

Research Paper

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Effects of elevated CO₂ concentration and increased temperature on leaf related-physiological responses of *Phytolacca insularis* (native species) and *Phytolacca americana* (invasive species)

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In the study, the effects of elevated CO₂ and temperature on the photosynthetic characteristics, chlorophyll content, nitrogen content, carbon content, and C/N ratio of *Phytolacca insularis* and *Phytolacca americana* were examined under control (ambient CO₂+ ambient temperature) and treatment (elevated CO₂+ elevated temperature) for 2 years (2008 and 2009). The photosynthetic rate, transpiration rate and water use efficiency of two plant species were higher under the treatment than the under the control. The stomatal conductance of *P. insularis* was higher under the control, but that of *P. americana* was not significantly affected by CO₂ and temperature under the treatment. The chlorophyll contents of two species were decreased about 72.5% and 20%, respectively, by elevated CO₂ and temperature. The nitrogen contents of two species were not significantly altered by increase in CO₂ and temperature. The carbon contents of the two species were higher under the treatment than under the control. The C/N ratio of *P. insularis* was higher under the treatment but that of *P. americana* was not significantly affected by CO₂ and temperature. These results demonstrated that the physiological responses of *P. insularis* native plants might be more sensitively influenced by a CO₂-mediated global warming situation than those of the *P. americana* invasive plants.

Key words: chlorophyll content, C/N ratio, global warming, nitrogen content, photosynthesis, Phytolaccaceae

INTRODUCTION

It has been theorized that, because atmospheric CO₂ concentration and air temperature appear to be linked, and elevations are occurring in both, the global environment should also be experiencing a concomitant change (Morison and Lawlor 1999).

Since the late 1950s, global atmospheric CO₂ concentration has increased by an average of 1.9 ppm per year (Intergovernmental Panel on Climate Change 2007). Within this century, atmospheric CO₂ concentration is expected to exceed 550 ppm (Hofmann et al. 2009), in turn generating a global mean surface temperature warming of 1.9-4.4°C (Intergovernmental Panel on Cli-

mate Change 2007). However, according to Lunt et al. (2010), the earth's temperature might be as much as 30-50% more sensitive to atmospheric CO₂ concentration than previously thought.

In Korea, since the late 1990s, atmospheric CO₂ concentrations rose from 370.7 ppm to 391.4 ppm in 2008 (Korea Meteorological Administration 2008). According to the observational data from six observation stations (in Seoul, Incheon, Gangneung, Daegu, Mokpo, and Busan) between 1912 and 2009, the annual mean temperature has risen by 1.7°C in that time (Korea Meteorological Administration 2009).

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Increased atmospheric CO₂ concentrations associated with increasing temperatures generally elicit two direct physiological responses on plants.

First, most of the plants increase the photosynthetic rate under elevated CO₂ and temperature (He et al. 2005, Geissler et al. 2009). Additionally, a common response of plants to elevated CO₂ concentration is reduced stomatal conductance (Leakey et al. 2009a). This frequently results in a reduced transpiration rate, coupled to a resultant increase in the plant's water use efficiency (Radoglou et al. 1992, Kanemoto et al. 2009).

Second, elevated CO₂ and temperature conditions tend to alter the foliar chemistry of plants. Generally speaking, the chlorophyll contents of leaves grown under elevated CO₂ concentrations are reduced (Wullschlegel et al. 1992, Hamid et al. 2009). Additionally, leaf nitrogen contents are reduced, but carbon contents are increased under such conditions (Gifford et al. 2000). Consequently, the change in the relative proportion of carbon to nitrogen is increased substantially under elevated CO₂ and temperature conditions (Rao et al. 2009).

These physiological responses of plants to elevated CO₂ and temperature are known to vary due to interspecific differences or varying experimental conditions, as well as for several other reasons (Enoch and Honour 1993, Hamilton et al. 2008). In foreign countries, many researchers have measured plants' physiological responses to global warming using a variety of techniques, methods and plant materials, as well as interactions among different environmental factors. While in Korea, the influence of elevated CO₂ or temperature on physiological responses of crops to enhance crop productivity has been studied (Lee and Choi 2001, Lee et al. 2009), but the effect of global warming on physiological responses of native plants have never been studied so far.

Native plants are generally less tolerant to environmental stresses and have lower phenotypic plasticity in acclimating to a broader range of environmental conditions than invasive species (Sakai et al. 2001, Baruch and Jackson 2005). For the reasons mentioned above, native species may be more negatively affected than invasive species under the global warming. According to Song et al. (2009), the photosynthesis and biomass production of native species under elevated CO₂ were lower than their invasive competitors.

In order to compare the physiological responses of native and invasive plants to elevated CO₂ and temperature, we measured the photosynthetic parameters, chlorophyll contents, nitrogen contents, carbon contents and C/N ratios of *Phytolacca insularis* (native species) and

Phytolacca americana (invasive species) under control (ambient CO₂-ambient temperature, AC-AT) and treatment (elevated CO₂-elevated temperature, EC-ET) in this study.

MATERIALS AND METHODS

Study species

A native species restrictively found in Ulleung-do of Korea, *P. insularis*, has been designated as a rare and endangered plant by the Korea Forest Service (Lee 2008). *P. americana* is a herbaceous perennial plant native to the American Northeast, which commonly grows to a height of 1 to 1.5 m (Lee 2006). *P. americana* is distributed widely throughout the country, occurring in diverse habitats including fields, roadsides, forest edges, etc. In particular, it is distributed broadly in environmentally polluted areas (Park et al. 1999). One of the principal morphological characteristics of *P. americana* is drooping racemes. By way of comparison, *P. insularis* features permanently erect racemes (Chae et al. 2007).

Experimental design and growth condition

This study was conducted in and out of a glass greenhouse. The control was maintained at ambient CO₂ concentration and temperature (AC-AT) of the immediately surrounding air, which averaged approximately 370-380 ppm on a 24-hour basis. In order to ensure the same light intensity in the treatment, the controls were covered by the glass roof as well.

Treatment with elevated CO₂ concentration and temperature (EC-ET) in a greenhouse was maintained by inputting a small quantity of pure CO₂ through two perforated plastic hoses.

In this fashion, the elevated CO₂ concentration was maintained at approximately twice that of the ambient (750-800 ppm). An LCI Ultra Compact Photosynthesis System (Lci Pro; ADC Bioscientific, Hoddesdon, UK) was used to evaluate the stability of the CO₂ concentration in the treatment. The CO₂ concentration was controlled from the planting throughout the experiment.

The mean temperature in the treatment was about 3°C higher than the control (Fig. 1). The air temperature was measured using an alcohol thermometer at the same height in the control and treatment during the study period.

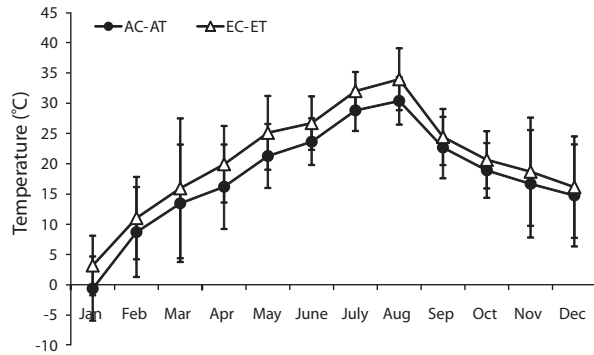


Fig. 1. Average monthly temperature in control (ambient CO₂- ambient temperature, AC-AT) and treatment (elevated CO₂- elevated temperature, EC-ET), 2008 and 2009.

Cultivation

In November 2007, the matured seeds of two species were collected from several individuals of a population in a glass greenhouse, respectively. In May 2008, the seeds of two species were sown in pots (51 cm × 15.3 cm × 12 cm) filled with equal proportions of sand, and we fertilized 0.5% of the sand weight. We subsequently applied organic fertilizer, which contains an ammonium nitrogen content of below 170 mg/L and nitrate nitrogen at a concentration of 150-330 mg/L. The plants were watered twice or three times per week to prevent them from suffering from water stress.

In June 2008, the plants were grown in the glass greenhouse until reaching the 2 to 3-leaf growth stage and were then transplanted in 2-seedlings into pots (22.5 cm × 27 cm) containing the sand.

For each species, three replicate pots were randomly assigned to the control and treatment respectively.

Photosynthetic measurements

The photosynthetic characteristics of the two species were measured at the vegetative stage, which was developmentally determined for the control and treatment using an LCI Ultra Compact Photosynthesis System (Lci Pro) from 10:00 am to 12:00 pm in June, 2009.

Leaf sections for measurements were selected in the upper parts of fully expanded leaves per an individual plant. The measured leaves from the controls were initially exposed to an air CO₂ concentration of 370-380 ppm and those from the treatment to a CO₂ concentration of 750-800 ppm.

Twenty four hours before measuring photosynthesis, water was supplied to the level of the moisture capacity (700 mL) of a pot, in order to reduce the difference

in relative humidity between the control and treatment. The light source utilized for the natural light and photosynthetic active radiation was 400-600 μmol m⁻² s⁻¹ in our measurements. Before the air entered the leaf chamber, the LCI Ultra Compact Photosynthesis System removed water vapor in the air through columns of soda lime.

All measurements were replicated more than 30 times. The items measured included the photosynthetic rate (μmol m⁻² s⁻¹), stomatal conductance (mol m⁻² s⁻¹), transpiration rate (mmol m⁻² s⁻¹) and water use efficiency (μmol CO₂/mmol H₂O).

Leaf water use efficiency was calculated as photosynthesis rate to transpiration rate.

Chlorophyll content measurements

The chlorophyll contents of the leaves of two species were measured using a hand-held chlorophyll content meter (CCM-20; ADC Bioscientific, Herts, UK), which measures the absorbance of a small portion of the leaf using differential transmission at two wavelengths, 665 nm and 940 nm. The samples of leaves were selected from the fully expanded uppermost leaves of the two species grown under the control and treatment conditions.

Nitrogen content measurements

The samples of leaves were dried for 2 days at 65°C. After the leaves were dried, the samples were pulverized into fine powder with a home blender (AKM-369s; Eupa, Seoul, Korea). At the time of measuring, the average specific leaf area of *P. insularis* was 633.16 cm²/g in the control and was 286.42 cm²/g in the treatment, and that of *P. americana* grown under control and treatment was 242.89 cm²/g and 347.83 cm²/g, respectively (Kim and You 2010). The nitrogen and carbon contents were determined using an automatic elemental analyzer (Flash EA 1112 series; Thermo Fisher Scientific, Rochester, NY, USA) at the Center for Research Facilities, Chungnam National University. The C/N ratio was calculated as the carbon content to the nitrogen content.

Statistical analysis

The effects of elevated CO₂ and temperature on the physiological parameters of two plant species measured in this study were confirmed via one-way ANOVA. Otherwise, the statistical differences between the control and treatment groups were evaluated via Fisher's least significant difference test. The data processing was conducted

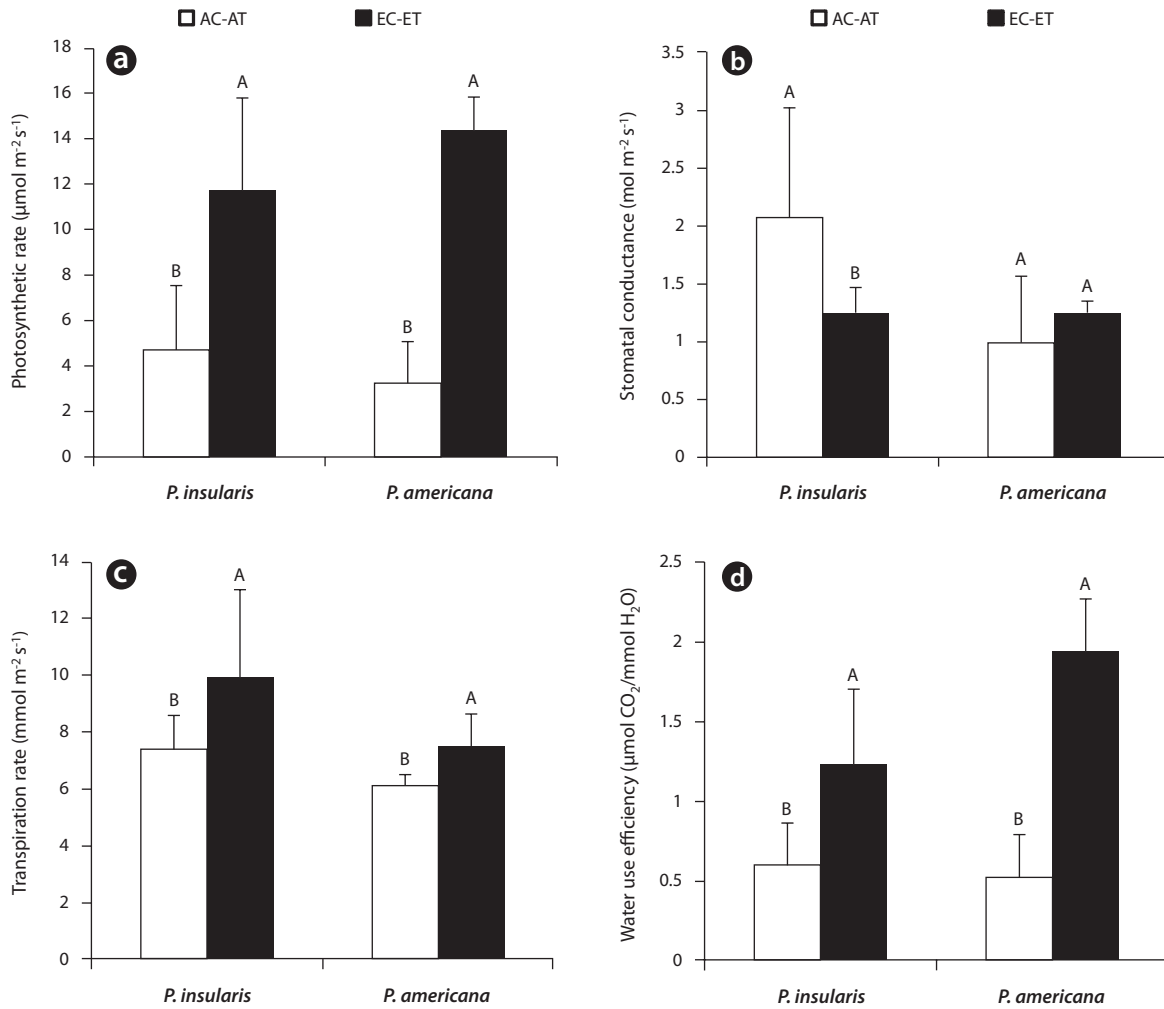


Fig. 2. Photosynthetic rate (a), stomatal conductance (b), transpiration rate (c) and water use efficiency (d) of *Phytolacca insularis* (closed bars) and *Phytolacca americana* (opened bars) under control (AC-AT) and treatment (EC-ET) conditions. The different letters on the bars refer to statistically significant differences between gradients within each species (Fisher's least significant difference, $P < 0.05$).

using STATISTICA 8 (Statsoft, Inc., Tulsa, OK, USA).

The percentage change of the measured physiological parameters of two species relative to the controls was represented via the method of Ghannoum et al. (2010).

RESULTS

Photosynthetic characteristics

The photosynthesis rate (Fig. 2a), transpiration rate (Fig. 2c) and water use efficiency (Fig. 2d) of the two plant species were higher under the treatment than under the control. Among the photosynthetic characteristics, photosynthesis rate and water use efficiency were found to be particularly related to plant growth. The photosynthesis rate of *P. insularis* and *P. americana* increased by

approximately 2.5- and 4.3-fold, respectively, in the treatment. The water use efficiency of *P. insularis* increased from 0.6 to 1.2 and that of *P. americana* increased from 0.5 to 1.9 as the result of elevated CO₂ and temperature.

At treatment, the stomatal conductance (Fig. 2b) of *P. insularis* was reduced by 38 percent as compared with the controls, but that of *P. americana* was not significantly affected by elevated CO₂ and temperature.

Chlorophyll content

The results of chlorophyll content of two plant species on elevated CO₂ and temperature are shown in Fig. 3. Chlorophyll content of two species significantly decreased by elevated CO₂ and temperature. *P. insularis* and *P. americana* decreased by 72.5% and 20% respectively at the treatment.

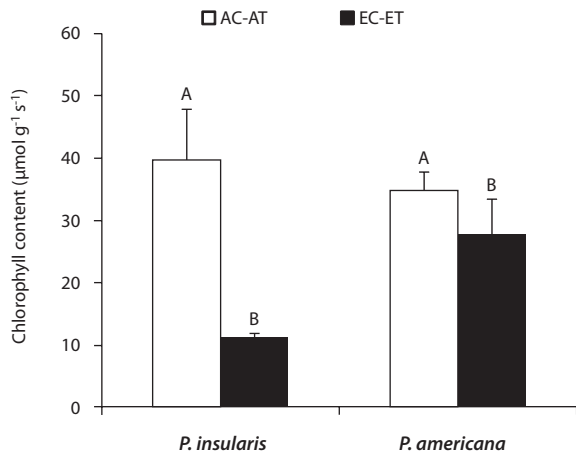


Fig. 3. Leaf chlorophyll content from *Phytolacca insularis* (closed bars) and *Phytolacca americana* (opened bars) grown under control (AC-AT) and treatment (EC-ET) conditions. The different letters on the bars refer to statistically significant difference among gradients within each species (Fisher's least significant difference, $P < 0.05$).

Nitrogen contents, carbon contents, and C/N ratio

The nitrogen contents of two plant species were not affected significantly by elevated CO₂ and temperature (Table 1), whereas the carbon contents of *P. insularis* and *P. americana* were increased by 16% and 9%, respectively, by the treatment. The C/N ratios of the two species were reduced by 24% and 7%, respectively, as compared with the control plants.

Table 1. Nitrogen content, carbon content and C/N ratio of *Phytolacca insularis* and *Phytolacca americana* grown in control (AC-AT) and treatment (EC-ET) conditions

| Gradient | Nitrogen (%) | Carbon (%) | C/N ratio |
|---------------------|--------------------------|---------------------------|---------------------------|
| <i>P. insularis</i> | | | |
| AC-AT | 3.78 ± 0.26 ^A | 33.85 ± 0.66 ^B | 9.00 ± 0.71 ^B |
| EC-ET | 3.51 ± 0.16 ^A | 39.22 ± 0.47 ^A | 11.20 ± 0.47 ^A |
| <i>P. americana</i> | | | |
| AC-AT | 4.19 ± 0.14 ^A | 36.40 ± 0.82 ^B | 8.69 ± 0.30 ^A |
| EC-ET | 4.28 ± 0.22 ^A | 39.66 ± 0.32 ^A | 9.27 ± 0.40 ^A |

Superscript letters mean significantly difference among gradients level within each species (Fisher's least significant difference, $P < 0.05$).

DISCUSSION

When we compared the two plant species grown under control and treatment conditions, the physiological responses of the two plant species grown under control

and treatment conditions were different (Fig. 4).

In general, elevated CO₂ and temperature enhance the photosynthetic rates of leaves (Lemon 1983, Lee and Choi 2001, Ghannoum et al. 2010) and water use efficiency (Nijs et al. 1989), and reduce the stomatal conductance and transpiration rates of the plants (Morison 1987, Ainsworth and Rogers 2007).

The results of our measurements demonstrated that the photosynthetic rates of *P. insularis* and *P. americana* were higher in the treatment than in the control. According to the results reported by Ryle et al. (1992), the photosynthetic rate of perennial ryegrass (*Lolium perenne*) grown for 49 days at a CO₂ concentration of 680 ppm was increased by 35-46%. During the growth of *L. perenne* over 10 years under elevated CO₂ conditions, the photosynthetic rate of *L. perenne* was stimulated by 36% (Ainsworth et al. 2003). Garbutt et al. (1990) determined that three C₃ plants and two C₄ plants were significantly increased in photosynthetic capacity at 700 ppm CO₂, relative to 350 ppm CO₂. The net photosynthetic rates of pigweed (*Chenopodium album*) and the sweet pea (*Pisum sativum*) were found to be higher with a doubling in the ambient CO₂ concentration (Hamilton et al. 2008). Those results were consistent with the results of our study. By way of contrast, cultivated tobacco (*Nicotiana tabacum*) grown at elevated CO₂ concentrations for a period of weeks evidenced a 20% reduction in the net photosynthetic rate (Raper and Peedin 1978). The photosynthetic rate of Mexican cotton (*Gossypium hirsutum*)

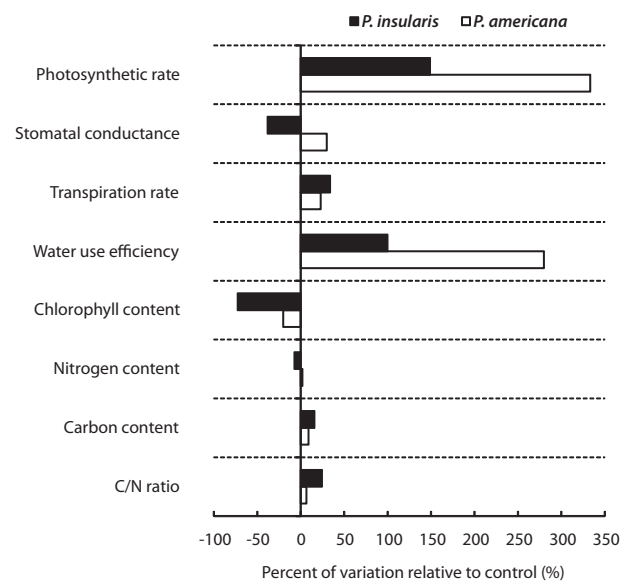


Fig. 4. Percentage variation of measured physiological parameters of *Phytolacca insularis* (closed bars) and *Phytolacca americana* (opened bars) under treatment (EC-ET) relative to control (AC-AT) conditions.

grown at 1,000 ppm CO₂ evidenced lower rates per unit leaf area than the plants grown at 350 ppm of CO₂ (Sasek et al. 1985).

Several previous studies have suggested that a reduction in photosynthesis was directly caused by excessive starch accumulation (Onoda et al. 2007, Leakey et al. 2009b), declines in chlorophyll content (Croonenborghs et al. 2009), reductions in Rubisco activity and RuBP regeneration (Zhang et al. 2008, Yamori and von Caemmerer 2009), etc.

We determined that the chlorophyll contents of *P. insularis* and *P. americana* were reduced under elevated CO₂ and temperature. However, the photosynthetic rates of two plant species were higher in the treatment, despite the observed decline in chlorophyll content. According to Wullschleger et al. (1992), the chlorophyll contents of the yellow-poplar (*Liriodendron tulipifera*) and white oak (*Quercus alba*) grown at double the ambient CO₂ concentration were reduced by 27% and 55% respectively, but photosynthesis per unit leaf area of two species increased by 60% and 39-51%, respectively. Wulff and Strain (1982) previously determined that the light harvesting capacity of plants grown under elevated CO₂ concentrations was affected by increases in the size and number of photosynthetic units, despite reduced chlorophyll contents. A photosynthetic unit was defined as a light-harvesting unit of photosynthesis, which encompassed approximately 300 light-absorbing molecules, with a molecule of chlorophyll functioning as the reaction center (Emerson and Arnold 1932).

This means that plants grown under elevated CO₂ concentration conditions tend to be more efficient in the capture or use of irradiance for photosynthesis than plants grown at ambient CO₂ levels. Thus, it is reasonable to suppose that increases in the photosynthesis of *P. insularis* and *P. americana* grown under treatment were caused by increases in light harvesting capacity per chlorophyll unit.

In most plants, stomatal conductance declined with increases in the levels of CO₂, because stomata were closed more often at high CO₂ concentrations (Bazzaz 1990). As a consequence, transpiration rates were reduced with consequent increases in water use efficiency (Bazzaz 1990). The stomatal conductance of *P. insularis* was reduced to 38.1% under the treatment, whereas that of *P. americana* was not significantly affected by elevated CO₂ concentrations and temperatures.

Lee et al. (2001) previously reported a 23% reduction in the stomatal conductance of 13 perennial species grown for 2 years under elevated CO₂ levels. The endangered

Western Himalayan herb, *Podophyllum hexandrum*, evidenced a significant reduction in stomatal conductance throughout the CO₂ enrichment (Chaturvedi et al. 2009).

Elevated CO₂ concentrations frequently reduce the stomatal conductance of plants and also may reduce the transpiration rate. However, elevated CO₂ concentration and temperature may not always reduce the transpiration rate (Dugas et al. 1997, Zheng et al. 2010), because of other compensatory effects occurring under elevated CO₂ and temperature conditions, such as increased leaf temperature--which might cause increased leaf-air vapor pressure deficits (Katul et al. 2009).

In our study, the transpiration rates of *P. insularis* and *P. americana* were increased by elevated CO₂ and temperature. In particular, the transpiration rate of *P. insularis* was increased by 33.8%, despite a 38.1% reduction in stomatal conductance occurring under elevated CO₂ and temperature.

According to Valle et al. (1985), the leaf temperature of soybeans was approximately 1.5°C higher at elevated CO₂ concentrations, and leaf resistance was more profound at elevated CO₂ concentrations than under ambient CO₂ conditions. As a consequence, the transpiration rate of soybeans grown under ambient or elevated CO₂ concentrations was not significantly affected by alterations in CO₂ levels. Because the increases in leaf resistance caused by high CO₂ were partially offset by increases in the leaf-to-air vapor pressure gradient induced by the increased transpiration rate owing to increased leaf temperature (Polley et al. 2008). In other words, higher temperatures can increase the transpiration rate by altering the vapor pressure deficit at the leaf surface. From the above discussion, the transpiration rates of *P. insularis* and *P. americana* would be more profoundly affected by increased temperature than by elevated CO₂ concentrations.

Increasing CO₂ concentration may generally have the effect of enhancing the water use efficiency of plants, because partial stomatal closure reduces transpiration (Ainsworth and Rogers 2007).

According to our results, the water use efficiency of *P. insularis* and *P. americana* was increased under elevated CO₂ and temperature. Runion et al. (2008) determined that *Cassia obtusifolia* (C₃) and *Sorghum halepense* (C₄) cultivated under elevated CO₂ conditions increased water use efficiency by 47% and 59%, respectively. A similar result was also reported for *Phaseolus vulgaris* (Radoglou et al. 1992). These findings were consistent with our results. Among the photosynthetic parameters, photosynthesis and water use efficiency was particularly

associated with plant growth and biomass production.

Invasive species generally evidence higher photosynthetic rates and greater water use efficiency than native species (McAlpine et al. 2008). Pattison et al. (1998) compared five invasive plants and four native plants, and determined that all invasive species evidenced higher photosynthetic rates than the native plants. Deng et al. (2004) also determined that the invasive plant, *Mikania micrantha*, maintained better water use efficiency than native *Mikania cordata*.

In EC-ET, photosynthetic rate and water use efficiency of *P. americana* as invasive plants were 2.2 times and 2.8 times respectively higher than *P. insularis* as native species. Song et al. (2009) determined that the invasive species evidenced a 67.1% stimulation of the photosynthetic rate, whereas the photosynthesis rate of the native species was increased by 24.8%. This result was consistent with our results. It can be inferred from our results that the photosynthetic characteristics of *P. americana* may be more profoundly positively affected by elevated CO₂ and temperature conditions than *P. insularis*.

Enhanced CO₂ concentration associated with increasing temperature was predicted to effect alterations in the biochemical components of plant tissues, including nitrogen contents, carbon contents, and C/N ratios (Cotrufo et al. 1998, Gifford et al. 2000, Zhou and Shangguan 2009).

Generally, the carbon contents increased but the nitrogen contents were reduced in the leaves, and resulted in higher C/N ratios under elevated CO₂ concentrations. A meta-analysis of the 75 reports of the effects of elevated CO₂ on herbivores and host plants determined that the nitrogen contents of plants were reduced by 16.4%, whereas the C/N ratios were increased by 26.6% (Stiling and Cornelissen 2007). Contrary to the prevalent view, the nitrogen contents of *P. insularis* and *P. americana* were not significantly affected by elevated CO₂ and temperature, but the carbon contents of the two species grown under EC-ET were increased by 15.6% and 9.1%, respectively. According to Chao and Ping (2009), the leaf carbon contents of *Onobrychis viciaefolia* were increased by more than 36%, but the leaf nitrogen contents were not significantly changed under elevated CO₂ concentration conditions.

The C/N ratio of *P. insularis* grown under treatment was increased by 24.4%, but that of *P. americana* was not significantly affected by elevated CO₂ and temperature. As the nitrogen content of *P. americana* was increased by 2.4%, rather than reduced as in *P. insularis*, the carbon content of *P. americana* was also increased to a lesser

degree than that of *P. insularis*. The higher C/N ratio frequently causes herbivores to increase their consumption to compensate for lower plant quality--the reduced nitrogen content--resulting in increased damage from herbivores (Stiling and Cornelissen 2007). Dermody et al. (2008) determined that elevated CO₂ levels increased the area of soybean leaves removed by insect herbivores. The leaf area loss was associated with reduced nitrogen in the soybean leaves and greater C/N ratios than those noted under elevated CO₂ concentrations.

According to our results, the C/N ratio of *P. insularis* was approximately 4 times that of *P. americana* under elevated CO₂ and temperature. Thus, elevated CO₂ and temperature appear to exert greater negative effects on the plant quality of *P. insularis* than on *P. americana* via alterations of the C/N ratios in leaves.

In conclusion, our results demonstrated that physiological responses of *P. insularis* in native plants might be more sensitively influenced than those of *P. americana* in invasive plants under the conditions relevant to global warming.

ACKNOWLEDGMENTS

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