J. ISSAAS Vol. 24, No. 2: 129-140 (2018)

GROWTH ANALYSIS AND PHYSIOLOGICAL CHARACTERISTICS OF SEVERAL TOMATO GENOTYPES UNDER THE LOW LIGHT INTENSITY

Dwi P. Sunaryanti[1], M.A. Chozin[2*], Sandra A. Aziz[2]
[1]Agronomy and Horticulture Study Program, Post Graduate School of Bogor Agricultural University, Jl. Meranti, Dramaga, Bogor, 11680, Indonesia
[2]Departement of Agronomy and Horticulture, Faculty of Agriculture, Bogor Agricultural University, Jl. Meranti, Dramaga, Bogor, 11680, Indonesia
*Corresponding author: ma_chozin@apps.ipb.ac.id

(Received: April 16, 2018; Accepted: November 17, 2018)

ABSTRACT

Light intensity is an important environmental factor affecting plants. Tomatoes (*Solanum lycopersicum* L.) have a wide response to light intensity. A field experiment was conducted at Cikarawang Experiment Station, Bogor, Indonesia from December 2015 to April 2016. The study was arranged in a factorial nested design with three replicates. Two shade-sensitive, two shade-tolerant, and two shade-loving genotypes of tomato were used in this experiment. The treatments were two shade levels (0 and 50%) applied on 23 day-old seedlings and maintained until harvest time. The study sought to evaluate the differences in adaptation mechanisms between shade-sensitive, shade-tolerant, and shade-loving tomato genotypes, based on their growth response and physiological characters. The study showed that low light intensity decreased significantly the Relative Growth Rate (RGR) and Net Assimilation Rate (NAR) of tomato plants. It also significantly affected physiological characters, i.e., the rate of photosynthesis, stomatal conductance, pigment content, sucrose and starch in leaves, and NPK nutrient status. In addition, shade had a significant effect on vegetative growth characters, including an increase in plant height and leaf area, as well as a decrease in stem diameter and generative growth variables (delayed flowering). Yield of shade-sensitive genotype was lower than the yield of both shade-tolerant and shade-loving genotypes because it has a different physiological response to low light intensity. On the other hand, the shade-tolerant and shade-loving genotypes showed similar responses. Under low light, the shade-sensitive genotype exhibited delayed generative phase, while having a lower of photosynthetic rate, stomatal conductance, pigment, and starch content compared with the shade-tolerant and shade-loving genotype.

Key words: growth, photosynthesis, physiology, shade, yields.

INTRODUCTION

Tomato is one of the horticultural commodities which have high economic value. Tomato production in Indonesia continuously decreased over the last few years. Statistical data from the Indonesian Ministry of Agriculture shows that production of tomato in 2013 was 992.780 tons. In 2014, there was a decline in tomato production to 915.987 tons. Tomato production in 2015 also decreased by 877.792 tons and further decreased in 2016 to 872.875 tons. The decline in tomato production may be caused by decreasing production area, which decreased by 7.56% in 2015. In 2016, there was an increase in tomato production area of 4.22% (Ministry of Agriculture, 2017). However, the increase was not been able to improve tomato production, as efforts turned out to be hampered by the limited availability of land due to the increased conversion of land for non-agricultural interests. Multiple cropping systems can however, increase the production area of tomato (Manurung et al. 2007). The cultivation of tomatoes with multiple cropping systems are constrained by low light intensity due to shade from other higher plants. The lack of light intensity causes physiological changes in plants, especially in photosynthetic activity (Susanto and Sundari 2011). Photosynthesis disturbances due to lack of light cause low carbohydrate (sucrose and starch) synthesis and decrease in photosynthetic enzyme activity (Rubisco) which will impact on low production of plants (Jian-lei et al. 2014). Low light intensity affects plant growth and flowering (Zhao et al. 2012; Miller et al. 2015), changes in agronomic and morpho-physiological characters (Chairudin et al. 2015), and also affect the production and quality of fruit (Ilic et al. 2012). The use of adaptive varieties with low light intensity is expected to be a more efficient method to prevent the decline of tomato production in multiple cropping systems. Shading at 50% produces a high diversity of tomato adaptation to shade, which can be grouped into three categories, i.e., shade-sensitive, shade-tolerant, and shade-loving genotype. The grouping is based on the relative production obtained during the treatment. It shows that each group of tomato genotypes has the different adaptability to low light intensity (Baharuddin et al. 2014).

The ability of plants to cope with low-light intensity is dependent on its ability to continue photosynthesis in conditions of lack of light (Sopandie 2014). The diversity of characters and responses of various tomato genotypes that appear in low light intensity are likely due to the differentiation of photosynthesis efficiency (Sulistyowati et al. 2016a). The mechanism of adaptation to shade is achieved by (i) the avoidance mechanisms which associated with changes in anatomy and leaf morphology to make photosynthesis more efficient, and (ii) the tolerance mechanism which associated with the decrease of light compensation point and efficiency of respiration (Levitt 1980). However, more specific information about the differences between shade-sensitive, shade-tolerant, and shade-loving tomato genotypes in the mechanism of adaptation to low light intensity is needed. This study sought to evaluate the different adaptation mechanisms between shade-sensitive, shade-tolerant, and shade-loving tomato genotypes based on growth response and physiological characters.

MATERIALS AND METHODS

Plant materials. The plant materials used in this experiment were six tomato genotypes which are part of the collection of the Genetic and Plant Breeding laboratory, Bogor Agricultural University. The six genotypes consisted of 2 shade-sensitive genotypes (Tora and F7005001-4-1-112-5); 2 shade-tolerant genotypes (F7003008-1-12-10-3 and F70030081-12-16-2); and 2 shade-loving genotypes (SSH 3 and Belgian Apples). The classification of tomato plant tolerance level to shade is determined based on the percentage of crop relative production. Relative production is a percent value against control. Tomato plants are divided into 4 groups according to their relative production of shade, i.e. shade-sensitive genotypes (relative production <60%), shade-moderate genotypes (relative production 60-80%), shade-tolerance genotypes (relative production >80%), and shade-loving genotypes (relative production >100%) (Baharuddin et al. 2014).

All genotypes tested were of the determinate type (growth ends with the emergence of flowers/fruit). Before planting in the field, the seeds of tomato plants first sowed in a medium of a mixture of ash husk and dried cow manure (1:1). The tomato plant seedlings were used in the field experiment.

Field experiments. The field experiment was conducted at Cikarawang Experiment Station, Bogor, Indonesia from December 2015 to April 2016. The study was arranged using a nested design consisting of two factors and three replications. The first factor consisted of two shade levels, i.e. 0% (control/without shade) and 50% shade level. The second factor consisted of 2 shade-sensitive genotypes namely Tora and F7005001-4-1-112-5; 2 shade-tolerant genotypes namely F7003008-1-12-10-3 and F70030081-12-16-2; and 2 shade-loving genotypes namely SSH 3 and Belgian Apples. Thus, there were 36 experimental units with a population of 60 plants, aged 23 DAS (Days After Sowing) per unit. Observations were made on five plant samples in each experimental unit. Shade treatment was done by making an artificial shade building from black shading-net which has 50% density level. The use of a 50% shade level is intended to show the responsiveness to sensitive, tolerant, and shade tomatoes clearly. The cultivation was done according to the standard cultivation of tomato plants in general.

Observation of plant growth parameters were done by measuring plant height, stem diameter, and leaf area every week from 3 to 7 WAT (Weeks After Transplanting). In addition, measurements of RGR (Relative Growth Rate) and NAR (Net Assimilation Rate) values were also carried out every 2 weeks when the plants were 3-5 and 5-7 WAT. Observations of RGR and NAR values were used to support plant growth parameters. To calculate RGR and NAR the following formulae were used:

$$\text{Relative Growth Rate} = \frac{\ln W2 - \ln W1}{t2 - t1}$$

Where, ln = natural log, W1 = Dry weight of plant/m^2 recorded at time t1, W2 = Dry weight of plant/m^2 recorded at time t2, t1 and t2 were the interval of time, respectively.

$$\text{NAR} = \frac{(W2-W1)(\ln A2-\ln A1)}{(t2-t1)(A2-A1)}$$

Where, A1 and A2 are total leaf are at time t1 and t2 respectively. W1 and W2 are total dry of plant/m^2 recorded at time t1 and t2 respectively.

The number of days when the flowers began to emerge was determined. Net photosynthetic rate and stomatal conductance were measured on the third leaf from the top of 6 WAT plants using a portable measurement system (LI-6400, LI COR Inc, Lincoln, USA) between 9:00 and 11:00 am.

Laboratory observations. Several observations on plant physiological characteristics were performed to determine the effect of low light on physiological and metabolism activity. Laboratory analysis was conducted at Post Harvest Laboratory and Quality Testing Laboratory, Department of Agronomy and Horticulture, Bogor Agricultural University. These observations were primarily performed on parameters associated with photosynthesis, consisting of leaf pigment content, starch-sucrose content, and NPK status in leaf tissue. Leaf pigment content (chlorophyll a, chlorophyll b, anthocyanin, and carotene) were determined using spectrophotometry (Sims and Gamon 2002). The samples used were fresh leaves derived from the third leaf from the top at 5 WAT plants. Starch and sucrose content were determined using a UV-VIS spectrophotometer (Yoshida et al. 1976). N status was analyzed by semi-micro Kjeldahl, while P and K were analyzed using an atomic absorption spectrophotometer. The samples used to analyzed sucrose-starch content and NPK status were dried leaves derived from the third and fourth leaf from the top of 5 WAT plants.

Statistical analysis. The effects of treatments were analyzed using analysis of variance (ANOVA) with SAS 9.1.3 portable program. Differences between treatments used Honestly Significant Difference (HSD) test at $P < 0.05$.

RESULTS AND DISCUSSION

Plant growth analysis

Plant growth analysis follows the dynamics of photosynthesis as measured by the production of dry matter. Plant growth can be measured without disturbing crops, but they often do not reflect quantitative accuracy. Dry matter accumulation is preferred as a measure of growth, as it may reflect the ability of plants to bind energy from sunlight through photosynthesis, and their interaction with other environmental factors. There was no interaction between shade levels and genotypes on RGR and NAR (Table 1). However, they have a significant effect on the value of RGR and NAR, respectively.

The 50% shade decreased RGR by 22.09% at 3-5 WAT and 23.07% at 5-7 WAT. The 50% shade also decreased the NAR by 32.69% at 3-5 MST and 20.83% at 5-7 WAT. Shaded plants are known to have lower RGR and NAR than plants receiving full light (Lautt et al. 2000). Light deficiency causes disruption of plant metabolism, resulting in decreased rate of photosynthesis and carbohydrate synthesis (Sopandie et al. 2003). Photosynthetic disorders can inhibit the accumulation of dry matter and have an impact on low RGR and NAR. The RGR and NAR values at 3-5 WAT is higher than at 5-7 WAT, either for control or at 50% shade level. The generative phase, at 5-7 WAT, caused the energy from photosynthesis to be used in the formation of generative organs (flowers and fruits) rather than for growth of vegetative organs (Gardner et al. 1991).

The six genotypes tested at 3-5 WAT showed significant diversity for NAR but not for RGR. The highest NAR at 3-5 WAT was genotype F7003008-1-12-16-2 (0.0054 g cm^{-2} per day) and the lowest was genotype F7005001-4-1-12-5 (0.0030 g cm^{-2} per day). Meanwhile, the NAR value of each genotype on 5-7 WAT did not show any significant difference (Table 1). NAR values are influenced by total leaf area. Shade-tolerant (F7003008-1-12-10-3; F7003008-1-12-16-2) and shade-loving (SSH 3; Belgian Apples) genotypes can maintain the value of NAR higher than shade-sensitive genotypes (Tora; F7005001-4-1-12-5), even when these are at 5-7 WAT. This may be due to the morphological form of tomato leaves of the shade-sensitive genotypes which is different from the shade-tolerant and shade-loving genotypes. The shade-tolerant and shade-loving genotypes have numerous, small, thin leaves. However, the shade-sensitive genotypes have few large, long, thick leaves. The number and weight of leaves affects the total leaf area. The more number of leaves that actively photosynthesize causing the amount of photosynthate produced and stored as dry matter also increases. Thus, shade-tolerant and shade-loving genotypes have NAR values higher than shade-sensitive genotypes, especially for F7005001-4-1-12-5.

Table 1. Relative growth rate (RGR) and net assimilation rate (NAR) of six tomato genotypes and two levels of shade

Treatment		RGR (g per day)		NAR (g cm^{-2} per day)	
		3-5	5-7	3-5	5-7
		WAT			
Level of shade (%)					
0		0.86 a	0.65 a	0.0052 a	0.0024 a*
50		0.67 b	0.50 b	0.0035 b	0.0019 b
Tomato genotypes					
Tora	(S)	0.72 a	0.48 bc	0.0047 ab	0.0017 b
F7005001-4-1-12-5	(S)	0.71 a	0.43 c	0.0030 c	0.0018 b
F7003008-1-12-10-3	(T)	0.81 a	0.60 ab	0.0041 bc	0.0027 a
F7003008-1-12-16-2	(T)	0.74 a	0.68 a	0.0054 a	0.0024 ab
SSH 3	(L)	0.79 a	0.59 abc	0.0038 bc	0.0024 ab
Belgian Apples	(L)	0.84 a	0.67 a	0.0051 ab	0.0019 b

*Means followed by the same letter(s) within each column are not significantly different according to HSD (Honestly Significant Difference) test at $P < 0.05$; S = shade-sensitive genotype, T = shade-tolerant genotype, L = shade-loving genotype; WAT= weeks after transplanting

Vegetative and generative growth

There was no interaction between shade levels and genotypes on vegetative growth parameters observed (plant height, stem diameter, and total leaf area). Shade levels had a very significant effect on vegetative growth parameters, whereas the genotype had no significant effect (Table 2). The 50% shade level increased significantly plant height and total leaf area but decreased stem diameter. Changes of plant morphological characteristics due to shade, especially in leaf organs are one of the forms of plant adaptation through the avoidance mechanisms so that photosynthesis can become more efficient (Levitt 1980).

The six tested tomato genotypes are the determinate type. However, the heights and total leaf areas are significantly different. Belgian Apples (shade-loving) has the lowest height (96.21 cm), which was significantly different from shade-sensitive F7005001-4-1-12-5 and shade-tolerant F7003008-1-12-10-3 and F7003008-1-12-16-2. However, the heights of the shade-loving genotypes, Belgian Apples and SSH 3, are not significantly different. The total leaf area of Tora is significantly larger from F7005001-4-1-12-5 although both are shade-sensitive genotypes. Similarly, the total leaf area of F7003008-1-12-10-3 is larger and significantly different from F7003008-1-12-16-2 although both are shade-tolerant genotypes. The total leaf area of the shade-loving genotypes, i.e., Belgian Apples and SSH 3, are not significantly different. The 50% shade level increased plant height and leaf area significantly to 68% and 45%, respectively (Baharuddin et al. 2014).

Table 2. Plant height, stem diameter, and total leaf area of six tomato genotypes and two shade levels at 6 WAT

Treatment		**Observed parameters**		
		Plant height (cm)	**Stem diameter (mm)**	**Total leaf area (cm^2)**
Level of shade (%)				
0		97.03 b	13.38 a	318.13 b
50		119.66 a	9.78 b	395.11 a
Tomato genotypes				
Tora	(S)	100.96 b	11.39 a	377.90 ab
F7005001-4-1-12-5	(S)	116.39 a	11.32 a	297.85 c
F7003008-1-12-10-3	(T)	114.83 a	11.96 a	429.21 a
F7003008-1-12-16-2	(T)	121.84 a	11.26 a	319.07 bc
SSH 3	(L)	99.83 b	11.95 a	356.14 abc
Belgian Apples	(L)	96.21 b	11.61 a	359.54 abc

*Means followed by the same letter(s) within each column are not significantly different according to HSD (Honestly Significant Difference) test at P < 0.05; S = shade-sensitive genotype, T = shade-tolerant genotype, L = shade-loving genotype; WAT= weeks after transplanting

There were interactions between shade levels and genotypes in the generative growth stage (flowering time). Shade levels and genotypes also had very significant effects on flowering time (Table 3).

Table 3. Flower initiation (days) of six tomato genotypes under different shade levels

Genotypes		**Level of shade (%)**	
		0	**50**
Tora	(S)	28.6 bc	31.0 ab
F7005001-4-1-12-5	(S)	28.0 bc	33.7 a
F7003008-1-12-10-3	(T)	27.3 c	29.7 bc
F7003008-1-12-16-2	(T)	27.6 bc	28.3 bc
SSH 3	(L)	28.0 bc	28.0 bc
Belgian Apples	(L)	29.3 bc	29.7 bc

*Means followed by the same letter(s) within each column are not significantly different according to HSD (Honestly Significant Difference) test at P < 0.05; S = shade-sensitive genotype, T = shade-tolerant genotype, L = shade-loving genotype

The vegetative period of tomato plants was extended at 50% shade level with varying responses. Flower initiation of shade-tolerant (F7003008-1-12-10-3; F7003008-1-12-16-2) and shade-loving genotype (SSH 3; Belgian Apples) are not different from control. Genotype F7005001-4-1-12-5 (shade-sensitive) flowered at 33.7 DAT, which is 5.7 days longer and significantly different from control (28.0 DAT) and is consistent with previous reports (Baharuddin et al. 2014; Sulistyowati et al. 2016b). Plant growth and development phase is affected by heat unit (Syakur 2012). The delay in flowering time under 50% shade may be due to lack of heat units required for flowering, as the average temperature under shading net is lower than without shade (Bahrun 2012).

Gas exchange activity

There are interaction between shade levels and genotypes on gas change activity observed (stomatal conductance and rate of photosynthesis). Stomatal conductance indicates the level of gas exchange activity required in the photosynthesis process. Shade-tolerant and shade-loving tomato genotypes are capable of maintaining stable stomatal conductance in 50% shade level. In contrast, stomatal conductance in shade-sensitive genotypes decreased significantly under 50% shade (Table 4). The stomatal conductance of genotype F7005001-4-1-12-5 grown in 50% shade level was 49% lower (0.54 mol CO_2 m^{-2} s^{-1}) and significantly different from control (1.07 mol CO_2 m^{-2} s^{-1}). The 50% shade level has been demonstrated to decrease stomatal conductance in all genotype groups (shade-sensitive, shade-tolerant, and shade-loving), but shade-loving genotypes were more able to maintain the rate of photosynthesis due to increased concentrations of internal CO_2. (Sulistyowati et al. 2016b)

Table 4. Stomatal conductance and net photosynthetic rate at 6 WAT of six tomato genotypes under different shade levels

Observed parameters	Genotypes		Level of shade (%)	
			0	50
Stomatal conductance (mol CO_2 m^{-2} s^{-1})	Tora	(S)	1.46 a	0.78 bc
	F7005001-4-1-12-5	(S)	1.07 ab	0.54 c
	F7003008-1-12-10-3	(T)	0.48 c	0.34 c
	F7003008-1-12-16-2	(T)	1.07 ab	0.79 bc
	SSH 3	(L)	0.58 c	0.48 c
	Belgian Apples	(L)	0.66 bc	0.49 c
Net photosynthetic rate (µmol CO_2 m^{-2} s^{-1})	Tora	(S)	59.44 a	52.80 ab
	F7005001-4-1-12-5	(S)	55.29 ab	35.52 c
	F7003008-1-12-10-3	(T)	58.70 a	64.77 a
	F7003008-1-12-16-2	(T)	63.32 a	62.53 a
	SSH 3	(L)	57.68 ab	45.92 bc
	Belgian Apples	(L)	60.70 a	53.74 ab

*Means followed by the same letter(s) within each column are not significantly different according to HSD (Honestly Significant Difference) test at $P < 0.05$; S = shade-sensitive genotype, T = shade-tolerant genotype, L = shade-loving genotype

Similar to its effect on stomatal conductance, the 50% shade level also did not cause a drastic reduction in the rate of photosynthesis for shade-tolerant (F7003008-1-12-10-3; F7003008-1-12-16-2) and shade-loving (SSH 3; Belgian Apples) genotypes. However, 50% shade level caused a decrease in photosynthetic rate drastically for F7005001-4-1-12-5 (shade-sensitive). Tora, a shade-sensitive genotype was not affected by 50% shade levels in terms of photosynthetic rate. Shade-tolerant genotypes have a higher photosynthetic rate than the shade-sensitive under low light conditions (Sulistyowati et al. 2016a). The photosynthetic rate of F7005001-4-1-12-5 (shade-sensitive) in 50%

shade levels is smaller and significantly different from control, while the photosynthetic rate of Tora at 50% shade levels is not significantly different from shade-tolerant and shade-loving. This is due to the higher chlorophyll content of Tora than F7005001-4-1-12-5 (Table 5).

Leaf pigment content

Leaf photosynthetic pigments, especially chlorophyll a and b can be used as indicators of plant tolerance to low light intensity. There are no interaction between shade levels and genotypes on leaf pigment content (Table 5). However, the leaf pigment content is significantly affected only by shade levels. The 50% shade level causes an increase in chlorophyll a by 27.84%, while chlorophyll b has increased by 37.93%.

This is consistent with previous studies which reported that low light intensity increased the content of chlorophyll a and b (Xiao-lei et al. 2012; Zhao et al. 2012). The ratio of chlorophyll b/a in 50% shade level is significant. Chlorophyll b is part of the photosynthetic antenna complex in charge of collecting and collecting and transferring light to the reaction center, which is composed of chlorophyll a. Light energy is changed into chemical energy which is used for reduction in photosynthesis (Taiz and Zeiger 2002). The higher percentage of chlorophyll b than chlorophyll a at low light intensity is related to the increase of chlorophyll protein, thus improving the efficiency of photosynthetic antenna function in Light Harvesting Complex II (LHCII) (Djukri and Purwoko 2003). The increase in antennas in Photosystem II (PSII) will increase the efficiency of light harvesting. Thus, plants in low light intensity will adapt by increasing the ratio of chlorophyll b/a.

F7005001-4-1-12-5 (shade-sensitive) has the lowest chlorophyll a and b content (Table 5). The chlorophyll ratio of F7005001-4-1-12-5 (0.37) is also lower and significantly different from Tora (0.39), although both belong to shade-sensitive genotype. Low pigment content is thought to be the cause of F7005001-4-1-12-5 not being able to adapt at low light. Meanwhile, Tora (shade-sensitive) which has higher photosynthetic pigment content was able to adapt to maintain the rate of photosynthesis although still lower than the shade-tolerant and shade-loving genotypes. Other pigments that can absorb the visible light are anthocyanin and carotenoid. In this study, the level of shade has a very significant influence on the content of anthocyanin and carotenoid, whereas genotypes have a significant effect only on carotenoids. The anthocyanin (0.076 mg 100 g^{-1}) and carotene (0.51 mg g^{-1}) content were higher and significantly different at 50% shade levels than controls. The carotenoid content of tomatoes in shade treatment increases significantly (Sulistyowati et al. 2016b).

Sucrose and starch content

Shade levels and genotype affected significantly starch content, but not sucrose content. The content of starch for control (5.62%) is lower and significantly different than 50% shade level (6.57%). The 50% shade level increased the leaf starch content up to 16.90%. The six genotypes tested showed diversity in starch content, but not in sucrose content. The highest starch content was 7.53% in Belgian Apples (shade-loving) and the lowest (4.97%) in F7005001-4-1-12-5 (shade-sensitive) (Table 6).

The increase of starch under shade conditions is due to the inhibition of photosynthate transport, causing carbohydrate accumulation (starch) in leaves (Calatayud et al. 2007). Under low light intensity, shade-tolerant rice genotypes are known to have lower starch and sucrose levels than the shade-sensitive genotypes (Lautt et al. 2000). The shade-tolerant genotype can survive better in low light because it has higher carbohydrate content which is used to maintain photosynthesis.

Table 5. Leaf chlorophyll content (a and b), total chlorophyll, chlorophyll b/a ratio, anthocyanin, and carotene at 5 WAT of six tomato genotypes and two shade levels

Treatment		**Observed parameters**					
		Chlorophyll a (mg g^{-1})	**Chlorophyll b (mg g^{-1})**	**Total chlorophyll (mg g^{-1})**	**Chlorophyll b/a ratio (mg g^{-1})**	**Anthocyanin (mg 100 g^{-1})**	**Carotene (mg g^{-1})**
Level of shade (%)							
0		1.58 b	0.58 b	2.17 b	0.37 b	0.065 b	0.42 b
50		2.02 a	0.80 a	2.81 a	0.39 a	0.076 a	0.51 a
Genotypes							
Tora	(S)	1.92 a	0.76 a	2.68 a	0.39 a	0.075 a	0.50 a
F7005001-4-1-12-5	(S)	1.55 b	0.57 b	2.13 b	0.37 b	0.066 a	0.42 b
F7003008-1-12-10-3	(T)	1.85 a	0.72 a	2.57 a	0.38 ab	0.076 a	0.48 a
F7003008-1-12-16-2	(T)	1.85 a	0.71 a	2.57 a	0.38 ab	0.068 a	0.48 a
SSH 3	(L)	1.81 a	0.68 ab	2.44 ab	0.38 ab	0.068 a	0.46 ab
Belgian Apples	(L)	1.84 a	0.72 a	2.57 a	0.39 a	0.070 a	0.48 a

*Means followed by the same letter(s) within each column are not significantly different according to HSD (Honestly Significant Difference) test at $P < 0.05$; S = shade-sensitive genotype, T = shade-tolerant genotype, L = shade-loving genotype.

WAT = weeks after transplanting.

Table 6. Starch and sucrose content at 5 WAT of six tomato genotypes under different shade levels.

Treatment		Starch (%)	Sucrose (%)
Level of shade (%)			
0		5.62 b	0.73 a
50		6.57 a	0.72 a
Genotypes			
Tora	(S)	5.66 ab	0.73 a
F7005001-4-1-12-5	(S)	4.97 b	0.72 a
F7003008-1-12-10-3	(T)	5.73 ab	0.71 a
F7003008-1-12-16-2	(T)	6.25 ab	0.72 a
SSH 3	(L)	6.42 ab	0.73 a
Belgian Apples	(L)	7.53 a	0.73 a

*Means followed by the same letter(s) within each column are not significantly different according to HSD (Honestly Significant Difference) test at P < 0.05; S = shade-sensitive genotype, T = shade-tolerant genotype, L = shade-loving genotype, WAT = weeks after transplanting.

NPK status of leaves

N (nitrogen), P (phosphorus), and K (potassium) are essential for the growth and development of plants. Shade levels have a very significant effect on N and P status, but it do not have an effect on K status (Table 7). While genotypes has a significant effect on P and K status, but it has no effect on N status. There are no interactions between shade levels and genotype on N, P, and K status in tomato leaves. N and P at 50% shade level are 5.39 and 0.55%, respectively, and are significantly higher and different from control (5.02% for N and 0.44% for P). The six genotypes showed only differences in P and K status. Tora (shade-sensitive) has a higher concentration of P and significantly different from F7003008-1-12-10-3 and F7003008-1-12-16- 2 (shade-tolerant). Meanwhile, K levels for F7005001-4-1-12-5 (shade-sensitive) are significantly lower from F7003008-1-12-10-3 (shade-tolerant) and SSH 3 (shade-loving).

Table 7. NPK levels of tomato genotypes and two shade levels at 5 WAT

Treatment		Observed parameters		
		N (%)	P (%)	K (%)
Level of shade (%)				
0		5.02 b	0.44 b	5.16 a
50		5.39 a	0.55 a	5.27 a
Genotypes				
Tora	(S)	5.20 a	0.54 a	4.94 bc
F7005001-4-1-12-5	(S)	5.28 a	0.52 ab	4.93 c
F7003008-1-12-10-3	(T)	5.27 a	0.47 b	5.45 ab
F7003008-1-12-16-2	(T)	5.14 a	0.47 b	5.03 bc
SSH 3	(L)	5.08 a	0.49 ab	5.56 a
Belgian Apples	(L)	5.23 a	0.48 ab	5.38 abc

*Means followed by the same letter(s) within each column are not significantly different according to HSD (Honestly Significant Difference) test at P < 0.05; S = shade-sensitive genotype, T = shade-tolerant genotype, L = shade-loving genotype. WAT = weeks after transplanting.

Nitrogen (N) is used in the formation of chlorophyll, protoplasm, proteins, and nucleic acids for vegetative growth. Plants with light deficiency will tend to increase N absorption. Shade-sensitive genotype had a higher N increase than the shade-tolerant genotype (Syafruddin et al. 2014). However, there are no significant differences in the N content of the three groups of tomato genotypes (Table 7). The shade-sensitive genotypes (Tora and F7005001-4-1-12-5) tends to use N for its vegetative growth (plant height) than the other groups (Table 2). On the other hand, shade-tolerant (F7003008-1-12-10-3 and F7003008-1-12-16- 2) and shade-loving (Belgian Apple and SSH 3) tend to use N to form chlorophyll (Table 5). This mechanism is most likely the cause for shade-tolerant and shade-loving genotypes having a higher photosynthetic rate than shade-sensitive. This study shows that 50% shade level increased P levels significantly compared to control. P is an important element for energy transfer (ATP and other nucleoproteins), genetic information systems (DNA and RNA), and forming cell membranes (phospholipids). Thus plants that live in low light environments have higher P than shade-tolerant and shade-loving genotypes to provide more energy for their metabolic activities (Salisbury and Ross 1995).

Tomato yield at different light intensities

There was a significant interaction between shade treatment and genotype on the number of fruits per plant. Except in the SSH 3 genotype, the number of fruits per plant under shaded conditions was not significantly different from the controls. The number of fruits per plant in the SSH 3 genotype grown under shade was 13.7 pieces, lower and significantly different from the controls (22.3 pieces). The effect of interaction between shade and genotype was shown in fruit size. In contrast to its effect on the number of fruits, shade significantly increases the size of the genotype SSH 3 tomato fruit. The weight of the genotype SSH 3 tomato on the shaded condition was 25.14 g, higher and significantly different than the control (18.38 g). The limited number of sinks and the high activity of photosynthesis on the source cause the photosynthate formed to be transferred only to the available sinks. This is thought to be the cause of higher fruit weight for genotype SSH in shade compared to control (Table 8).

Table 8. Number of fruit per plant and fruit weight of tomato genotypes under different shade levels.

Parameters	Genotypes		Shade level (%)	
			0	50
Number of fruits (per plant)	Tora	(S)	6.5 de	4.9 e
	F7005001-4-1-12-5	(S)	10.3 cde	6.6 de
	F7003008-1-12-10-3	(T)	15.2 abc	17.8 ab
	F7003008-1-12-16-2	(T)	16.9 abc	21.8 a
	SSH 3	(L)	22.3 a	13.7 bcd
	Belgian Apples	(L)	18.8 ab	17.9 ab
Fruit weight (g per fruit)	Tora	(S)	63.89 a	50.08 b
	F7005001-4-1-12-5	(S)	38.06 c	26.13 d
	F7003008-1-12-10-3	(T)	25.89 d	19.22 ef
	F7003008-1-12-16-2	(T)	20.04 e	14.17 g
	SSH 3	(L)	18.38 ef	25.14 d
	Belgian Apples	(L)	16.28 fg	16.37 efg

*Means followed by the same letter(s) within each column are not significantly different according to HSD (Honestly Significant Difference) test at $P < 0.05$; S = shade-sensitive genotype, T = shade-tolerant genotype, L = shade-loving genotype

The effect of low light treatment on the production of tomatoes per plant is varied between genotypes (Fig. 1). Shade decreased yield significantly for the shade-sensitive group, but not for shade-tolerant and shade-loving group. The decrease in yield due to the shade treatment in Tora and F7005001-4-12-5 genotypes were 39.64% and 56.57%, respectively. The results of this study support earlier findings that demonstrate tomatoes have a high diversity of response to shade (Baharuddin et al. 2014; Sulistyowati et al. 2016b). It is therefore necessary to select appropriate genotypes for multiple cropping systems (Bahrun 2012; Manurung et al. 2007).

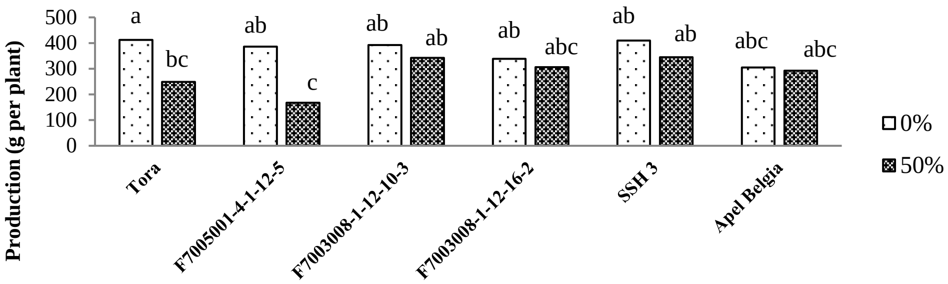

Fig. 1. Interaction effect of shade treatment and genotype on the production of tomatoes per plant.

CONCLUSION

Six tomato genotypes tested gave varied responseS to low light intensity. Shade-loving and shade-tolerant genotypes have better adaptation to shade resulting in higher growth and production compared to shade-sensitive genotypes. The differences in the adaptability of the tested tomato genotypes are thought to be closely related to differences in plant physiological responses to light especially the photosynthetic physiological characteristics such as net photosynthetic rate, stomatal conductance, chlorophyll content, and leaf sucrose-starch content.

ACKNOWLEDGMENTS

We thank the Directorate of Higher Education that funded this research through Strategic Research of Higher Education Program chaired by Prof. Dr. Ir. M.A. Chozin, M.Agr.

REFERENCES CITED

Bahrun, A.H. 2012. *Kajian ekofisiologi tanaman semusim penyusun agroforestri pada beberapa zona agroklimat di DAS Ciliwung Hulu.* Disertasi. Sekolah Pascasarjana Institut Pertanian Bogor, Bogor (in Bahasa Indonesia).

Baharuddin, R., M.A. Chozin, and M. Syukur. 2014. Shade tolerance of 20 genotypes of tomato (*Lycopersicon esculentum* Mill.). J. Agron. Indonesia. 42 (2): 130-135.

Calatayud, A., D. Roca, E. Gorbe, and P.F. Martinez. 2007. Light acclimation in rose (*Rosa hybrida* cv. Grand Gala) leaves after pruning: effects on chlorophyll *a* fluorescence, nitrate reductase, ammonium, and carbohydrates. Sci. Hort. 111: 152-159.

Chairudin, Effendi, and Sabarudin. 2015. Impact of shades to changes of characters of agronomy and morpho-physiology leaves in soybean (*Glycine max (L.) Merrill*). J. Floratek. 10: 26-35.

Djukri and B.S. Purwoko. 2003. Effects of paranets shade to tolerance characters of Taro (*Colocasia esculenta* (L.) Schott). Ilmu Pertanian. 10 (2): 17-25.

Gardner, F.P., Pearce, R.B., Mitchell, R.I. 1991. *Physiology of Crop Plant.* UI Pr, Jakarta, Indonesia.

Ilic, Z.S., L. Milenkovic, L. Stanojevic, D. Cvetkovic and E. Fallik. 2012. Effect of the modification on light intensity by color shade nets on yield and quality of tomato fruits. Sci Hort. 139:90-95.

Jian-lei, S., S. Xiao-lei, H. Hong-yu, W. Shao-hui, W. Yu-xia, and Z. Zhen-xian. 2014. Low light stress down-regulated rubisco gene expression and photosynthetic capacity during cucumber (*Cucumis sativus* L.) leaf development. J. Integr. Agr. 13 (5): 997-1007.

Lautt, B.S., M.A. Chozin, D. Sopandie, and L.K. Darusman. 2000. The balance of sucrose-starch and the enzyme activity of sucrose phosphate synthase in tolerant and sensitive upland rice under the shade. Hayati 7: 31-34.

Levitt, J. 1980. Response of Plants to Enviromental Stress. Academic Press, New York, United States**.**

Manurung, G., A.D. Susila, J. Roshetko, and M.C. Palada. 2007. Finding and challenges: Can vegetables be productive under tree shade management in West Java?. SANREM-TMPEGS Pub. 8: 2-17.

Miller, S.S., C. Hott, and T. Tworkoski. 2015. Shade effect on growth, flowering, and fruit of apple. J. Appl. Hort. 17 (2): 101-105.

Ministry of Agriculture 2017. Agricultural statistics for 2012-2016, Indonesian Ministry of Agriculture, Jakarta, Indonesia.

Salisbury, F.B. and Ross, C.W. 1995. Plant Physiology. 4th ed., CA: Wadsworth Publishing Company, Belmont. 682 p.

Sims, D.A. and J.A. Gamon. 2002. Relationship between leaf pigment content and spectral reflectance across a wide range of species, leaf structure and developmental stages. Remote. Sens. Environ. 81: 337-354.

Sopandie, D. 2014. *Fisiologi adaptasi tanaman terhadap cekaman abiotic pada agroekosistem tropika*. IPB Press, Bogor (in Bahasa Indonesia). 93 p.

Sopandie, D., M.A. Chozin, S. Sastrosumarjo, T. Juhaeti, and Sahardi. 2003. Shading tolerance in upland rice. Hayati 10 (2): 71-75.

Sulistyowati, D., M.A. Chozin, M. Syukur, M. Melati, and D. Guntoro. 2016a. Selection of shade-tolerant tomato genotypes. J. Appl. Hort. 18 (2): 154-159.

Sulistyowati, D., M.A. Chozin, M. Syukur, M. Melati, and D. Guntoro. 2016b. The photosynthetic characters of loving-shade tomato genotypes at low light intensity. J. Hort. 26 (2): 181-188.

Susanto, G.W.A. and T. Sundari. 2011 The changes of agronomy characters of soybean germplasm under shading condition. J. Agron. Indonesia. 39 (1): 1-6.

Syafruddin, Suwarti, and M. Azrai. 2014. *Penyaringan cepat dan toleransi tanaman jagung terhadap intensitas cahaya rendah*. Penelitian Pertanian Tanaman Pangan. 33 (1): 36-43.

Syakur, A. 2012. Heat unit approach for determining growth and development phases of tomato plants in greenhouse. J. Agroland. 19 (2): 96-101.

Taiz, L. and Zeiger, E. 2002. Plant Physiology. 3rd ed., Sinauer Associates, Sunderland. 690 p.

Xiao-lei, S., M. Sheng-li, W. Li-hao, Z. Bao-xi, and Z. Zhen-xian. 2012. Effect of low light on the characteristics of photosynthesis and chlorophyll *a* fluorescence during leaf development of sweet paper. J. Integr. Agr. 11(10): 1633-1643.

Yoshida, S., D.A. Forno, J.H. Cock, and K.A. Gomez. 1976. *Laboratory manual for physiological studies of rice*. IRRI, Los Banos, Philippines.

Zhao, D., Z. Hao, and J. Tao. 2012. Effect of shade on plant growth and flower quality in the herbaceous peony (*Paeonia lactiflora* Pall.). Plant. Physiol. Biochem. 61: 187-196.