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Effects on Net Photosynthesis in Field-Grown Hot Peppers Responding to the Increased CO_2 and Temperature

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ABSTRACT: The increased CO_2 and temperature (700 μmol·mol^{-1} CO_2 and 30ºC) was compared with ambient growth conditions (400 μmol·mol^{-1} CO_2 and 25ºC) in hot pepper. Gas exchange measurements, including net photosynthesis (P_{net}) and stomatal conductance (g_s), were taken according to treatment in fields of peppers grown in Suwon and Asan during 2008. The increased treatment P_{net} by 35-45% throughout the season and was statistically significant in *t*-tests ($p < 0.001$); however, it did not significantly affect g_s. In addition, the gas exchange parameters in sun and shade leaves were measured. The difference between the sun and shade leaves was much greater than that between the elevated and ambient treatments, especially at harvest. Four commercial cultivars of hot pepper, Chunhasangsa, Ryukang, Manitta, and Olympic, were also compared by ANOVA. Chunhasangsa had the highest P_{net}, which decreased by 30% from the vegetative to the harvest stage. Based on a factorial design, the effect of the increased CO_2 and temperature was assessed based on the temperature, CO_2, and their interaction effects. Orthogonal contrasts showed that the effects of temperature on P_{net} and g_s were significant, whereas CO_2 and their interactions were not.

Key Words: doubled CO_2, hot pepper, net photosynthesis, stomatal conductance, shade leaf

Introduction

The carbon dioxide concentration ([CO_2]) has risen from 270 μmol·mol^{-1} since the industrial revolution due to increased fossil fuel use. According to International Panel on Climate Change (IPCC) projections, the [CO_2] is predicted to exceed 700 μmol·mol^{-1} by the end of the century[1)]. In addition, global warming due to greenhouse gases may raise temperatures by 3-5ºC, depending on the scenario. The fertilization effect of CO_2 on crops may enhance net photosynthesis (P_{net}) and water use efficiency (WUE)[2)], and may lead to yield increases of about 33% according to more than 1,000 studies[3)].

Free-air CO_2 enrichment (FACE) technology has been investigated in terms of future food security to project the CO_2 fertilization effect at 550 μmol·mol^{-1} by 2050. FACE was developed to overcome such chamber effects as reduced light, increased temperatures, humidity, and water vapor pressure deficits, as well as altered air flow, intercepted rainfall, and the restriction of pests and diseases[4)]. Such FACE studies have revealed an approximately 20% increase in P_{net} in rice, wheat, and soybean. In addition, P_{net} was consistently higher than the growth or yield of the crop, and neither measure was proportional to P_{net}.

Stomatal conductance (g_s) is decreased at elevated [CO_2][5-8)] by an average of 22%[9)]. Decreases in stomatal density at elevated [CO_2] are, at best, 5% and not statistically significant. The main reason for the decrease is a change in stomatal aperture. In addition, acclimation of the g_s to elevations in [CO_2] is rare and environmental factors such as dry conditions in the field rapidly alter the response of g_s to increases in [CO_2][8,10)].

Climate change could increase host resistance to

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pests[11]. Elevations in the [CO_2] can change Rubisco biochemistry, stomatal physiology, and the phenology of a host plant. Increases in P_{net} can increase the non-structural carbohydrate content, which may potentially enhance pest resistance[12]. Increased temperatures due to global warming may cause the breakdown of the temperature-sensitive resistance of oat cultivars to diseases through *Pg3* and *4*[13]. Before the impact of climate change on pepper-pathogen interactions occurs in Korea, we need to understand the changing pepper ecophysiology caused by global warming.

Gas exchange measurements in peppers have been conducted in a greenhouse[14,15] and in a recirculation hydroponic system[16,17]. In this study, we measured the P_{net} and g_s in hot pepper grown in the field in Korea using four commercial cultivars to compare the effects of simulated global warming (doubled [CO_2] and 30℃) and ambient conditions (400 μmol·mol^{-1} [CO_2] and 25℃). In addition, gas exchange was compared between the sun and shade leaves of fully-grown plants at the vegetative and harvest stages in order to understand the responses of pepper at the canopy level.

Materials and Methods

Plant materials and gas exchange measurements

Four cultivars of hot pepper (*Capsicum annum* L.) were grown in the field at Asan (cv. Chunhasangsa) and Suwon (cv. Ryukang, Manitta, and Olympic) in 2008. A Li-Cor 6400 (Li-6400) photosynthesis measurement system (Li-Cor, Lincoln, NE) was used to measure P_{net} and g_s. Sun and shade leaves were measured in 2- × 3-cm cuvettes under 1,500 μmol m^{-2}·s^{-1} obtained from light-emitting diodes (LED). The sun leaves (70-80% of the canopy) received direct sunlight in the upper canopy regions and were smaller than the shade leaves, which were thinner and hung vertically. Once a leaf was clamped in the chamber, data were automatically collected every 10 s for 3 min while mid-point measurements were collected as representative data. All measurements were taken on 6-8 July at the fully-grown vegetative stage, on 4-5 August at the green fruit stage, and on 2-9 September at the red fruit stage. All measurements on cv. Chunhajangsa, Ryukang, Manitta, and Olympic were conducted on sunny days between 11:00 and 13:00.

Increasing CO_2/temp treatment and ambient treatment in the Li-Cor cuvette

The temperature and [CO_2] used in the cuvettes were 25℃ and 400 μmol·mol^{-1} or 30℃ and 700 μmol·mol^{-1}. Liquid CO_2 (Li-Cor 6400-01) was supplied to the measuring system at variable concentrations. Sun and shade leaves were taken from individual pepper plants. Three plants per cultivar were selected each day for replication of the gas exchange measurements.

CO_2, temperature, and their interaction effects on P_{net} and g_s

To investigate CO_2, temperature, and their interactive effects, Chunhasangsa plants were subjected to four different treatments (700 μmol·mol^{-1} [CO_2] and 30℃, 700 μmol·mol^{-1} [CO_2] and 25℃, 400 μmol·mol^{-1} [CO_2] and 30℃, and 400 μmol·mol^{-1} [CO_2] and 25℃) in a measuring chamber on 19 August and 9 September at Asan. Three replicates were subjected to each set of conditions.

Statistical analysis

To examine gas exchange in response to the two treatments during the growing season in the four cultivars, a one-tailed *t*-test was performed. We expected that the treatment of increasing CO_2 and temperature have more of an effect on P_{net} and g_s than the ambient conditions. In addition, gas exchange in the four cultivars was compared in terms of P_{net} and g_s using one-way analysis of variance. The effects of CO_2 and temperature were analyzed using a 2x2 factorial design (two-way completely randomized design). CO_2, temperature, and their interactive effects on P_{net} and g_s were analyzed by orthogonal contrasts. We used a 95% significance level and the statistics software program S-link (ver. 2.2, Seoul, Korea).

Results

P_{net}

P_{net} in the sun leaves of the four pepper cultivars at an elevated [CO_2] and temperature was 38-45 μmol CO_2 m^{-2}·s^{-1}, while that in the plants subjected to ambient conditions was 28-31 μmol CO_2 m^{-2}·s^{-1} early in the season (Table 1). The treatment effects were significant in all four cultivars. P_{net} in the shade leaves was 26-40 μmol CO_2 m^{-2}·s^{-1} at an elevated

Table 1. Net photosynthesis in response to simulated global warming (700 μmol·mol^{-1} CO_2 and 30℃) or under ambient conditions (400 μmol·mol^{-1} CO_2 and 25℃) in the sun and shade leaves of four pepper cultivars. Comparisons between the two treatments were made by *t*-tests and ANOVA among the four cultivars

Measured Date	Cultivar	Sun-leaf			Shade-leaf		
		$CO_2$700/30℃	$CO_2$400/25℃	*t*-test	$CO_2$700/30℃	$CO_2$400/25℃	*t*-test
Jul. 6~8	Chunhajangsa	45.8 ± 0.7	31.5 ± 0.1	>0.001	40.3 ± 1.3	21.5 ± 2.0	0.001
	Ryukang	43.2 ± 0.4	29.5 ± 0.3	>0.001	26.6 ± 4.6	16.6 ± 2.3	0.062
	Manitta	38.7 ± 1.3	29.1 ± 0.7	0.001	30.7 ± 3.6	19.2 ± 1.4	0.021
	Olympic	38.0 ± 0.3	28.3 ± 0.2	>0.001	29.0 ± 2.8	19.6 ± 1.9	0.025
	ANOVA	>0.001	0.003		0.080	0.385	
Aug. 4~5	Chunhajangsa	40.7 ± 1.5	34.6 ± 3.1	0.074	17.4 ± 2.7	17.2 ± 2.9	0.481
	Ryukang	34.5 ± 0.9	23.6 ± 0.5	>0.001	-	-	-
	Manitta	33.9 ± 0.8	23.4 ± 0.2	0.001	19.6 ± 2.4	9.7 ± 1.2	0.011
	Olympic	33.8 ± 0.9	24.6 ± 0.3	0.001	-	-	-
	ANOVA/*t*-test	0.004	0.003		0.569	0.080	
Sep. 2~9	Chunhajangsa	32.7 ± 0.1	19.4 ± 0.4	>0.001	18.2 ± 3.8	11.9 ± 1.0	0.094
	Ryukang	33.7 ± 1.2	17.9 ± 1.9	0.001	-	-	-
	Manitta	37.6 ± 1.3	26.8 ± 2.0	0.005	13.7 ± 3.1	11.4 ± 2.4	0.298
	Olympic	27.9 ± 1.8	19.6 ± 0.3	0.005	-	-	-
	ANOVA/*t*-test	0.004	0.008		0.209	0.429	

Shade leaves were measured only from cv. Chunhasangsa and Manitta in Aug. and Sept. Thus, comparisons between the varieties during those months were made using *t*-tests. The numbers represent the mean ± standard error.

temperature and [CO_2] and 16-21 μmol CO_2 $m^{-2}\cdot s^{-1}$ under ambient conditions; both sets of results were statistically significant. Within the same treatment, P_{net} in the shade leaves was about 5-10 μmol CO_2 $m^{-2}\cdot s^{-1}$ (p = 0.05), which is lower than that in the sun leaves. The treatment effects in the sun leaves were maintained throughout the growing season, whereas those in the shade leaves were not significant at the green and red fruit stages. The differences in P_{net} among the four cultivars throughout the season were significant in the sun leaves (p = 0.008 to > 0.001). At the green fruit stage, P_{net} was similar in both the Asan and Suwon fields; however, the highest values were calculated for Manitta at the red fruit stage.

There was a decrease of about 10 μmol CO_2 $m^{-2}\cdot s^{-1}$ from the vegetative to the harvest stage in the sun leaves under both treatment regimens (Fig. 1). The effect of simulated global warming on P_{net} in the shade leaves was significant in July but gradually disappeared. Because P_{net} in the sun leaves (solid lines) was always higher than that in the shade leaves (dotted line) during the growing season, leaf type was more important than global warming.

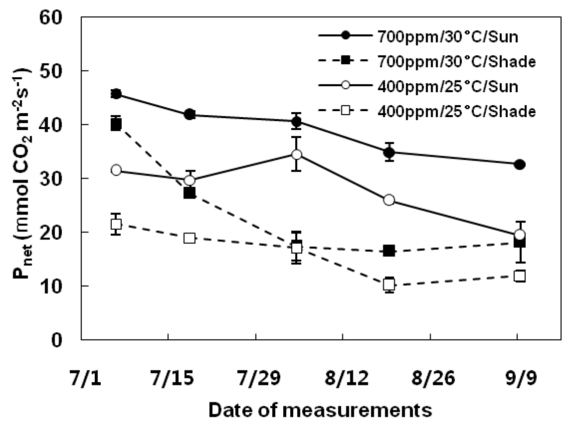

Fig. 1. Net photosynthesis (P_{net}) in the sun (solid line) and shade leaves (dotted line) of cv. Chunhasangsa collected at the fully-grown vegetative stage (6 July) and at harvest (9 Sept.) following exposure to simulated global warming (closed) and ambient (open) conditions in Asan field in 2008.

g_s

g_s in the sun leaves of the four pepper cultivars was 1.13-0.28 mmol H_2O $m^{-2}\cdot s^{-1}$, whereas it was 0.59-0.10 mmol H_2O $m^{-2}\cdot s^{-1}$ in the shade leaves regardless of treatment (Table 2). Most shade leaves

Table 2. Stomatal conductance in response to simulated global warming (700 $\mu mol \cdot mol^{-1}$ CO_2 and 30℃) or under ambient conditions (400 $\mu mol \cdot mol^{-1}$ CO_2 and 25℃) in the sun and shade leaves of four pepper cultivars. Comparisons between the two treatments were made by *t*-tests and ANOVA among the four cultivars

Measured Date	Cultivar	Sun-leaf			Shade-leaf		
		$CO_2$700/30℃	$CO_2$400/25℃	*t*-test	$CO_2$700/30℃	$CO_2$400/25℃	*t*-test
Jul. 6~8	Chunhajangsa	0.73 ± 0.03	0.74 ± 0.07	0.558	0.59 ± 0.09	0.48 ± 0.08	0.218
	Ryukang	1.07 ± 0.17	0.84 ± 0.02	0.150	0.25 ± 0.08	0.28 ± 0.07	0.590
	Manitta	0.92 ± 0.05	1.13 ± 0.12	0.895	0.26 ± 0.07	0.36 ± 0.05	0.842
	Olympic	0.85 ± 0.20	1.12 ± 0.12	0.842	0.28 ± 0.09	0.43 ± 0.10	0.840
	ANOVA	0.382	0.004		0.052	0.358	
Aug. 4~5	Chunhajangsa	0.56 ± 0.15	0.30 ± 0.07	0.091	0.12 ± 0.02	0.18 ± 0.04	0.860
	Ryukang	0.71 ± 0.11	0.83 ± 0.03	0.810	-	-	-
	Manitta	0.56 ± 0.06	0.73 ± 0.03	0.973	0.17 ± 0.03	0.17 ± 0.06	0.502
	Olympic	0.67 ± 0.09	0.88 ± 0.04	0.951	-	-	-
	ANOVA/*t*-test	0.660	0.001		0.240	0.936	
Sep. 2~9	Chunhajangsa	0.38 ± 0.01	0.28 ± 0.00	>0.000	0.10 ± 0.04	0.13 ± 0.02	0.751
	Ryukang	0.41 ± 0.00	0.33 ± 0.02	0.031	-	-	-
	Manitta	0.70 ± 0.06	0.74 ± 0.09	0.652	0.26 ± 0.10	0.27 ± 0.11	0.515
	Olympic	0.36 ± 0.08	0.38 ± 0.02	0.594	-	-	-
	ANOVA/*t*-test	0.005	>0.001		0.901	0.839	

Shade leaves were measured only from cv. Chunhasangsa and Manitta in Aug. and Sept. Thus, comparisons between the varieties during those months were made using *t*-tests. The numbers represent the mean ± standard error.

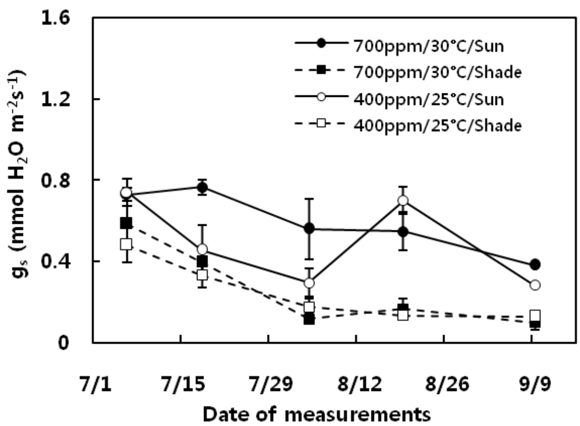

Fig. 2. Stomatal conductance (g_s) in the sun (solid line) and shade leaves (dotted line) of cv. Chunhasangsa collected at the fully-grown vegetative stage (6 July) and at harvest (9 Sept.) following exposure to simulated global warming (closed) and ambient (open) conditions in Asan field in 2008.

had a g_s of less than 0.3 mmol H_2O $m^{-2} \cdot s^{-1}$ ($p > 0.1$). *t*-tests showed that the effects of global warming were not significant in all cultivars, except in Chunhasangsa and Ryukang in September. Differences in g_s among the four cultivars throughout the growing season were significant in the sun leaves of plants exposed to ambient conditions (p = 0.004 to >0.001), but not in those exposed to global warming (p = 0.382-0.668). Like P_{net}, g_s gradually decreased towards the end of the season, and was significant in the sun leaves under either set of conditions in September due to the high g_s in Manitta.

Similar to our P_{net} results, g_s in the sun leaves (solid line) was always higher than that in the shade (dotted line) leaves throughout the growing season (Fig. 2). Both the average g_s and standard deviation in the sun leaves were higher than in the shade leaves. g_s decreased throughout the season by about 60-70% (i.e., much more than P_{net}). g_s was different between the sun and shade leaves, rather than in response to global warming.

CO_2, temperature, and their interactive effects

The effects of temperature on P_{net} were significant (p = 0.005 and 0.025 on the two measured dates; Table 2). The effect of CO_2 on P_{net} was significant only on 19 August (p = 0.001), whereas the effects of temperature on g_s were significant (p = 0.003) on both dates (Table 3). No significant effects of the interaction were found.

Table 3. Photosynthesis and stomatal conductance in the sun leaves of pepper cv. Chunhasangsa were measured using three replicates. A 2 x 2 factorial design with two concentrations of CO_2 (700 vs. 400 $\mu mol \cdot mol^{-1}$) and temperatures (30 vs. 25℃). The effects of CO_2, temperature, and their interactions were analyzed based on the *p*-value of the orthogonal contrasts using a two-way completely randomized design

Gas-Exchange parameters	Measured date	$CO_2$700/30℃	$CO_2$700/25℃	$CO_2$400/30℃	$CO_2$400/25℃	CO_2effect	Temp. effect	Interaction
Net photosynthesis	Aug. 19	34.9 ± 1.7	25.9 ± 0.6	28.4 ± 2.2	19.4 ± 1.9	0.001	0.005	0.993
	Sep. 9	32.7 ± 0.1	19.4 ± 0.4	12.9 ± 0.1	19.9 ± 7.0	0.397	0.025	0.020
Stomatal conductance	Aug. 19	0.55 ± 0.09	0.70 ± 0.06	0.29 ± 0.05	0.29 ± 0.09	0.355	0.003	0.342
	Sep. 9	0.38 ± 0.01	0.28 ± 0.00	0.16 ± 0.02	0.17 ± 0.07	0.292	0.003	0.206

Discussion

Simulated global warming increased P_{net} in pepper by about 33-45% in the sun leaves, depending on the cultivar. Although our treatment regimen was restricted to the clamped parts of the measured leaves, our P_{net} data were quite reliable, with low coefficients of variation. Gas exchange measurements in the field are much better for obtaining realistic measurements than controlled environment chambers. Branch chambers were used for air pollution studies[18] before the advent of open-top chambers and FACE studies.

P_{net} and g_s were much higher on 4 September in cv. Manitta, suggesting that it can better acclimate to global climate change than the other cultivars. Although we used an environmental scenario for 100 years in the future, the actual ecophysiological responses of pepper are unlikely to match their predicted values because acclimation will continuously change according to global warming. However, it is worth selecting well-adapted cultivars in order to prepare for the future.

Rubisco activity is critical for photosynthesis, especially at an elevated [CO_2], and should be considered in the breeding of pepper. The downregulation of P_{net} at an elevated [CO_2] typically involves a decrease in the amount and activity of Rubisco[19,20]. Sun or upper canopy leaves do not change their Vc_{max} with growth, whereas it is reduced by 10% in the lower levels of the canopy[21].

It is difficult to quantitatively predict pepper yields in response to global warming. An increase in P_{net} in the plant canopy in response to a rise in the [CO_2] was not found in most FACE studies. P_{net} decreased as the fruits ripened, and differed between the sun and shade leaves. Shade leaves, which are broader and thinner than sun leaves, constitute 30% of the pepper canopy. Plant leaf age also affects acclimation[22]. Developmental stage, leaf age, and canopy position all affect the sink activity of plants; therefore, P_{net} will be affected at a higher [CO_2]. This is one reason why FACE studies on pepper are needed to obtain more precise parameters.

Our treatment increased both [CO_2] and temperature; however, P_{net} and g_s were more affected by the increase in temperature than by the increase in the [CO_2]. Scenario A1B predicts that global temperatures will be 3-5ºC higher than current temperatures. Thus, pepper fields should be relocated to taller mountains or further north[11].

Anthracnose infection is expected to increase due to global warming because of increased humidity in the plant canopy. Excess carbon due to global warming may increase plant size resulting in increased canopy humidity, which may increase disease susceptibility or be used to produce non-structural carbohydrates, which may reduce the incidence of pest attacks. More *Colletotrichum gloeosporioides* spores were collected in a *Stylosanthes* canopy under elevated [CO_2][23].

Instantaneous water use efficiency (IWUE), the relative ratio of P_{net} to g_s in a cuvette where the boundary layer is reduced, overestimates g_s[24]. Our results show that IWUE was reduced in response to global warming because of a greater increase in P_{net} than g_s. Many FACE studies have found that a rise in the [CO_2] increases the WUE[6,19,21], which may alter the geographical distribution of plants to more marginal climates[25].

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