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Original research article

Response of 'Hua-ruea' Chili Pepper (*Capsicum annuum* L.) to Salicylic Acid under Heat Stress

Sudchai Locharoen, Pariyanuj Chulaka*

Department of Horticulture, Faculty of Agriculture, Kasetsart University, Bangkok 10900, Thailand

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ABSTRACT

Environmental stress, especially high air temperature (T_{air}) and high vapour pressure deficit (VPD) affect photosynthesis which is directly related to productivity. In this study, salicylic acid (SA), at concentrations of 10^{-5} and 10^{-7} M, was tested for the ability to ameliorate physiological stress, improve the protein profile, and increase chili pepper yield under extreme environmental conditions. Salicylic acid at a concentration of 10^{-7} M ($SA10^{-7}$) increased the net photosynthetic rate (P_n), stomatal conductance (g_s), intercellular CO_2 concentration, transpiration rate, and maximum quantum efficiency of PSII photochemistry (F_v/F_m) when temperature was lower than 37 °C and VPD was less than 3 kPa. In addition, $SA10^{-7}$ could stimulate the synthesis of proteins associated with photosynthesis, such as chloroplast Rubisco activase, which promoted photosynthesis in chili pepper leaves. However, fruit number and fruit quality were not significantly different between the SA treatments (10^{-5} and 10^{-7} M) and control. Based on the results, SA application can improve photosynthesis of chili pepper plants, if the temperature does not exceed 37°C and VPD is less than 3 kPa.

Keywords: Heat stress; Leaf gas exchange; Chili pepper; Plant hormones; Proteomic

1. Introduction

Chili is an important cash crop in Asia. The chili production of Asian countries jointly accounted for 71 percent of the total world production. From 2013 to 2017, Thailand was the second largest producer of dried chilies in Asia and has earned the reputation as a major chili exporter in the world market [1]. Popular varieties of chili pepper for fresh and dried chili production in Thailand include 'Yod-son', 'Hua-ruea', 'Chinda', and hybrid varieties [2]. Additionally, chilies are used in domestic consumption as a raw material for cooking, processed food products, and medicine. Chili crops are exposed to the prevailing weather

***Corresponding author:** pariyanuj.c@ku.ac.th
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conditions such as temperature, radiation, and vapor pressure deficit (VPD). They are therefore vulnerable to extreme weather events. Previous research revealed that the temperature tends to be highest at midday. This results in reductions in photosynthetic output. When leaves are exposed to high air temperature, plants do not always reach their full photosynthetic capacity [3]. In the case of chili plants, if the air temperature rises higher than 33°C, plants stop the photosynthesis process and will start to dissipate heat in order to survive [4]. Furthermore, a reduction in photosynthesis may be the cause of flower abortion [5]. High temperature during chili production is frequently the cause of flower dropping and fruit abortion, which negatively influences crop yield. Bell peppers grown under high temperature conditions (33°C) during the post- pollination stage resulted in inhibited fruit set [6]. Also, low VPD has been shown to lead to an increase in the photosynthetic rate [7]. The relationship between air temperature and VPD is positive, which means that as the temperature rises, the VPD also increases [8].

Climate change prediction models showed that the air temperature will rise by 1 to 4°C by the end of the 21st century, due to increased greenhouse gases in the atmosphere [9]. The average temperature in Thailand from 1955 to 2009 increased by 0. 95°C, which was higher than the world average temperature change [10].

Extreme temperature change in Thailand would have a substantial negative socio- economic impact, especially in the agricultural sector.

Salicylic acid (SA) is classified as a plant hormone [11]. Recent evidence also suggests that SA is an important regulator of photosynthesis because it affects leaf chloroplast structure and stomatal closure [12]. The effects of exogenous SA depend on concentration of the application and plant species; in one study, a lower concentration of SA (10^{-5} M) improved the net photosynthetic rate (P_n) and CO_2 assimilation in *Brassica juncea* L. [13]. However, in a different study, higher SA concentrations (1 mM) caused a reduction in P_n and Rubisco activity in barley [14]. SA has been found to be an important signalling molecule for modulating plant response to environmental stress [15-16]. SA could protect the aspects of the photosynthetic process that are related to electron transport rate, quantum yield of photosystem II, and relative contents of D1 protein and Deg1protease in *Satsuma mandarin* leaves under heat stress [17]. Moreover, heat stress- related damage to membranes of *Cicer arietinum* could be reduced by the application of SA. The treatment also enhanced the protein content significantly with an induction of various stress enzymes [18]. Therefore, the objective of this study was to investigate the effects of SA on photosynthesis, protein synthesis, and crop yield under high temperature conditions.

2. Materials and Methods

2.1 Experimental conditions and plant material

The experiment was conducted inside a plastic-roof net house under ambient conditions at the experimental field, Department of Horticulture, Faculty of Agriculture, Kasetsart University (latitude 13°84´N, longitude 100°56´E). The daytime ambient conditions recorded include photosynthetic photon flux (PPF), air temperature (T_{air}), and VPD, which were collected by a weather station data logger (Watchdog 1450, Spectrum Technology Company, USA) which was placed in the center of the net house 2.5 m above the floor (Table 1 and 2). The experiment was carried out during the time period of March, 2015 to July, 2015.

'Hua-ruea #13' chili pepper seeds (*Capsicum annuum* L.) were obtained from Si Sa Ket Horticultural Research Center, Thailand. Seeds were germinated in peat moss substrate. At 45 days after sowing, the

Table 1. Mean, minimum, and maximum of PPF, T_{air}, and VPD inside the net house throughout planting time.

Month	Min PPF (µmol $m^{-2}s^{-1}$)	Max PPF (µmol $m^{-2}s^{-1}$)	Mean PPF (µmol m-2s-1)	Min T_{air} (°C)	Max T_{air} (°C)	Mean T_{air} (°C)	Min VPD (kPa)	Max VPD (kPa)	Mean VPD (kPa)
March[*1]	305.1	876.4	639.2	25.3	37.5	31.6	0.6	2.7	1.4
April	299.8	928.1	726.6	26.6	39.7	32.8	0.4	3.5	1.7
May	189.9	947.2	643.0	28.0	39.5	33.5	0.6	3.3	1.7
June	215.2	880.6	663.4	26.1	39.6	32.7	0.4	3.3	1.6
July[*2]	376.9	786.4	634.3	28.3	37.7	32.9	0.7	2.7	1.8

[*1]: average of the data from 14th-31st March
[*2]: average of the data from 1th-11st July

Table 2. Mean PPF, T_{air}, and VPD from 11:00 am to 01:00 pm on the day of photosynthesis measurement.

Date	PPF (µmol $m^{-2}s^{-1}$)	T_{air} (°C)	VPD (kPa)
15 May 2015	850.5±157.9	38.0±1.4	2.7±0.3
22 May 2015	516.7±148.0	37.1±0.5	2.6±0.1
29 May 2015	870.1±136.6	39.0±1.3	3.0±0.3

Values are show as mean±SD

seedlings were transplanted into 8-inch pots (4 liters) containing a mixture of coconut coir dust and coconut husk chips (2:1 v/v). Resh's Tropical Dry Summer nutrient solution [19] with an electrical conductivity of 2.4 mS cm^{-1} was applied by fertigation. When the plants developed 6 reproductive nodes, flowers at the lower sixth reproductive nodes were removed and foliar sprayed with salicylic acid at a concentration of 10^{-5}($SA10^{-5}$) or 10^{-7} ($SA10^{-7}$) M, using a volume of 50 ml/plant, by hand sprayer. A control (C) group of plants was foliar sprayed with deionized water. All treatment applications were performed at intervals of 7 days for 3 times each during the whole experiment at 102, 109, and 116 days after sowing. Leaf gas exchange and chlorophyll fluorescence were measured at 3 days after salicylic acid treatment from 11:00 am to 01:00 pm.

2.2 Photosynthesis measurements

P_n, stomatal conductance (g_s), intercellular CO_2 concentration (C_i), transpiration rate (E), and leaf temperature (T_{leaf}) were measured with a LI-COR 6400 portable photosynthesis measurement system. Gas exchange was measured in fully expanded leaves in a similar position (4th leaf node from top) on each plant with the artificial saturating photosynthetic photon flux (PPF) at 1200 µmol $m^{-2}s^{-1}$ using a red-blue light source, CO_2 concentration at 400 µmol CO_2 mol^{-1}, relative humidity at 60% and air flow rate into assimilation chamber at 500 $\mu mols^{-1}$.

The measurement of chlorophyll fluorescence was taken after gas exchange measurements on the same leaves which were used for primary photochemistry detection. Measured leaves were dark-adapted with leaf clips for 30 min prior to measurements, the induction curve (F_v/F_m ratio) was then estimated by a Hansatech Pocket PEA (Hansatech Instruments Ltd., King's Lynn, Norfolk, UK) with 3500 µmol $m^{-2}s^{-1}$ of a peak wavelength 625 nm light intensity (excitation intensity). F_v/F_m provides an estimation of the maximum quantum efficiency of photosystem II.

2.3 Determination of protein profile

After the leaf gas exchange and chlorophyll fluorescence measurements, a young leaf in a similar position (4th leaf node from top) was harvested to determine the proteins present. The leaves were stored at -80 °C until protein extraction was performed.

The leaf samples were taken at the 2nd photosynthesis measurement (22 May 2015). The samples were ground in liquid nitrogen to powder and total soluble protein was extracted using the tissue extraction I kit (Invitrogen, USA). Protein content was estimated using the Bradford reagent kit (Ameresco, USA). Protein samples were subjected to one-dimensional gel electrophoresis (4-12% NUPAGE® SDS-PAGE, Invitrogen, USA) for visualization of protein profiles using Coomassie Brilliant Blue staining. The size of polypeptides was estimated by comparison with a molecular weight protein standard marker (GeneDirex, Bio-Helix Co., Ltd., Taiwan). The resulting vertical protein lanes were sliced into eight pieces giving fraction1: 3.5-8 kDa, fraction2: 8-15 kDa, fraction3: 15-24 kDa, fraction4: 24-42 kDa, fraction5: 42-57 kDa, fraction6: 57-93 kDa, fraction7: 93-125 kDa and fraction8: 125-240 kDa (Fig. 1). The sample pieces were sent to the Institute of Molecular Biosciences, Mahidol University for protein identification using LC-MS analysis and the NCBI database. Their biological functions were defined using the UniProt database (http://www.uniprot.org).

2.4 Yield and fruit quality

Chili pepper fruits were harvested at the fully ripened stage. Fruits per plant (yield) from each treatment were collected every other week. For measurements of fruit width, fruit length, and fruit weight, 10 fruits were randomly taken from each treatment.

2.5 Statistical analyses

The experiment was conducted in a randomized complete block design (RCBD) manner.

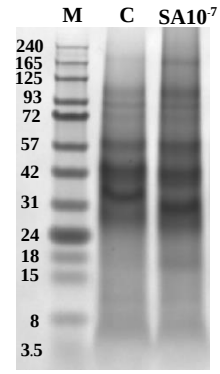

Fig. 1. Leaf protein performance in one dimensional gel electrophoresis of control (C) and Salicylic acid 10^{-7} M ($SA10^{-7}$). Molecular weight markers (M) are also shown.

Five replicates per treatment were evaluated. Data was statistically analyzed by the analysis of variance (ANOVA) technique and the means were separated using the Duncan Multiple Range test. All results were presented as means and standard deviation (SD). Means differing at $p<0.05$ were considered significant.

3. Results

3.1 Microclimate

The mean, minimum, and maximum values of PPF, T_{air}, and VPD throughout the planting time were measured and are shown in Table 1.

On the days of measurement, 22nd May 2015 showed the lowest PPF, T_{air} and VPD values. The highest PPF, T_{air}, and VPD values were recorded on 29th May 2015 (Table 2).

3.2 Effects of SA on photosynthesis

The application of $SA10^{-7}$ on 22nd May 2015 showed that P_n, g_s, C_i, E, F_v/F_m, but not T_{leaf}, were significantly different when compared to control, whereas $SA10^{-5}$ did not show a significant difference. The measurements of all photosynthetic parameters on 15th May and 29th May 2015 were similar and lower than on 22nd May 2015 but the values were not significantly different for all parameters (Fig. 2).

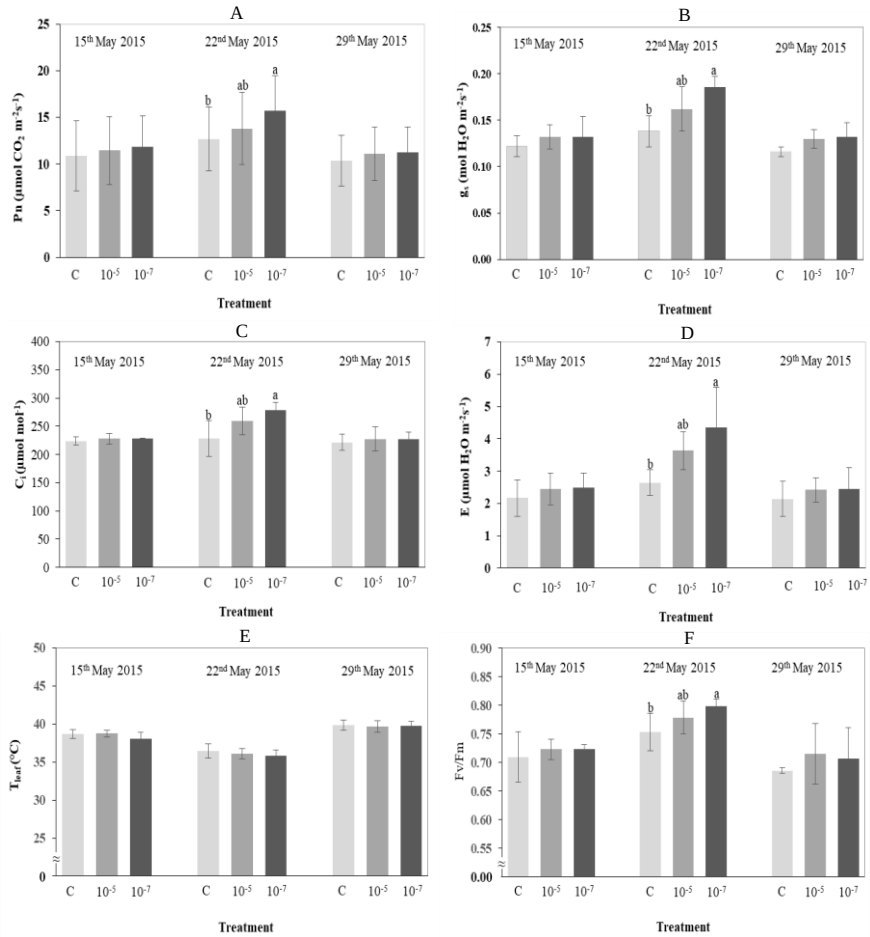

Fig. 2. The net photosynthetic rate (A), stomatal conductance (B), intercellular CO_2 concentration (C), transpiration rate (D), leaf temperature (E), and F_v/F_m (F) of chili pepper leaves sprayed with salicylic acid at concentrations of 10^{-5} M (10^{-5}) or 10^{-7} M (10^{-7}) and control (C) on 15th, 22nd, and 29th May 2015. Data are the means of 5 replicates. Vertical bars show ±SD of mean. The same letters indicate no significant difference at $p<0.05$ base on DMRT.

3.3 Effects of SA on the protein profile

The $SA10^{-5}$ treatment group was not the significantly different from the control in photosynthesis, therefore proteins present in leaves of $SA10^{-5}$ plants were not shown. Thirteen proteins were found in both control and treatment leaf samples. There were 7 proteins specifically regulated by $SA10^{-7}$ and 6 proteins were detected in both $SA10^{-7}$ and control groups. Furthermore, the protein matches were also classified according to their biological function, divided into 6 categories including photosynthesis (5 proteins), metabolism (3 proteins), stress defense (2 proteins), energy (1 protein), transporter of photosynthesis process (1 protein), and unclassified (1 protein) (Table 3).

3.4 Effects of SA on yield and fruit quality

The total fruit numbers, fruit width, fruit length, and fruit weight from both of the SA treatments were slightly higher than the control treatment but not significantly different from each other (Table 4).

Table 3. Identification and protein function in chili pepper leaves of the control and salicylic acid 10^{-7} M treatments.

No.	Protein Accession	Protein name	Organism	Protein function	Control Sample	SA10^{-7} sample
1	gi|404474510	ATP synthase CF1 alpha subunit (chloroplast)	*Arabidopsis thaliana* (L.) Heynh.	photosynthesis		/
2	gi|404474511	ATP synthase CF0 subunit I (chloroplast)	*Arabidopsis thaliana* (L.) *Heynh.*	photosynthesis		/
3	gi|404474532	ATP synthase CF1 beta subunit (chloroplast)	*Arabidopsis thaliana* (L.) *Heynh.*	photosynthesis	/	/
4	gi|6899972	chloroplast ferredoxin-NADP+ oxidoreductase precursor	*Nicotiana tabacum* L.	metabolism		/
5	gi|283049930	chloroplast manganese stabilizing protein	*Capsicum annuum* L.	photosynthesis		/
6	gi|169930138	chloroplast rubisco activase	*Solanum tuberosum* L.	photosynthesis		/
7	gi|641803824	cytochrome f (chloroplast)	*Lolium perenne* L.	transporter of photosynthesis process	/	/
8	gi|62910196	cytosolic ascorbate peroxidase	*Solanum lycopersicum* L.	stress defense	/	/
9	gi|222820578	NAD(P)H:quinone oxidoreductase	*Nicotiana tabacum* L.	stress defense	/	/
10	gi|193290694	putative ferredoxin-dependent glutamate synthase	*Capsicum annuum* L.	metabolism	/	/
11	gi|193290696	putative glutamine synthase 2	*Solanum lycopersicum* L.	metabolism		/
12	gi|222159965	putative ML domain protein	*Capsicum annuum* L.	unclassified		/
13	gi|390098824	triose phosphate isomerase cytosolic isoform-like protein	*Capsicum annuum* L.	energy	/	/

/ = found protein in control and/or salicylic acid 10^{-7} M (SA10^{-7})

Table 4. Fruit numbers and fruit traits of 'Hua ruea' chili pepper affected by SA.

Treatment	Number of fruit/plant	Fruit width (cm)	Fruit length (cm)	Fruit weight (g)
Control	31.6±3.05	0.73±0.04	4.30±0.27	1.31±0.25
SA10^{-5}	34.4±9.15	0.74±0.05	4.53±0.77	1.33±0.10
SA10^{-7}	33.8±4.97	0.76±0.02	4.69±0.36	1.42±0.09
CV	18.58	5.32	8.05	11.28
F-test	ns	ns	ns	ns

ns = nonsignificant at $p < 0.05$ based on DMRT. Values are shown as mean±SD

4. Discussion

The optimum PPF that supports pepper growth ranged from 450-1200 µmol $m^{-1}s^{-1}$ [20-22]. The PPF mean value throughout the experiment (Table 1) and all the days measured (Table 2) were in range of optimum conditions for chili pepper growth. The optimum temperature range and VPD for chili pepper growth ranged from 16 to 32°C [23] and 0.3-2.1 kPa [24, 6], respectively. In this experiment, both temperature and VPD were above the optimum range for pepper growth (Table 1 and 2).

On 15th and 29th May 2015, high temperature (38°C and 39°C, respectively) and high VPD (2.7 kPa and 3.0 kPa, respectively) indicated heat stress conditions. High temperature (35-40 °C) and high VPD (over 2.5 kPa) increased stomatal closure which is related to a decrease in the uptake of CO_2 into the leaves, transpiration rate, and P_n [25-27]. The results of this current study showed that the chili pepper leaves in all treatments were exposed to high T_{air} and VPD which induced stomatal closure and consequently caused the suppression of photosynthesis (Fig. 2A, 2B, 2C and 2D). The value of F_v/F_m on both 15th and 29th May 2015, in all treatment groups, was lower than 0.80, indicating that plants were exposed to stress and sustained damaged in the light reaction center [28-29]. Both SA 10^{-5} and SA

10^{-7} treatments on 15th and 29th May 2015 were not found to have a positive effect on photosynthesis, a similar result was found in grapevine leaf; SA treatment at a concentration of 10^{-8} M did not influence photosynthesis under heat stress at 43°C [30].

On 22nd May 2015, plants sprayed with $SA10^{-7}$ showed the highest values of P_n, g_s, C_i, and E (Fig. 2A-D) and also the value of F_v/F_m was 0.8 (Fig. 2E), indicating that plants were in a good physiological state and that the flow of electrons was undisturbed.

Table 5. Correlation coefficient of photosynthetic photon flux (PPF), air temperature (T_{air}), vapor pressure deficit (VPD), net photosynthetic rate (Pn), stomatal conductance (gs), intercellular CO2 concentration (Ci), transpiration rate (E), leaf temperature, and maximum quantum efficiency of photosystem II (F_v/F_m) for chili pepper plants applied with salicylic acid at a concentration of 10^{-5} ($SA10^{-5}$) or 10^{-7} ($SA10^{-7}$) M and deionized water (C).

Parameters	PPF	T_{air}	VPD	P_n	g_s	C_i	E	T_{leaf}	F_v/F_m
PPF		0.065	-0.013	-0.725**	-0.788**	-0.554*	-0.786**	0.626*	-0.687**
T_{air}			0.982**	-0.480	-0.405	-0.322	-0.291	0.667**	-0.369
VPD				-0.403	-0.334	-0.279	-0.247	0.627*	-0.314
P_n					0.723**	0.426	0.620*	-0.668**	0.510
g_s						0.726**	0.771**	-0.800**	0.697**
C_i							0.818**	-0.697**	0.823**
E								-0.673**	0.869**
T_{leaf}									-0.770**
F_v/F_m									

*, ** Significant at $p < 0.05$ and $p < 0.01$ respectively

In this study, the effects on photosynthesis from $SA10^{-7}$ treatment were more beneficial than $SA10^{-5}$; the low SA concentration could not largely induce the accumulation of reactive oxygen species (ROS), but in another study it significantly promoted stress tolerance [31].

The results from the correlation coefficient analysis of the ambient daytime conditions and physiological parameters (Table 5) in plants treated with SA and deionized water revealed that PPF, T_{air}, and VPD were significantly and positively associated with T_{leaf}. Also, T_{leaf} showed negative correlations with P_n, g_s, C_i, and E. These findings confirm that extreme weather conditions affect photosynthesis through T_{leaf} [4]. Although T_{leaf} did not show a statistically significant difference (Fig. 2E).

In addition, it was found that $SA10^{-7}$ treatment stimulated synthesis of proteins associated with photosynthesis such as chloroplast Rubisco activase, but these proteins were not found in the control treatment (Table 3). SA may affect certain metabolic factors in carbon uptake or fixation including Rubisco enzyme concentration and activity, and/ or the photosynthetic carbon reduction cycle [32]. Consequently, the application of SA to chili pepper leaves significantly affected the photosynthesis process. Moreover, the results show that SA at a concentration of 10^{-7} M can improve photosynthesis in chili pepper leaves when

the temperature is below 37°C and VPD is lower than 3 kPa.

The weather conditions throughout the experiment indicated heat stress conditions. The maximum T_{air} and VPD of each month were often over 37°C and 3 kPa, respectively (Table 1). Hence, SA applications did not successfully activate essential reactions as predicted, which was related to poor photosynthesis outcomes in the chili pepper leaves. The temperature over several days was more important in its impact on fruit production and quality of fruit [24]. In the current study, the results show no significant difference in yield and fruit quality of SA applications treatments (10^{-5} or 10^{-7} M) compared to the control group (Table 4). This outcome is demonstrative of the relationship between photosynthesis and crop production; as was shown in another study, a reduction of P_n resulted in a reduced fruit yield and increased incidence of poor fruit quality in tomato plants [33]. The present results show that the weather conditions, especially T_{air} and VPD, affected the efficiency of SA treatment. Therefore, the chili pepper production in net houses may require a fogging system to maintain suitable T_{air} and VPD.

5. Conclusion

Salicylic acid at a concentration of 10^{-7} M can improve photosynthesis in chili pepper leaves if temperatures do not exceed 37°C and VPD is less than 3 kPa. Yield and fruit quality of chili peppers were not significantly different between the SA treatments (10^{-5} and 10^{-7} M) compared to the control.

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References

[1] FAOSTAT. Production data [Internet] . [cited 2020 Jan 19]. Available from:http://www.fao.org/faostat/

[2] Pakuthai W, Sriwaranan Y. Chili peppers: How to grow in global warming. The Thailand Research Fund (TRF); 2014. [in Thai]

[3] Hirasawa T, Hsiao TC. Some characteristics of reduced leaf photosynthesis at midday in maize growing in the field. Field Crops Res. 1999;62(1):53-62.

[4] Espinosa-Calderon A, Torres-Pacheco I, Padilla-Medina JA, Chavaro-Ortiz RM, Xoconoste-Cazares B, Gomez-Silva L, et al. Relationship between leaf temperature and photosynthesis carbon in *Capsicum annuum* L. in controlled climates. J Sci Ind Res. 2012;71:528-33.

[5] Berry J, Bjorkman O. Photosynthetic response and adaptation to temperature in higher plants. Ann. Rev. Plant Physiol. 1980;31:491–543.

[6] Erickson AN, Markhart AH. Flower developmental stage and organ sensitivity of bell pepper (Capsicum annuum L.) to elevated temperature. Plant Cell Environ. 2002;25(1):123-30.

[7] Bunce, JA. Effects of humidity on photosynthesis. J. Exp. Bot. 1984; 35:1245-51.

[8] Williams LE, Baeza P. Relationships among ambient temperature and vapor pressure deficit and leaf and stem water potentials of fully irrigated, field-grown grapevines. Am J Enol Vitic. 2007; 58(2):173-81.

[9] Intergovernmental panel on climate change. Climate change the physical science summer for policymakers. Contribution of working group I to the fourth assessment report of the intergovernmental panel on climate

change [Internet]. [cited 2019 May 24]. Available from: http://www.ipcc.ch/

[10] The Thailand Research Fund. Thailand's first assessment report on climate change 2011 Volume 1 [Internet]. [cited 2019 May 24] . Available from: https://www.trf.or.th/e-book/ [in Thai]

[11] Raskin I. Salicylate, a new plant hormone. Plant Physiol. 1992;99: 799-803.

[12] Uzunova AN, Popova LP. Effect of salicylic acid on leaf anatomy and chloroplast ultrastructure of barley plants. Photosynthetica. 2000;38(2): 243–50.

[13] Hayat S, Park EG, Son BG, Choi YW, Lee YJ, Park YH, et al. Growth of indian mastad (*Brassica juncea* L.) in response to salicylic acid under high temperature stress. Braz. J. Plant Physiol. 2009; 21(3):187-95.

[14] Pancheva TV, Popova LP. Effect of the salicylic acid on the synthesis of ribulose-1,5- bisphosphate carboxylase/ oxygenase in barley leaves. Plant Physio. 1998;152: 381–6.

[15] Bergmann H, Machelett LV, Geibel M. Increase of stress resistance in crop plants by using phenolic compounds. In Geibel,M, Treutter D, Feucht W. (eds.) International symposium on natural phenols in Plant resistance: Acta Horticulturae, Weihenstephan, Germany. 1994;1(2): 381–90.

[16] Breusegem, FV, Vranova E, Dat JF, Inze D. The role of active oxygen species in plant signal transduction. Plant Sci. 2001;161(3): 405–14.

[17] Qiu C, Ji W, Guo Y. Effects of high temperature and strong light on chlorophyll fluorescence, the D1 protein, and Deg1protease in satsuma mandarin and the protective role of salicylic acid. Acta Eco Sin. 2011;31: 3802-10.

[18] Chakraborty U, Tongden C. Evaluation of heat acclimation and salicylic acid in treatment as potent inducers of thermotolerance in *Cicer arietinum* L. Curr. Sci. 2005;89(2): 384-9.

[19] Resh MH. Hydroponic food production. California: Woodbridge Press Publishing Company; 1978.

[20] Bhatt RM, Rao NKS, Anand N. Response of bell pepper (*Capsicum annuum* L.) to irradiance photosynthesis, reproductive attributes and yield. Indian J Hortic. 1999;56 (1): 162-6.

[21] Hirun-on S, Yingjajaval S, Wasee S. Leaf photosynthesis potential of hot pepper (*Capsicum annuum* L.) in parental lines 38- 168 and KKU cluster, F1 and F1 reciprocal. J. Agric. Sci. 2006;37(1):66-75. [in Thai]

[22] Fu QS, Zhao B, Wang YJ, Ren S, YD Guo. Stomatal development and associated photosynthetic performance of capsicum in response to differential light availabilities. Photosynthetica 2010;48(2): 189-98.

[23] Bosland PW, Votava J. Pepper: Vegetable and Spice Capsicums. London: CABI Publishing; 2000.

[24] Bakker, JC. The effects of air humidity on growth and fruit production of sweet pepper (*Capsicum annuum* L.). J. Hortic. Sci. 1989;64: 41–6.

[25] Santarius KA. Sites of heat sensitivity in chloroplasts and differential inactivation of cyclic and noncyclic photophosphorylation by heating. J. Therm. Biol. 1975;1(2):101-7.

[26] Yingjajaval S. Basic physiology on leaf gas exchange and water potential of tangerine. Faculty of Liberal Arts and Science, Kasetsart University, Kamphaeng Saen, Thailand; 2001. [in Thai]

[27] Xu DQ, Shen YG. External and internal factors responsible for midday depression of photosynthesis. In Pessarakli M. (eds.)

Handbook of photosynthesis, 2nd ed. USA: CRC Press. Boca Raton, FL; 2005. p.287-94.

[28] Bjorkman O, Demmig-Adams B. Regulation of photosynthesis light energy capture, conversion, and dissipation in leaves of higher plants. In: Schulze ED, Caldwell MM. (eds.). Ecophysiology of Photosynthesis. Berlin, Heidelberg, New York; 1995. p. 13-47.

[29] Schreiber U, Bilger W, Neubauer C. Chlorophyll fluorescence as a nonintrusive indicator for rapid assessment of in vivo photosynthesis. In Schulze ED, Caldwell MM. (eds.) Ecophysiology of Photosynthesis. Berlin, Heidelberg, New York: Springer; 1995. p 49-69.

[30] Wang L, Fan L, Loesher W, Duan W, Liu GJ, Cheng JS, et al. Salicylic acid alleviates decreases in photosynthesis under heat stress and accelerates recovery in grapevine leaves. BMC Plant Biol [Internet] . 2010 [cited 2018 Aug 15] ;10: 34. Available from: https://doi.org/10.1186/1471-2229-10-34

[31] Yuan S, Lin H.-H. Role of salicylic acid in plant abiotic stress. Z. Naturforsch. C. 2008;63: 313-20.

[32] Janda T, Gondor OK, Yordanova R, Szalai G, Pal M. Salicylic acid and photosynthesis: signaling and effects. Acta Physiol Plant. 2014;36(10):2537-46.

[33] Nilsen S, Hovland K, Dons C, Sletten SP. Effect of CO_2 enrichment on photosynthesis, growth and yield of tomato. Sci Hortic. 1983;20(1):1-14.