/10.1007/s10681-005-6149-0>
- Purnamasari, I., Sobir, & Syukur, M. (2019). Diversity and inheritance in cowpea (*Vigna unguiculata*) on protein and yield components characters: Diversity and inheritance in cowpea (*Vigna unguiculata* (L.) Walp) on protein and yield components characters. *Biodiversitas Journal of Biological Diversity*, 20(5), 1294–1298. <https://doi.org/10.13057/biodiv/d200507>

- Ramos Guimarães, P. H., Guimarães Santos Melo, P., Centeno Cordeiro, A. C., Pereira Torga, P., Nakano Rangel, P. H., & Pereira de Castro, A. (2021). Correction to: Index selection can improve the selection efficiency in a rice recurrent selection population. *Euphytica*, 217, Article 133. <https://doi.org/10.1007/s10681-021-02858-0>
- Rini, H., Suwarno, Sintho Wahyuning, A., Munif, G., & Hajrial, A. (2018). Pedigree selection to obtained rice varieties adapted truso low phospho conditions. *Russian Journal of Agricultural and Socio-Economic Sciences*, 82(10), 234–243. <https://doi.org/10.18551/rjoas.2018-10.26>
- Ritonga, A. W., Chozin, M. A., Syukur, M., Maharijaya, A., & Sobir, S. (2018). Short Communication: Genetic variability, heritability, correlation, and path analysis in tomato (*Solanum lycopersicum*) under shading condition. *Biodiversitas Journal of Biological Diversity*, 19(4), 1527–1531. <https://doi.org/10.13057/biodiv/d190445>
- Ritonga, A. W., Syukur, M., Yunianti, R., & Sobir. (2018). Assessment of natural cross-pollination levels in chili pepper (*Capsicum annum* L.). *IOP Conference Series: Earth and Environmental Science*, 196, Article 012008. <https://doi.org/10.1088/1755-1315/196/1/012008>
- Rosminah, Maharijaya, A., & Syukur, D. M. (2019). Selection response pattern of chili pepper (*Capsicum annum* L.) species. *Jurnal Agronomi Indonesia*, 47(1), 47–52. <https://doi.org/10.24831/jai.v47i1.21922>
- Said, A. A. (2014). Generation mean analysis in wheat (*Triticum aestivum* L.) under drought stress conditions. *Annals of Agricultural Sciences*, 59(2), 177–184. <https://doi.org/10.1016/j.aos.2014.11.003>
- Saratayophat, T., & Nualsri, C. (2010). The efficiency of pedigree and single seed descent selections for yield improvement at generation 4 (F4) of two yardlong bean populations. *Kasetsart Journal (Natural Science)*, 44, 343–352.
- Sinha, P., Singh, V. K., Bohra, A., Kumar, A., Reif, J. C., & Varshney, R. K. (2021). Genomics and breeding innovations for enhancing genetic gain for climate resilience and nutrition traits. *Theoretical and Applied Genetics*, 134(6), 1829–1843. <https://doi.org/10.1007/s00122-021-03847-6>
- Syukur, M., Sujiprihati, S., & Yunianti, R. (2015). *Plant Breeding Techniques*. Penebar Swadaya.
- Thien Tran, L., Tuan Nguyen, A., Hong Nguyen, M., Tien Nguyen, L., Thi Nguyen, M., Thi Trinh, L., Thi Tran, D. -T., Viet Ta, S., Hoshikawa, K., Sugimoto, K., & Ezura, H. (2021). Developing new parthenocarpic tomato breeding lines carrying iaa9-3 mutation. *Euphytica*, 217, Article 139. <https://doi.org/10.1007/s10681-021-02853-5>
- Varghese, A., Joseph, J., Sarath, P. S., Sunil, R., Mathew, D., Biju, S., & Sindhumole, P. (2021). Development of dual purpose cowpea culture (*Vigna unguiculata* (L.) Walp.) with high grain yield. *Journal of Tropical Agriculture*, 59(1), 45–54. <https://jtropag.kau.in/index.php/ojs2/article/view/819/580>
- Wanga, M. A., Shimelis, H., Mashilo, J., & Laing, M. D. (2021). Opportunities and challenges of speed breeding: A review. *Plant Breeding*, 140(2), 185–194. <https://doi.org/10.1111/pbr.12909>
- Wibisono, K., Aisyah, S. I., Nurcholis, W., & Suhesti, S. (2021). Performance of putative mutants and genetic parameters of *Plectranthus amboinicus* (L.) through mutation induction with colchicine. *AGROSAINSTEK: Jurnal Ilmu Dan Teknologi Pertanian*, 5(2), 89–99. <https://doi.org/10.33019/agrosainstek.v5i2.247>
- Wibisono, K., Aisyah, S. I., Nurcholis, W., & Suhesti, S. (2022). Sensitivity in callus tissue of *Plectranthus amboinicus* (L.) through mutation induction with colchicine. *AGRIVITA Journal of Agricultural Science*, 44(1), 82–95. <https://doi.org/10.17503/agrivita.v44i1.3058>

- Wibisono, K., Aisyah, S. I., Suhesti, S., & Nurcholis, W. (2019). Optimization of Total Flavonoids Extraction and α -glucosidase inhibitory activity from *Plectranthus amboinicus* (Lour.) spreng. Leaves using the simplex-centroid design. *Molekul*, 14(2), 84–91. <http://dx.doi.org/10.20884/1.jm.2019.14.2.497>
- Yadav, S., Sandhu, N., Dixit, S., Kumar Singh, V., Catolos, M., Rani Mazumder, R., Rahman, M. A., & Kumar, A. (2021). Genomics-assisted breeding for successful development of multiple-stress-tolerant, climate-smart rice for southern and southeastern Asia. *The Plant Genome*, 14(1), Article e20074. <https://doi.org/10.1002/tpg2.20074>