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Evaluation of Progress Selection of F2 - F6 Population, A Cross between Two Lowland Tomato Genotypes

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Abstract

One of the parameters that can be measured from the activities of selection is progress selection. The population of a plant which has been selected is expected to be good against a derivative of a crop which was selected. The aim of this research is to study the results of progress selection varieties superior of tomato plants down the generations in the population F2 005001 until F6 005001-4-1-12-3 with a standard tomato cultivar, "Ratna". The result showed that the selected genotypes have shown improvements over the standard cutivar in terms of weight per fruit, fruit weight per plant, the number of fruits per plant, fruit thickness and the age of harvested plants in the population F2-005001 until F6 005001-4-1-12-3. The mean against the character being observed in the population F2 005001 until F6 005001-4-1-12-3 indicated that the result is better if compared with both parents, P1 (SSH-5) and P2 (Intan) and the standard cultivar "Ratna". The value of heritability a wider sense indicate its value being on each character of being selected, while the value of heritability in a more narrow sense showed a low value on every character. The value of progress against character selection of weights per fruit, the weight of the fruit per plant, the number of fruit per plant, thick flesh fruit and the age of harvest showed increased slow progress in a genotype F2 005001 followed by a period of rapid progress in a genotype F4 005001-4-1 and very slow in a genotype F6 005001-4-1-12-3.

Keywords: progress selection, population, genotype, mean, heritability

Introduction

Production of tomatoes, *Solanum lycopersicum*, in 2010-2011 increased by 7% from 891,616 tons (2010) to 954,046 tons (2011) with productivity average of 16.65 tons per ha (Dirjenhorti, 2012). National demand for tomatoes consistently increases every year, so many superior varieties are developed which are able to produce high production. High productivity is one of the major breeding objectives (Hidayat et al., 1997). However, with the limitations of high environmental factors conducive to tomato growing, high yielding varieties of tomatoes were developed that are able to adapt in lowland with high productivity.

One of the stages in the assembling of superior varieties of tomatoes is by selection, a process of separation of plants from a mixed population based on the appearance of certain characters (Arif, 2008). The purpose of selection is to select particular desired phenotypes to obtain a better genotype (Wahdina, 2004). There are two forms of selection for character enhancement, namely the selection between the existing population to enhance the desired character, and selection in the population to create new varieties, resulting in the offspring of the crosses usually consisting of segregation (Syukur et al., 2012). Evaluation of the selection between the existing populations is conducted to determine the response of a population selection to the expected characters.

One of the measurable parameters of the selection activity is the progress of selection. The estimates of selection progress will depend largely on the value of heritability, the standard intersection of selected populations, and the intensity of selection (Mejaya et al., 2010). Selected crop populations are expected to provide better results for derivatives of selected plants. Heritability value is the ratio of genotype with the total amount of phenotypes. Generally, narrow sense of heritability gets much attention because the additive effect of each allele is inherited from the elder to its derivatives (Memen et al., 2007). In this study, evaluation of selected characters is expected to get good selection progress. This study aims to study the progress of selection of superior varieties of tomato plants between generations in the population F2 - F6 with the "Ratna" variety as the comparing variety.

Materials and Methods

The research was conducted at the Leuwikopo experimental station and Plant Breeding Education Laboratory of Agronomy and Horticulture Department, Bogor Agricultural University, Indonesia, from December 2013 until April 2014. The materials used in this research were tomato parents SSH-5 (40 plants), tomato parents Intan (40 plants), and five generations of selfing derivatives (F2 005001) (100 plants), the third derivative (F3 005001-4) (100 plants), the fourth derivative (F4 005001-4-1) (100 plants), the fifth derivative (F5 005001-4-1 -12) (100 plants), and the sixth derivative (F6 005001-4-1-12-3) (100 plants).

Two seeds of tomato were planted per hole on seedling trays containing media soil mixture and manure (1:1 v/v). Gandasil D at the rate of 2 $g.L^{-1}$ was applied in a liquid form. Watering was conducted twice a day, morning and afternoon. Land clearing was done before it was prepared and leveled after which the land was then divided into seven plots for each varieties tested. The size of each bed was 1 m x 5 m with 80 cm as the distance between beds.

Fertilizers were applied after planting with half dose 50 kg N per ha (5 g Urea per plant), 100 kg P_2O_5 per ha (16 g TSP per plant) and 120 kg K2O per ha (20 g KCl per plant) (Harjadi and Sunaryono, 1989). Plant pest and disease control were conducted twice a week using Mancozeb 80% or Propinep 70% (2 $g.l^{-1}$), Profenofos (2 $ml.L^{-1}$) and Dicofol (2 $ml.L^{-1}$). Harvesting was conducted when the fruit skin were yellow reddish in colour.

Results and Discussion

Harvest Age

Heritability values are referred to as low if less than 20%, medium if between 20-50% and high if the value is more than 50% (Sujiprihati et al., 2003). The width sense of heritability value character of tomato harvest age was in the medium range of 40.66 to 54.03%, while the narrow sense of heritability was in the low range of 6.24 to 15.13% (Table 5). Based on the additive ratio contained in Table 1, it is known that the value of the additive variety of harvest age characters is low. The low variety of additives affecting the age of harvest suggests that selection done in the early generations did not provide much genotype progress. A study by Arif et al. (2012) showed thatthe width sense of heritability value in the character of harvest age is in the medium-high range, while heritability in the narrow sense is in the low range. Our findings are in line with this study, where the width sense of heritability was in the medium range and narrow sense of heritability was in the low range.

The mean value of the harvest age character decreases from the genotype F2 005001 - F6 005001-4-1-12-3 which was in the range of 67 to 65 DAP. The decline in the mean values on the character of harvest age indicated that there was a great selection of progress from the parents to the progenies. Idris et al. (2011) reported that there was a positive correlation between harvest age of maize and seed weight per ear. Our study had shown a similar result where increasing harvest age in each genotype affects the weight increase per fruit in each genotype. The addition of harvested lifespan had an enormous impact on the opportunities for plants to accumulate more organic matter and photosynthates in the fruit ripening process.

Weight of Fruit per Plant

Heritability value of the broad mean of fruit weight character per plant was in the medium range of 18.75 to 61.24%. A high heritability value is caused by a relatively homogenous environment (Arifin, 2008), The low heritability value in the F3 005001-4 genotype (18.75%) was influenced by environmental factors

Table 1. Component variety (?) and heritability of tomato harvest age

Population	Harvest age					
	Range (days)	Mean (days)	Diversity	h^2_{bs} (%)	h^2_{ns} (%)	a ratio
P1 (SSH-5)	65 – 76	70.25	13.69			
P2 (Intan)	55 – 64	57.93	5.55			
F2 005001	58 – 75	65.43	16.48	41.64	6.24	0.15
F3 005001-4	58 – 75	66.81	19.50	50.68	8.96	0.18
F4 005001-4-1	56 – 75	63.14	16.21	40.66	16.94	0.42
F5 005001-4-1-12	56 – 73	67.48	16.70	42.42	16.11	0.38
F6 005001-4-1-12-3	56 – 79	65.29	20.93	54.03	15.13*	0.28
"Ratna"	57 – 73	62.60	11.78			

Note : * = Based on extrapolation of the additive ratio

(Table 2), including pest and diseases. The severe pest and disease attack occurredd in the population of F3 005001-4 had directly affected the fruit yield per plant.

Table 2. Various components and heritability of fruit weight per tomato plant

Population	Fruit weight per plant					
	Range (g)	Mean (g)	Diversity	h^2_{bs} (%)	h^2_{ns} (%)	a ratio
P1 (SSH-5)	30.05 - 63.25	49.23	151.55			
P2 (Intan)	54.42 - 805.53	309.28	53996.48			
F2 005001	89.28 - 1023.23	231.53	35557.66	23.86	11.09	0.46
F3 005001-4	83.17 - 768.35	235.22	33322.38	18.75	17.96	0.96
F4 005001-4-1	94.7 - 1276.53	389.80	69841.74	61.24	29.54	0.48
F5 005001-4-1-12	69.86 - 975.02	430.46	56990.66	52.29	24.24	0.46
F6 005001-4-1-12-3	384.76 - 1193.03	806.15	40090.63	32.47	14.29*	0.44
"Ratna"	23.27 - 1257.83	434.25	108786.46			

Note : * = Based on extrapolation of additive ratio

The narrow sense of heritability value of character of fruit weight per plant was in the low range of 11.09 to 29.54%. According to Masruroh et al. (2009), the value of heritability in the narrow sense indicates the magnitude of additive influence on phenotype appearance. A narrow sense of heritability value indicated a low proportion of additive variance (Table 2). This was less favorable in the selection process because of the low possibility to improve fruit weight per plant.

The Number of Fruits per Plant

The width sense of heritability value of the character of the number of fruit was in the medium range of 44.32 to 51.95%, except in the genotype F3 005001-4 which is in the low range of 10.16% (Table 3). The narrow sense of heritability value of the number of fruit was in the low range of 7.4 to 26.33%. The low value of heritablitas in genotype F3 005001-4 was caused by pest and disease attack resulting in a decrease in population hence influenced the value of genotype varieties.

Based on the results on the number of fruits per plant it can be seen that the highest variety of values was in the genotype F2 005001 (51.95%) (Table 3) whereas the value of the highest narrow sense of heritability is in the genotype F4 005001-4-1 (26.33%). According to Gaswanto et al. (2009) the narrow sense of heritability becomes more important in an inheritance to its derivatives due to the diversity caused by the role of the additive gene as part of the total genetic diversity. The higher narrow sense of heritability value of the genotype F4 005001-4-1 indicated the effect of higher additive varieties so that the nature of the number of fruits will be inherited from the offspring of the crosses occurring in the F4 005001-4-1 generation.

Thickness of Fruit Flesh

The width sense of heritability value of the thickness of the fruit flesh was in the medium range of 24.64

Table 3. Various components and heritability of the number of fruits per plant

Population	The number of fruit per plant					
	Range (fuits)	Mean (fuits)	Diversity	h^2_{bs} (%)	h^2_{ns} (%)	a ratio
P1 (SSH-5)	2 – 12	3.75	9.94			
P2 (Intan)	3 – 31	11.78	52.54			
F2 005001	2 – 43	11.25	65.01	51.95	13.55	0.26
F3 005001-4	3 – 26	11.38	34.78	10.16	7.40	0.73
F4 005001-4-1	6 – 36	16.20	59.07	47.11	26.33	0.56
F5 005001-4-1-12	8 – 40	19.00	56.11	44.32	19.64	0.44
F6 005001-4-1-12-3	10 – 41	26.29	58.15	46.27	14.81*	0.32
"Ratna"	2 – 45	18.24	135.13			

Note : * = Based on extrapolation of additive ratio

Table 4. The thickness of tomato flesh and its heritability

Population	Thickness of fruit flesh					
	Range (mm)	Mean (mm)	Diversity	h^2_{bs} (%)	h^2_{ns} (%)	a ratio
P1 (SSH-5)	0.96 - 4.03	2.17	0.72			
P2 (Intan)	0.90 - 4.03	2.32	0.36			
F2 005001	1.50 - 4.83	3.04	0.76	28.86	8.92	0.31
F3 005001-4	2.04 - 5.45	3.08	0.84	35.95	14.96	0.42
F4 005001-4-1	2.11 - 5.95	3.81	1.22	55.88	8.69	0.16
F5 005001-4-1-12	2.57 - 6.15	4.50	0.80	32.89	8.18	0.25
F6 005001-4-1-12-3	3.19 - 6.98	5.37	0.72	24.64	8.62*	0.35
"Ratna"	1.51 - 7.02	4.59	1.55			

Note : * = Based on extrapolation of additive ratio

Table 5. Various components and heritability weights per tomato fruit

Population	Weight per fruit					
	Range (g)	Mean (g)	Variation	h^2_{bs} (%)	h^2_{ns} (%)	a ratio
P1 (SSH-5)	15.03 - 59.09	25.09	9.95			
P2 (Intan)	18.13 - 50.52	32.66	81.90			
F2 005001	6.98 - 40.41	20.15	76.03	39.60	11.72	0.30
F3 005001-4	10.40 - 43.62	20.49	70.01	34.40	19.13	0.56
F4 005001-4-1	20.35 - 48.37	31.95	69.69	34.11	26.4	0.77
F5 005001-4-1-12	24.24 - 64.18	35.72	64.94	29.28	21.63	0.74
F6 005001-4-1-12-3	36.44 - 66.62	48.87	56.82	19.18	13.43*	0.70
"Ratna"	12.21 - 55.73	29.18	100.12			

Note : * = Based on extrapolation of additive ratio

to 55.88%, while the narrow sense of heritability value was in the low range of 8.18 to 14.96% (Table 4). Based on the thickness and heritability of tomato flesh (Table 4), the highest mean value of heritability was in F4 005001-4-1 genotype (55.88%) and the lowest value was in F6 006001-4-1-12-3 genotype (24.64%). The highest narrow sense of heritability value is in the genotype F3 005001-4 (14.96%). This indicated that effective selection was performed on the F4 005001-4-1 generation. However, in the final population of the F6 005001-4-1-12-3 genotype the selection was not effective.

Weight per Fruit

The width sense of heritability value of the character of weight per fruit was in the medium range of 29.28 to 39.60%, in the genotype F2 005001- F5 005001-4-1-12. However heritability decreased to as low as 19.18% in the genotype F6 005001-4-1-12-3 (Table 5) while the narrow sense of heritability value of weight character per fruit was in the low range of 11.72 to 26.63%. A similar study on chilly by Syukur (2012) indicated a high weight per fruit. However, the results of this study are somewhat different and it is thought to be due to differences in population and the methods employed.

The value of heritability shows the effectiveness of selection of a character. According to Arifin (2008) heritability estimates are used as a first step in the selection work of segregated populations. The low diversity value of the genotype F6 005001-4-1-12-3 shows that selection of weight per fruit in the F6 generation will result in a low selection progress. According to Arif et al. (2012) the narrow sense of heritability in approaching the width sense of heritability shows that the proportion of the additive diversity is greater than the dominant diversity. This is in accordance with the additive ratio (Table 1), which shows a high diversity of additives compared to the dominant.

Progress Selection

Progress selection is a value that becomes the parameter of success on the selection of a population. In simple terms the progress of selection is the difference between the mean of the descendants of the selection with the median selection of the population (Gratitude et al., 2012). The value of selection of weight per fruit, weight of fruit per plant, number of fruits per plant, fruit flesh thickness and plant harvest age showed a slow increase in genotype F2 005001 followed by a period of rapid advancement in genotype F4 005001-4-1, and progressively slowed down in genotype F6 005001-4-1-12-3.

which had the character of harvest age. In the study of Barmawi et al. (2013) the value of the genetic progress of the harvest age is low suggesting that there was a slow progress in the selection in every generation of selection.

Estimated progress of selection will be highly dependent on the heritability value, standard intersection of selected population and the selection

Table 6. Progress of selection of tomato yield characters

Population	Harvest age			Fruit weight per plant			Fruit number per plant		
	S	G_m	G_t	S	G_m	G_t	S	G_m	G_t
F2 005001	-4.56	-0.28	-0.45	231.80	25.70	36.80	13.75	1.86	1.92
F3 005001-4	-4.81	-0.43	-0.70	156.80	28.16	57.69	7.62	0.56	0.77
F4 005001-4-1	-4.94	-0.84	-1.20	381.11	112.58	137.40	12.70	3.34	3.56
F5 005001-4-1-12	-6.03	-0.97	-1.16	312.70	75.79	101.83	13.00	2.55	2.59
F6 005001-4-1-12-3	-5.89	-1.08	-1.48	260.31	37.19	50.34	11.41	1.69	1.99

Note : G_m = Progress selection based on differential selection; G_t = Progress selection based on theory (i =1.76)

This is in line with Zulfarosda et al. (2012) where the weight of fruit per grain, fruit weight per plot, flowering age, and harvest age of ten tomato genotypes tested had slow selection progress. Susiana (2006) demonstrated that most chili characters had high genetic expectation values except for flowering age, harvest age, marketable fruit weight and thick bark of fruit having low genetic progress value (0%).

The age of tomato harvest showed the decline of the days of each generation with values from 0.45 to 1.48 (Table 6). This means that each generation experiences an acceleration of harvest time between 0.45 days to 1.48 days after planting. Graph of the mean age of harvest (Figure 1) shows the average yield of harvest age of each generation was between the second harvest age of P1 (SSH-5) which has a long harvesting age character with P2 (Intan)

intensity (Mejaya et al., 2010). The comparison of selection progress using the difference between the selected middle value and the middle of the initial population (differential selection) using the selection intensity has a small difference, where the value of selection progress using differential selection always has lower value than the value of selection progress by using intensity of selection (Table 6 and Table 7). This was because the differential selection used had not been standardized for the deviation, so the difference of the units in comparing the selection power of two or more characters could not be used differential magnitude of selection.

Quantitative characters are influenced by many genes whose influence is cumulative (Murti et al., 2015). The value of selection of weight per fruit, the weight of fruit per plant and the number of fruit

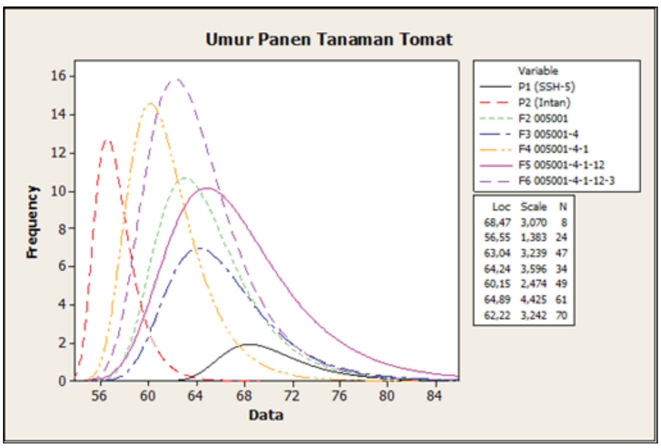

Figure 1. The mean values of harvest age of tomato from population F2-F6 and both parents.

Table 7. Progress of selection of advanced tomato yield characters

Population	Thickness of fruit flesh			Weight per fruit		
	S	G_m	G_t	S	G_m	G_t
F2 005001	1.20	0.11	0.14	13.17	1.54	1.80
F3 005001-4	1.49	0.22	0.24	12.10	2.32	2.82
F4 005001-4-1	1.58	0.14	0.17	11.63	3.07	3.88
F5 005001-4-1-12	1.32	0.11	0.13	12.18	2.64	3.07
F6 005001-4-1-12-3	1.06	0.09	0.13	8.81	1.18	1.78

Note : G_m = Progress selection based on differential selection; G_t = Progress selection based on theory (i =1.76)

per plant had the highest selection progress on the genotype F4 005001-4-1 and decreased in the next generation. In contrast to the progress of selection on the thickness of fruit flesh and fruit harvest age, the highest thickness of the flesh was observed on the genotype F3 005001-4 with a value of 0.22 indicating a progressively differential selection and 0.24 was progressively selection with the intensity of selection (Table 7). While the highest selection of fruit harvest age on genotype F6 005001-4-1-12-3 with a value of 1.08 in progress differential selection and 1.48 in progress selection with the intensity of selection (Table 7).

Fruit weight per plant with cycles of 36.80 to 137.40 (Table 6). This means that each generation contains additional fruit per plant with an added value of 36.80 grams per plant up to 137.40 grams per plant. Graph of the median fruit-per-plant value (Figure 2) shows an improvement in the larger F6 005001-4-1-12-3 genotype compared to both parents P1 (SSH-5) and P2 (Intan), and the genotype of each generation. In the study of Idris et al. (2011) fruit weight per plant is positively correlated with the weight per fruit, so the increase in fruit weight per fruit could potentially increase yield. There was an increased progress of high selection of fruit weight per plant on genotype F4 005001-4-1 and genotype F5 005001-4-1-12 (Table 6). This is due to the mean value and narrow sense of heritability value that influenced the selection of a population. On the other hand, the additive ratio level in the F3 005001-4 genotype of 0.96 (Table 2) gives a greater impact on subsequent generations, so the selection of the F3 005001-4 genotype provides higher upgrades in the next generation.

The number of fruits per plant shows the progress of selection of each cycle with values from 0.77 to 3.56 (Table 6). This means that each generation has an additional number of fruits per plant with an additional value of 0.77 fruits up to 3.56 fruits per plant. Graph of the mean value of the number of fruits per plant (Figure 3) shows an increase in the number of fruits per generation with the genotype F6 005001-4-1-12-3 showing the highest number of fruits when compared with both parents ie P1 (SSH-5) fruit per plant is very low and P2 (Intan), as well as the genotype of each generation.

The parental crossover of P1 (SSH-5) had a low number of fruits per plant compared to the P2 (Intan) parent which yielded a high number of fruits per plant producing saplings that inherit the number of fruits per plant with average yields between the two ages in genotype F2 005001 (Figure 3). This shows that the influence of P2 (Intan) is stronger than P1 (SSH-5). Therefore it is possible that the gene P2 (Intan) is dominant for the character of the number of fruits

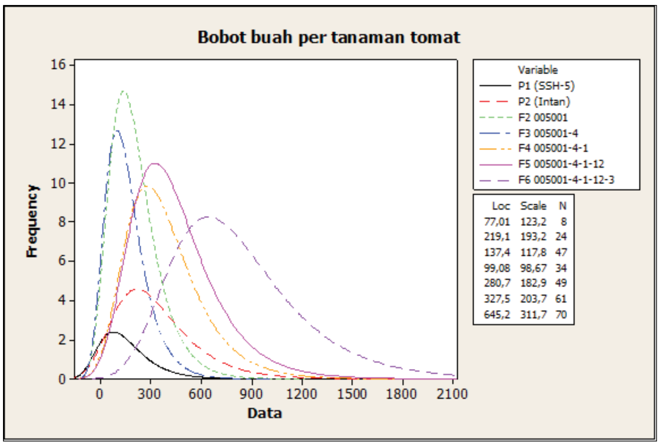

Figure 2. The mean values of fruit weight per plant of population F2-F6 and both parents

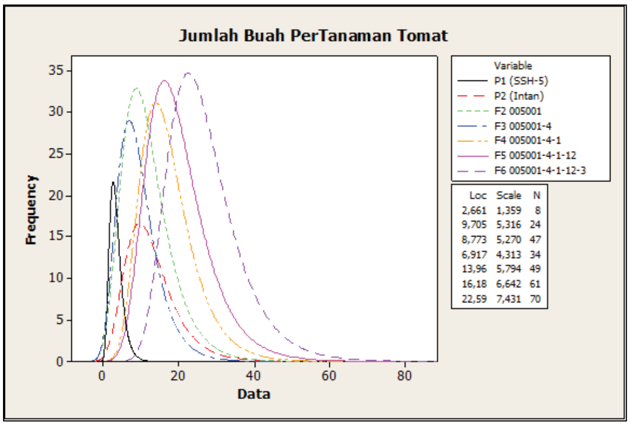

Figure 3. The mean values of the number of fruits per plant of population F2-F6 and the two parents

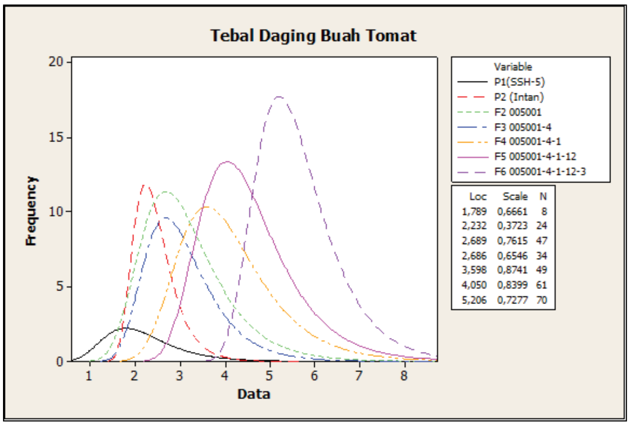

Figure 4. The mean values of the tomato flesh thickness of population F2-F6 and both parents

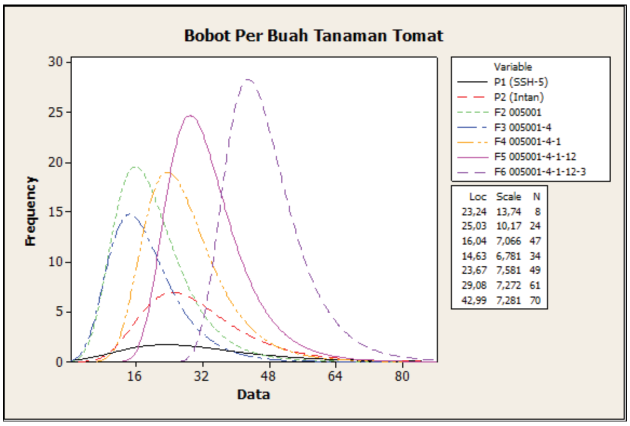

Figure 5. The mean values of weight per fruit of the F2-F6 population and the two parents

per plant. The results of research by Masruroh et al. (2009) showed that the number of fruit on the tomato crossing LV6123 X LV5152 fully influenced the action of additive gene. The existence of additive gene action provides an increase in the number of fruit per plant that occurs after the best population selection.
The thickness of the tomato flesh shows a progress in the selection of each cycle with values from 0.13 to 0.24 (Table 7). This means that every generation had increased thickness in fruit flesh with an additional value of 0.13 to 0.24 mm per generation of selection. Graph of mean value of thickness of fruits flesh (Figure 4) shows an increase in the thickness of fruit flesh of each generation with genotype F6 005001-4-1-12-3 having the largest fruit thickness as compared to the two parents namely P1 (SSH-5) which has thin flesh and P2 (Intan) with character of medium flesh thickness.

The weight per fruit shows the progress of selection of each cycle with the values of 1.78 to 3.88 (Table 7). Each generation had an average weight per fruit ranging from 1.78 grams to as high as 3.88 grams per fruit in the genotype F4 005001-4-1. The weight character per fruit is one of the most important selection criteria that correlated with other characters and showed the potential outcomes (Zulfarosda et al., 2012). Graph of weight mean value per fruit (Figure 1) shows a selection progress on genotype F6 005001-4-1-12-3 which has the biggest weight per fruit when compared to both parents P1 (SSH-5) and P2 (Intan), as well as the genotype of each generation.

Increased progress of low weight selection per fruit was shown in genotype F2 005001 and F3 005001-4 when compared to both parents (Figure 5). This is consistent with the data in Table 1 where there is a modest advancement of mean values on the genotype F2 005001 and F3 005001-4. The low advancement of mean values in this initial genotype was due to the high value of variance indicating high levels of heterozygosity compared with the final genotype. The high genetic diversity of early generations in a population indicated that selection can be performed on the desired variables according to the purpose of plant breeding activities performed (Susiana, 2006).
The result of the t-test was conducted on population F6 005001-4-1-12-3 as genotype of selection result

with "Ratna" as varieties of comparison on weight per fruit, fruit weight per plant and number of fruit per plant there is a real difference (Table 8). This result demonstrated that the weight character per fruit, the weight of the fruit per plant and the number of fruits per plant F6 005001-4-1-12-3 has a better value compared to the standard cultivar "Ratna". However t-test results was conducted on population F6 005001-4-1-12-3 with "Ratna" on the thickness of fruit flesh and harvest age showed no significant difference. This is due to the low selection progress in harvest age and flesh thickness as well as the good character of the "Ratna" variety that has a thick fruit flesh that is large and the age of the shorter harvest. The selection improvement of thick character of fruit flesh and harvest age did not show tangible results when compared with "Ratna". The characters that have low selection progress, generally indicated that the character was a quantitative that was controlled by many genes (Komariah and Amalia 2012).

Table 8. Test the t-student tomato yield characters of population F6 005001-4-1-12-3 against the standard cultivar "Ratna"

Populasi	Average fruit weight (g)	Fruit weight per plant (g)	Number of fruits per plant	Fruit flesh thicnkess (mm)	Harvest age (day)
F6 005001-4-1-12-3	48.87 ± 7.54	806.15 ± 200.23	26.29 ± 7.63	5.37 ± 0.85	65 ± 5
"Ratna"	29.18 ± 10.01	434.25 ± 329.83	18.24 ± 11.62	4.59 ± 1.24	63 ± 3
T-test	10.09*	6.09*	3.79*	3.45^{ns}	3.65^{ns}
Prob > |t|	0.000	0.000	0.000	0.001	0.000

Note : * = significantly different to "Ratna"; ^{ns} = not significantly different from "Ratna"

Conclusion

The result of this research demonstrated that there were progress of selection on character of weight per fruit, fruit weight per plant, number of fruit per plant, fruit flesh thickness and plant harvest age in population F2-005001 to F6 005001-4-1-12-3. The mean values of the characters observed in the population F2 005001 - F6 005001-4-1-12-3 showed better results when compared to both P1 (SSH-5) and P2 (Intan) parents, and to the standard cultivar "Ratna". The width sense of heritability value indicates the current value of each selected characterwhile the narrow sense of heritability value indicated a low value on each character. The value of selection of weight per fruit, weight of fruit per plant, number of fruits per plant, thickness of fruit flesh and harvest age showed a slow increasd in the genotype F2 005001 and followed by a period of rapid advancement in genotype F4 005001-4-1 and progressively slowed down in the genotype F6 005001-4-1-12-3.

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