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Elevated CO_2 and Temperature Effects on the Incidence of Four Major Chili Pepper Diseases

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Four major diseases of chili pepper including two fungal diseases, anthracnose (*Colletotrichum acutatum*) and Phytophthora blight (*Phytophthora capsici*), and two bacterial diseases, bacterial wilt (*Ralstonia solanacearum*) and bacterial spot (*Xanthomonas campestris* pv. *vesicatoria*), were investigated under future climate-change condition treatments in growth chambers. Treatments with elevated CO_2 and temperature were maintained at 720 ppm±20 ppm CO_2 and 30°C±0.5°C, whereas ambient conditions were maintained at 420 ppm±20 ppm CO_2 and 25°C±0.5°C. Pepper seedlings or fruits were infected with each pathogen, and then the disease progress was evaluated in the growth chambers. According to paired *t*-test analyses, bacterial wilt and spot diseases significantly increased by 24% (p=0.008) and 25% (p=0.016), respectively, with elevated CO_2 and temperature conditions. On the other hand, neither Phytophthora blight (p=0.906) nor anthracnose (p=0.125) was statistically significant. The elevated CO_2 and temperature accelerated the progress of bacterial wilt by two days and bacterial spot by one day compared to the ambient treatment. Temperature regime studies of the diseases without changes in CO_2 confirmed that the accelerated bacterial disease progress was mainly due to the increased temperature rather than the elevated CO_2 conditions.

Keywords **:** anthracnose, bacterial spot, bacterial wilt, climate change, chili pepper

The background level of CO_2 has increased about 30% since 1750 (Percy et al., 2002) and is projected to double from the current level by 2100 (IPCC, 2007). Extensive studies on the response of plants to elevated CO_2 levels show that increased photosynthesis and water-use efficiency lead to higher biomass and yield (Ainsworth et al., 2002; Kimball, 1983). However, most C_3-type crops may not increase their yields in the future because of other limiting factors, such as ozone, pests, diseases, or weed competition.

Several peer-reviewed papers have reported that various plant diseases increased, decreased, or remained unchanged in severity under elevated CO_2 (Chakraborty et al., 2008; Coakley et al., 1999; Manning and Tiedemann, 1995). For example, among 10 biotrophic pathogens, disease severity increased in six and decreased in four at elevated CO_2, and among 15 necrotrophic pathogens, disease severity increased in nine, decreased in four, and remained unchanged in two (Chakraborty et al., 1998). Since plant disease under elevated CO_2 may or may not change in incidence or severity, we need to investigate each pathosystem associated with important agricultural crops or forest trees to properly predict disease susceptibility under future climate conditions.

Prospective future climate and atmospheric composition varies depending on emission scenarios for greenhouse gases. Global mean temperature has been projected to rise between 0.9 and 3.5°C by 2100 (Chakraborty et al., 2000b; IPCC, 2007). In addition, more substantial change is anticipated for high northern latitudes (Harris et al., 2006). The National Institute of Meteorological Research (NIMR) in Korea has predicted more than a 4°C changed in Korea by 2100 in the Kyunggi Province area based on an ECHO-G model under scenario A1B of the Intergovernmental Panel on Climate Change (IPCC), which assumes a moderate emission level of greenhouse gases (Min et al., 2006). Increased CO_2 raises temperatures, resulting in complex changes in plant pathosystems. For example, a 3°C increase from ambient temperature increased potato-yield loss caused by late blight demonstrated by the 3-year-long controlled-environment study (Kaukoranta, 1996), reducing potential benefits from yield increases due to warmer temperatures.

The importance of major crop diseases may also be changed under a warmer future climate. Three economically important soybean diseases, downy mildew, Septoria brown spot, and sudden death syndrome (SDS), were investigated under higher CO_2 and O_3, with results showing Septoria brown spot as the most serious under the changed environment (Eastburn et al., 2010). Chili pepper is the second most economically important crop in Korea and is grown on over 4,000 ha. Yun and Ahn (2009) reported that

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under 700 ppm CO_2 and a 5°C temperature rise, chili pepper leaves increased net photosynthesis by 35%, but no previous study has evaluated the influence of future atmospheric conditions on pepper diseases. Anthracnose, Phytophthora blight, bacterial spot and wilt are the main diseases of pepper in Korea (Myung et al., 2006).

Among three key components - a susceptible host, a virulent pathogen, and a favorable environment - warmer and elevated CO_2 environments in plant disease are known to exacerbate disease symptoms (McElrone et al., 2001) or result in new disease emergence (Anderson et al., 2004). The possible mechanisms of modifying plant disease occurrence include directly changing host resistance (Chakraborty et al., 2000b, 2008; Manning and Tiedemann, 1995), indirectly increasing canopy size for more favorable conditions (Pangga et al., 2003), or changing pathogen aggressiveness and fecundity (Chakraborty et al., 2000a). In addition, preferable environments enhanced substrate pathogen growth, resulting in an increase in diseases under elevated CO_2 (Runion, 2003).

The objective of this study was to predict changes in pepper disease occurrence under future warmer climate conditions. Under the condition of a doubled CO_2 level and 5°C temperature increase, we quantitatively compared the incidences of four main pepper diseases: anthracnose, Phytophthora blight, bacterial spot, and wilt. In addition, environmental change treatments were divided between CO_2 and temperature effects in diseased pepper tissues or on a pure culture medium of each pathogen.

Materials and Methods

Elevated CO_2 and temperature (Elevated CO_2+Temp.) treatment on four major diseases

Pepper seedlings (cv. Dabotop) or fruits were grown in two growth chambers which were controlled at 25°C/400 ppm CO_2 or 30°C/700 ppm CO_2, respectively. Carbon dioxide levels at 400 ppm and 700 ppm were monitored and controlled. The two separate chambers provided 70% relative humidity and a 12 h photoperiod with 200 μmol $m^{-2}s^{-1}$ photon flux density.

Infection of anthracnose. A fully grown green pepper fruit without wounds was sprayed with a suspension of *Colletotrichum acutatum* (1×10^5 spores/ml) SM017 isolated from Asan, Korea, in 2007. To maintain saturated humidity, an infected fruit was suspended on wires in a 4-cm-wide test tube with a water-saturated Kimwipe at the bottom for 2-3 days. Twenty infected fruits were placed in each chamber and typical anthracnose symptoms on the fruit were observed from days 4-8 after infection. Anthracnose incidence was rated as the percentage of diseased fruits among the infected ones. Experiments were replicated five times.

Infection of Phytophthora blight. The Phytophthora isolate was *Phytophthora capsici* No. 40476 provided by the Korea Agricultural Culture Collection (KACC). The pathogen was cultured on carrot agar media (10% carrot juice, 1% $CaCO_3$, 2% agar) for 5 days at 25°C. Ten to 12 agar blocks (1×1 cm pieces) covered with a dense hyphal mat were soaked in a Petri plate with 20 ml of sterilized water and then cultured for 5 days at 25°C. Zoospores were released from the soaked block by cold treatment for 3 hr in a refrigerator at 4°C. Pepper seedlings with 2-3 leaves were prepared for Phytophthora infection. Soil was removed from roots, and then seedling roots were dipped in a suspension of 10^4 zoospores/ml for 30 min. The inoculated seedlings were transferred to a 9-cm pot with commercial soil, and treated in the respective controlled chambers. Twelve infected pots were put in each chamber, and Phytophthora symptoms on the seedlings were observed for 5 days after inoculation. Phytophthora blight was rated for incidence on a five-point scale (0=no symptom; 1=a cotyledon was blighted or had dropped, 0%; 2=most of the leaves were diseased, 50%; 3=stem was broken or all leaves had fallen, 100%; 4=typical blight symptom appeared, 100%). The rate of incidence was calculated from the average percentage for the 12 pots per treatment in each experiment. Experiments were replicated four times.

Infection of bacterial wilt. The bacterial wilt isolate, *Ralstonia solanacearum* SW1001, was kindly provided by Dr. Seon-Woo Lee (Department of Applied Biology, Dong-A University, Pusan, Korea). The bacterial suspension was prepared from the basal liquid medium (1% peptone, 0.1% casamino acid) for 2 days at 30°C and shaking at 150 rpm, with the concentration of the suspension adjusted at OD=0.5 at 600 nm. The prepared inoculum was injected on the stems of 3–4-leaf seedlings at the node of cotyledon. Ten infected seedlings were put in each chamber and bacterial wilt on the stems was observed from days 1-6 after infection. Bacterial wilt was rated for incidence on a five-point scale (0=no symptom, 0%; 1=a cotyledon was wilted or had dropped, 0%; 2=most of the leaves were wilted without discoloration, 50%; 3=stem was broken at the inoculated site or all leaves had fallen, 100%; 4=above-ground part was dead, 100%). The rate of incidence was calculated from the average percentage of 10 pots per treatment in each experiment. Experiments were replicated seven times.

Infection of bacterial spot. The bacterial spot isolate was *Xanthomonas campestris* pv. *vesicatoria* No. 11157, provided by KACC. The bacterial suspension was prepared

from a liquid medium (0.5% glucose, 1.5% $CaCO_3$, 0.1%, 0.25% yeast extract at 7.0 pH) for 2 days at 30°C and shaking at 150 rpm, with the concentration of suspension adjusted at OD=0.135 at 600 nm. The prepared inoculum was injected on two leaves per seedling. A total of 12 infected leaves of six pots were put in each chamber and bacterial spot on the leaves was measured from days 1-5 after infection. Bacterial spot was rated for incidence on a five-point scale (0=no symptom, 0%; 1=center of the inoculated area was water soaked, 0%; 2=the discolored area was enlarged and changed to brown color, 50%; 3=the infected leaf was entirely yellow or curled, 100%; 4=the infected leaf had dropped, 100%). The rate of incidence was calculated from the average percentage of 12 leaves per treatment in each experiment. Experiments were replicated independently six times.

Elevated CO_2+Temp treatment effects on cultures and temperature effect on the four diseases

Hyphal growths of the fungal and oomycete pathogens under the elevated CO_2+Temp. treatment. *In vitro* growth rates of *C. acutatum* and *P. capsici* on PDA media in the 25°C/400 ppm CO_2 or 30°C/700ppm CO_2 treatments were determined. Hyphal plugs with 5-mm diameters from the two pathogens on PDA were placed in the centers of 9-cm Petri plates on PDA. Ten replications were placed in the 25°C/400 ppm CO_2 and 30°C/700 ppm CO_2 growth chambers. Radial hyphal growth was measured daily for 6 d. Experiments were replicated independently five times.

Bacterial growth of the two pathogens under the elevated CO_2+Temp. treatment. *In vitro* growth rates of *R. solanacearum* and *X. campestris* pv. *vesicatoria* on each liquid media in the 25°C/400 ppm CO_2 or 30°C/700 ppm CO_2 were determined. In test tubes with silicon plugs allowing for atmosphere control, 50 ml of each bacterial suspension were inoculated in 5 ml of the liquid cultures for the two pathogens. Three test-tube replications were shaken with a 3D mini shaker (MyLab, SL3D, Korea) for 48 hr in the treatment chambers. Absorbance was measured at 600 nm at 12, 24, 36, and 48 hrs after inoculation. Because $CaCO_3$ interfered with the absorbance of *X. campestris* pv. *vesicatoria*, it was removed from the liquid culture for *X. campestris* pv. *vesicatoria* Experiments were replicated five times independently.

Temperature treatment on four major diseases. To separate the elevated CO_2+Temp. treatment into CO_2 and temperature effects on the progress of the four pepper diseases, artificial infection of the four major diseases was conducted in a multi-thermo incubator (Eyela, MTI-201, Japan) at different temperature regimes. The temperature regimes were 25°C and 30°C for Phytophthora blight and the two bacterial diseases, while those for anthracnose were 28°C and 33°C because the optimal temperature for anthracnose was found to be 28°C. The inoculation and evaluation methods of the four diseases were the same as those for the elevated CO_2+Temp. treatment. Replications in each experiment consisted of 10 fruits for anthracnose, five seedlings for Phytophthora blight, five seedlings for bacterial wilt, and six leaves for bacterial spot. Experiments were replicated three times for anthracnose, two times for Phytophthora blight, and five times for the two bacterial diseases.

Statistical analysis. To compare the two treatments between the elevated CO_2+Temp. and the ambient, one-tailed paired *t*-test was conducted in each disease and a datum of the paired *t*-test was a difference (*d*) between the elevated CO_2+Temp. minus the ambient incidence in each experiment. The number of experiments in each disease was a data set of a paired *t*-test. Since the paired *t*-tests of the four diseases did not satisfy the assumption of a normal distribution, non-parametric analyses: Wilcoxon singled-rank tests of the paired *t*-test were performed. In addition, the alternative hypothesis of the test was that the incidence of the elevated CO_2+Temp. is higher than that of the ambient, therefore the paired *t*-test was one-tailed. We used a 95% significance level and the statistics software program S-link (ver. 2.2, Seoul, Korea).

Results

Elevated CO_2 and temperature increased the incidences of Phytophthora blight, bacterial wilt, and bacterial spot, but

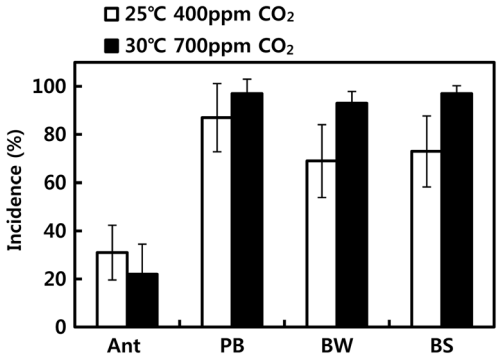

Fig. 1. Comparison between elevated CO_2+Temp. and ambient treatments. Four major diseases were anthracnose (Ant), Phytophthora blight (PB), bacterial wilt (BW), and bacterial spot (BS). And they were artificially inoculated on pepper seedlings, and the infected seedlings were placed in controlled chambers. Data were calculated as averages and standard errors. Experiments for each disease were repeated at least four times.

Table 1. The changes of the disease incidence on pepper due to the elevated CO_2 and temperature. Paired *t*-tests were conducted for each disease. Each experiment was pair-analyzed since the incidence of disease is highly variable depending on environmental conditions

Diseases of pepper (Observation time)	Experiment	Incidence of disease on last day of experiment		*p* value[a]
		25°C, 400 ppm CO_2	30°C, 700 ppm CO_2	
Anthracnose (192h)	5	31.0 (11.4)[b]	22.0 (12.5)	0.9063^{NS}
Phytophthora blight (96h)	4	87.3 (14.2)	97.0 (6.0)	0.1250^{NS}
Bacterial wilt (144h)	7	69.3 (15.1)	92.9 (4.9)	0.0078**
Bacterial spot (120h)	6	72.5 (14.7)	97.3 (3.3)	0.0156*

[a] *p* value is the result of one tailed pared *t*-tests in each disease. The paired *t*-test was a nonparametric alternative: Wilcoxon singed-rank test. The alternative hypothesis of the tests was the incidence of the elevated CO_2+Temp. treatment is higher than that of the ambient treatment.
[b] Data were calculated as averages and standard deviations.

decreased the incidence of anthracnose (Fig. 1). The incidences of bacterial wilt and spot were increased about 24% (p=0.0078) and 25% (p=0.0156) by the treatment and were statistically significant. In contrast, the incidences of fungal and oomycete diseases, anthracnose (p=0.9063) and Phytophthora blight (p=0.1250), were not statistically significant through the final observation day of disease progress (Table 1). Disease progress curves show that the pepper diseases (Fig. 2) progressed faster under the elevated CO_2+Temp. treatment than under the ambient treatment, except for anthracnose (Fig. 2a). The progress of the two bacterial diseases differed between the two treatments from day 3 after infection to the last day of observation (Fig. 2c, d). The difference in Phytophthora blight progress between treatments was largest at 2 days after infection, after which differences progressively decreased until the end of the measurement (Fig. 2b).

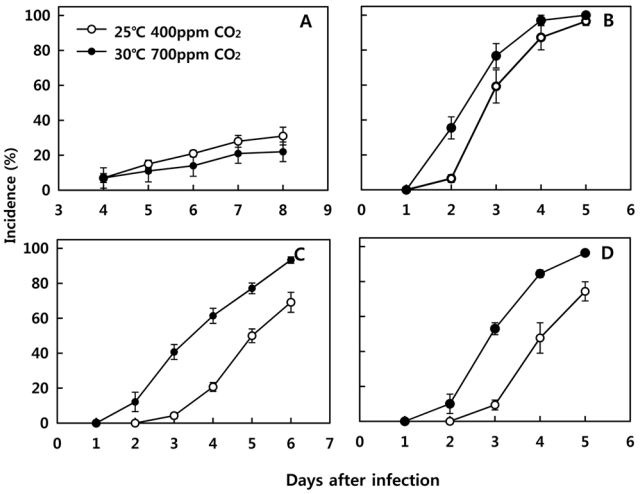

Fig. 2. Incidence of four major diseases on pepper seedlings or fruits under ambient (25°C and 400 ppm CO_2) and elevated CO_2+Temp. (30°C and 700 ppm CO_2) treatments. The incidence of anthracnose on fruits is the percentage of disease among the infected fruits and each point was taken from 100 fruits per experiment over five independent experiments (A). The incidence of Phytophthora blight is the average of the levels (0-4) and each point was taken from 12 seedlings per experiment over four independent experiments (B). The incidence of bacterial wilt is the average of the levels (0-4) and each point was taken from 10 seedlings per experiment over seven independent experiments (C). The incidence of bacterial spot is the average of the levels (0-4) and each point was taken from 12 leaves per experiment over seven independent experiments (D). The levels of Phytophthora blight and of the two bacterial diseases on pepper seedlings were determined as described in the materials and methods section.

To determine if the disease increases observed in peppers under higher temperature and CO_2 were due to improved growth rates of the pathogens, the rates of the fungal and oomycete hyphal growths and those of the two bacterial absorptions (Fig. 3) were studied in the two treatments. The rate of hyphal growth of *C. acutatum* under ambient

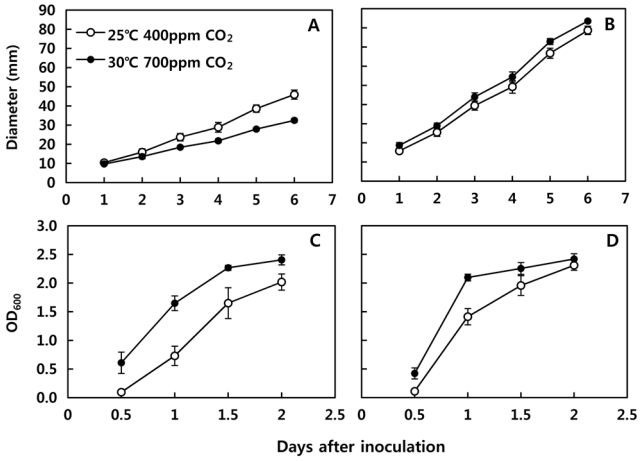

Fig. 3. *In vitro* growth of the four pepper pathogens. Radial growths of *Colletotrichum acutatum* (A) and *Phytophthora capsici* (B) cultured on potato dextrose agar media and the levels of pathogenic bacterial cells of *Ralstonia solanacearum* (C) and *Xanthomonas campestris* pv. *vesicatoria* (D) were measured at the 600 nm OD value in the liquid cultures under ambient (25°C and 400 ppm CO_2) and elevated CO_2+Temp. (30°C and 700 ppm CO_2) treatments. A 3D shaker and silicon plugs were used for the test-tube liquid culture, which allowed for controlled air conditions in each growth chamber. Each data point shows the average and standard error.

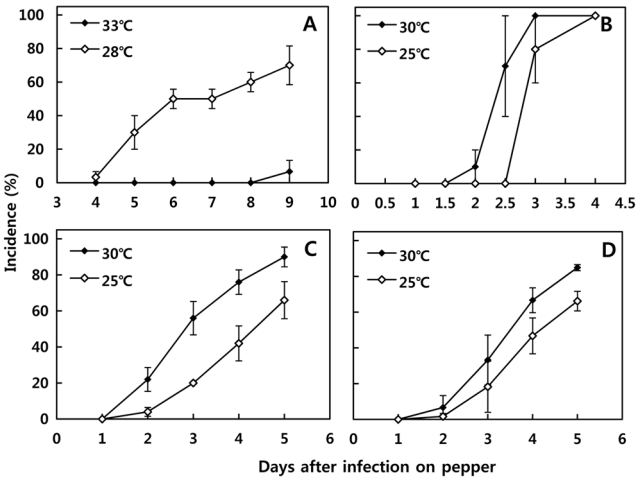

Fig. 4. Incidence of the four major diseases on pepper seedlings under the 25°C and 30°C treatments with the exception of anthracnose. The incidence of anthracnose on fruit was examined between 28°C and 33°C and was calculated as the percentage of diseased fruits among the infected fruits; each point was taken from 30 fruits per experiment over three independent experiments (A). The incidence of Phytophthora blight is the average of the levels (0-4), and each point was taken from five seedlings per experiment over two independent experiments (B). The incidence of bacterial wilt is the average of the levels (0-4), and each point was taken from five seedlings per experiment over five independent experiments (C). The incidence of bacterial spot is the average of the levels (0-4), and each point was taken from six leaves per experiment over five independent experiments (D). The levels of Phytophthora blight and the two bacterial diseases on pepper seedlings were determined as described in the materials and methods section.

conditions was faster than that in the elevated CO_2+Temp. treatment. Hyphae of *C. acutatum* under ambient conditions increased by approximately 0.7 cm d^{-1} over the 6 days, but under the elevated CO_2+Temp. treatment increased by approximately 0.4 cm d^{-1} (Fig. 3a). In contrast, hyphal growth of *P. capsici* did not differ under the two treatments and increased by approximately 1.0 cm d^{-1} over the 6 days (Fig. 3b). Bacterial cells of *R. solanacearum* under the elevated CO_2+Temp. treatment were consistently observed at higher levels than under ambient conditions. It appeared that the log phase of *R. solanacearum* was from 12 to 36 h after inoculation (Fig. 3c). On the other hand, *X. campestris* pv. *vesicatoria* growth under the elevated CO_2+Temp. treatment was higher only at 24 h after inoculation (Fig. 3d). The log phase of *X. campestris* pv. *vesicatoria* appeared to be from 12 to 24 h, but the faster growth of *X. campestris* pv. *vesicatoria* compared to *R. solanacearum* made differentiation difficult.

The patterns of the four disease progressive curves for the temperature treatment (Fig. 4) were quite similar to those of the elevated CO_2+Temp. treatment (Fig. 2), except for the pattern of anthracnose disease progress (Figs. 2a and 4a). The CO_2 effects on the four diseases seemed to be much less important than the temperature effects, which were dramatically different for anthracnose. However, the other three diseases seemed to show similar patterns under the elevated CO_2+Temp. treatment. Temperature effects on disease progress on pepper seedling or fruits (Fig. 4) were substantially different than those on pathogen growth on pure cultural media (Fig. 3). These significant differences highlight the need for further global warming studies in host tissues as pathogens in host tissues may be routinely affected by warming treatment.

Discussion

This study revealed that elevated CO_2 and temperature significantly increased the incidence of two bacterial diseases on pepper plant after a successive infection stage and that fungal and oomycete diseases, anthracnose and Phytophthora blight, would increase under conditions of elevated CO_2 and temperature. These results suggest that bacterial diseases on pepper may become more serious than the fungal and oomycete diseases under global warming. Preparation for such future conditions is needed, such as breeding of resistant pepper varieties especially for the bacterial diseases. Comparison of results from the elevated CO_2+Temp. (Fig. 2) and temperature (Fig. 4) treatments showed that temperature had more significant effects that did CO_2 for the four studied pepper diseases. As future temperatures are predicted to increase, the most important environmental factors in pepper-disease epidemics would be rising temperatures rather than elevated CO_2 (Luo et al., 1995).

Our results of the elevated CO_2+Temp. effects on the four pepper diseases can be separated by the infection ability of anthracnose and Phytophthora blight and the accelerating disease progress inside the host tissues of bacterial wilt and spot diseases. Anthracnose infection on *Stylosanthes scabra* under the 700 ppm CO_2 treatment was delayed initially, but once colonies were established they then grew faster inside the host tissue (Chakraboty et al., 2000a). Delayed anthracnose infection ability on pepper under the elevated CO_2 was similar to the finding for *Stylosanthes scabra* anthracnose infection (Chakraboty et al., 2000a; Chakraborty and Datta, 2003). Because the two bacterial diseases were injected via an artificial wound, there was no way to test the infection abilities of the bacterial pathogens; only disease progress under elevated CO_2 and temperature conditions could be observed after successful infection. Once the bacterial pathogens entered the interior plant tissue, the disease progressed faster. It has been previously observed that pathogens can colonize rapidly after they invade the host

tissue under elevated CO_2 (Pangga et al., 2003).

Fungal and oomycete growths *in vitro* were not affected by the elevated CO_2+Temp. treatment (Fig. 3). The hyphal growth of *Phytophthora capsici* in this study was the same as that of *Phytophthora parasitica* (Jwa and Walling, 2001) and *Colletotrichum acutatum* result was the same as that of *Colletotrichum gloesporioides* (Chakraborty et al., 2000a). In other words, the fungal pathogens were not sensitive to the treatment, which did not affect their pathogenicity. Like the results of the two bacterial growths, fungal growth of *Phyllosticta minima* was stimulated by about 17% higher under elevated CO_2 compared to ambient conditions. However, infected red maple under elevated CO_2 was found to be 8-22% less diseased than under ambient conditions (McElrone et al., 2005). Our results for disease severity under temperature regimes and pathogen growth under the elevated CO_2+Temp. for the two bacterial diseases consistently and directly showed that increased temperature was the major factor of the bacterial disease increases.

The altered environmental conditions affected the amount of bacterial diseases on pepper, but the two bacterial growth patterns under the treatment did not correspond. Rising temperature changed the pepper tissue directly, but the bacterial pathogens inside the plant may have been affected much less by the increased temperature due to plant homeostasis that moderated the environmental changes. Study of disease on pepper under elevated CO_2 and temperature can indicate future changes in diseases under global climate change. In addition, study of *in vitro* growth of the pathogens is not only useful to verify the mechanism of changing disease patterns but is also relevant to predict future disease pattern changes. Thus, temperature treatments without change in CO_2 levels can directly confirm the effects of temperature changes on pathogens in the future.

Our previous ecophysiological study reported that net photosynthesis substantially increased under elevated CO_2 (Yun and Ahn, 2009). Even though changes in pepper resistance under doubled CO_2 were not verified, several studies have reported that modified host physiology may induce disease resistance (Coakley et al., 1999; Hibberd et al., 1996a; Hibberd et al., 1996b; Hibberd et al., 1996c). Suggested mechanisms of enhanced resistance may include the mobilization of resources for plant defense (Hibberd et al., 1996c), reduced stomatal conductance and density (Hibberd et al., 1996a), and increased waxes and fiber content (Mouseau and Saugier, 1992). However, increases of resistance at elevated CO_2 levels are transient (Farrar and Gunn, 1996) and the development delays in pathogen growth are only at the pre-penetration stages (Hibberd et al., 1996b; Hibberd et al., 1996c).

Our studies dealt only with future temperature and CO_2 changes. Other environmental factors such as moisture should be considered as well. The NIMR has projected the frequent occurrence of heavy rain in Korea by 2100. According to a model study of pepper anthracnose (Kang et al., 2009), moisture is a much more important factor than temperature. In addition, rain splash is an important factor in bacterial diseases and rain is necessary to the movement of Phytophthora zoospores. For better prediction of future changes in plant disease patterns, long-term field studies such as those of free-air CO_2 enrichment (FACE) are needed for chili pepper. Our results from seedlings or fruit for 7-10 day treatment are not sufficient to predict the amount of disease on chili pepper in the future.

In conclusion, the climate change treatment, which added 5°C and 700 ppm of CO_2, increased the incidence of bacterial wilt and spot on pepper by 24% and 25%, respectively. Anthracnose decreased and Phytophthora blight slightly increased but the fungal diseases were not statistically significant, suggesting that bacterial diseases on chili pepper will likely be of more serious in the future. Also, temperature will be a more important factor in changing pepper diseases patterns in the future than CO_2. Our bacterial study showed a 2-day or 1-day faster rate of disease progress mainly due to temperature increases. The infection ability of the two fungal diseases did not change significantly. Although net photosynthesis in pepper under elevated CO_2 levels and temperature may contribute to disease resistance, improved disease resistance may be transient, and the duration of our growth chamber treatment was too short to allow for increases in net photosynthesis.

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