

ORIGINAL ARTICLE

Leaf temperature of soybean grown under elevated CO₂ increases *Aphis glycines* (Hemiptera: Aphididae) population growth

Bridget F. O'Neill¹, Arthur R. Zangerl¹, Evan H. DeLucia^{2,3}, Clare Casteel², Jorge A. Zavala^{4,5}, and May R. Berenbaum^{1,3}

Departments of ¹Entomology and ²Plant Biology and ³Institute of Genomic Biology, University of Illinois, Urbana-Champaign, Urbana, Illinois USA, ⁴Consejo Nacional de Investigaciones Científicas y Técnicas, Catedra de Bioquímica, Facultad de Agronomía, University of Buenos Aires and ⁵Pontificia Universidad Católica Argentina, Buenos Aires, Argentina

Abstract Plants grown under elevated carbon dioxide (CO₂) experience physiological changes that influence their suitability as food for insects. To determine the effects of living on soybean (*Glycine max* Linnaeus) grown under elevated CO₂, population growth of the soybean aphid (*Aphis glycines* Matsumura) was determined at the SoyFACE research site at the University of Illinois, Urbana-Champaign, Illinois, USA, grown under elevated (550 μ L/L) and ambient (370 μ L/L) levels of CO₂. Growth of aphid populations under elevated CO₂ was significantly greater after 1 week, with populations attaining twice the size of those on plants grown under ambient levels of CO₂. Soybean leaves grown under elevated levels of CO₂ were previously demonstrated at SoyFACE to have increased leaf temperature caused by reduced stomatal conductance. To separate the increased leaf temperature from other effects of elevated CO₂, air temperature was lowered while the CO₂ level was increased, which lowered overall leaf temperatures to those measured for leaves grown under ambient levels of CO₂. Aphid population growth on plants grown under elevated CO₂ and reduced air temperature was not significantly greater than on plants grown under ambient levels of CO₂. By increasing *Glycine max* leaf temperature, elevated CO₂ may increase populations of *Aphis glycines* and their impact on crop productivity.

Key words *Aphis glycines* Matsumura, elevated CO₂, *Glycine max* Linnaeus, leaf temperature

Introduction

Atmospheric carbon dioxide (CO₂) levels have risen steadily since the start of the Industrial Revolution, from 280 μ L/L to 386 μ L/L today (IPCC, 2007). This concentration is predicted to double within the next

100 years (Ehhalt *et al.*, 2001). While elevated CO₂ stimulates photosynthesis and results in increased productivity in C₄ plants (Curtis & Wang, 1998), the indirect effects on interactions with herbivores vary greatly.

Multiple studies with lepidopteran herbivores have shown delayed larval development (Reddy *et al.*, 2004; Gang *et al.*, 2007) and higher mortality (Agrell *et al.*, 2000, Knepp *et al.*, 2007) when feeding on plants grown under elevated CO₂. However, several studies have documented that coleopterans and hemipterans experience increased survivorship (Xing *et al.*, 2003; Gao *et al.*, 2008) and fecundity (Chen *et al.*, 2004, 2006; O'Neill *et al.*, 2008). The causative factor for these changes

Correspondence: Bridget O'Neill, University of Illinois, Urbana-Champaign, Department of Entomology, 320 Morrill Hall, 505 S. Goodwin Avenue, Urbana, IL 61801, USA

Present address: Bridget O'Neill, Trinity College, Department of Botany, College Green, Dublin 2, Ireland. Tel: +353 1 896 4238; email: oneillb6@tcd.ie

differs depending on which plant species the insects are consuming.

One of the most recent pest species found on soybean in the USA is the soybean aphid, *Aphis glycines* Matsumura (Venette & Ragsdale, 2004). A native of Asia, *A. glycines* was first documented in the USA in July 2000 (Ragsdale *et al.*, 2004). It has spread throughout the USA's Midwest and is one of the few pests that consistently has an economic impact on soybean (*Glycine max*) yield (Ragsdale *et al.*, 2007). *Aphis glycines* are ectotherms and their physiological functions are dependent on the temperature of their environment (McCornack *et al.*, 2004). McCornack *et al.* (2004) showed that soybean aphid growth and reproduction changes dramatically depending on leaf temperature.

Aphid populations were surveyed at the SoyFACE research site at the University of Illinois, Urbana-Champaign and populations were larger on soybeans grown under elevated CO₂ conditions than on soybeans grown under ambient CO₂ conditions (Dermody *et al.*, 2008). *Glycine max* plants grown under elevated CO₂ have increased leaf area, increased C : N ratio, and higher amounts of leaf sugars (Ainsworth *et al.*, 2007). They also have decreased evapotranspiration, which increases leaf temperatures (up to 2°C), due to reduced stomatal conductance (Bernacchi *et al.*, 2007). As stated above, temperature is one of the most important factors for ectotherm growth.

In this study we examined the effects of living on soybean exposed to elevated CO₂ atmospheres on *A. glycines* population growth. As stated, one of the most important factors for ectotherm growth is temperature. For small-bodied aphid species, such as *A. glycines*, one of the most important of these factors is the temperature of the leaves they live upon for their entire lives. As higher leaf temperatures were previously measured for soybean grown under elevated CO₂ atmospheres (Bernacchi *et al.*, 2007), we hypothesized that *A. glycines* population growth would increase on plants grown under elevated CO₂ as the result of changes in leaf temperature. To test this hypothesis, we manipulated air temperature in the elevated CO₂ treatment to nullify the resultant increased leaf temperature on aphid population growth.

Materials and methods

Aphis glycines population growth on FACE plants

All field studies were done during July and August 2005 at the soybean free air gas concentration enrichment (SoyFACE) research site at the University of Illinois,

Urbana-Champaign, USA. SoyFACE is an open Free Air gas Concentration Enrichment system that exposes large field plots of *G. max* to elevated levels of CO₂ (Long *et al.*, 2004). *Glycine max* plants were grown under ambient (384 µL/L CO₂) and elevated CO₂ (550 µL/L) atmospheres at the SoyFACE site. The *G. max* cultivar used was Pioneer 93B15. Treatment plots covered 350 m², had a diameter of 20 m, and were at least 100 m from any other plot. The SoyFACE plots were designed in a randomized block with each treatment replicated four times. CO₂ concentration at all of the plots in the site was measured with an infrared gas analyzer (Model SBA-1, PP Systems, Hitchin, UK). As the entire field site is open to the elements, air temperature, day length and rainfall were the same for both treatments.

Ten soybean plants were chosen in each atmospheric treatment plot for a total of 40 plants per treatment. Fifty wingless adult *A. glycines* were confined on one leaf on each plant with fine mesh (size 30) at the R4 growth stage. The R4 stage was chosen as this was the plant stage that coincided most often with the period of aphid peak population growth at the SoyFACE research site (end of July, early August). Populations were undisturbed for 1 week. At the end of the week, leaves within bags were cut and placed at -80°C until aphids could be counted. Population growth of only 1 week was counted as *A. glycines* can easily double their populations in that period and we were concerned that if we left them longer they would become overcrowded and switch to producing only alates (Wang *et al.*, 1962). Population growth, estimated from the final counts in the two treatments minus the size of the original population placed on each leaf, was analyzed by a one-way analysis of variance (ANOVA) with treatment as the independent variable (SPSS 9.0: SPSS Inc., Chicago, IL, USA). Results at the 0.05 level were considered significant, and as there were only two treatments, use of post-hoc tests was unnecessary. Air temperatures were recorded at the SoyFACE site for the week of the experiment with a humidity and temperature probe (Vaisala INTERCAP HMP50 SecondWind, Somerville, MA, USA) attached to a data logger (Campbell CR23X logger: Campbell Scientific, Inc., Logan, UT, USA). Leaf temperatures in the ambient and elevated carbon dioxide atmospheric research plots were previously reported by Bernacchi *et al.* (2007).

Aphis glycines population growth under elevated CO₂ conditions with controlled temperatures

Growth chamber studies were done in environmental growth chambers during spring 2008 to isolate the

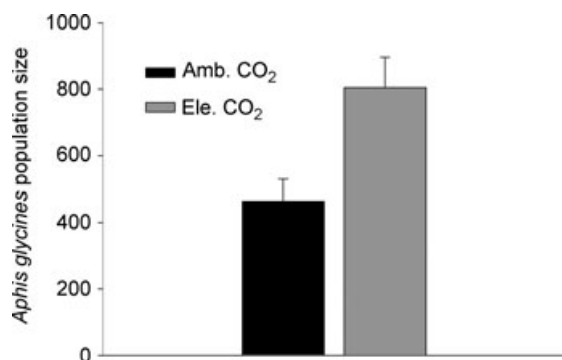


Fig. 1 *Aphis glycines* population growth on *Glycine max* grown under ambient and elevated levels of CO₂. Mean ± standard deviation air temperature for the week of the experiment was 23.878 ± 4.759°C. Black bars = *A. glycines* population growth on *G. max* grown under ambient levels of CO₂; grey bars = *A. glycines* population growth on *G. max* grown under elevated levels of CO₂.

potential effects of elevated temperature caused by stomatal closure, one of the indirect effects of CO₂, on aphid population growth rate. Chambers were built of an aluminium frame and walls made of clear cellulose acetate (Maherali & DeLucia, 2000). *Glycine max* were grown under ambient (400 µL/L CO₂) and elevated CO₂ (700 µL/L) atmospheres. Seeds of Pioneer 93B15 were planted in Sunshine[®] LC1 soil growth mix (SunGro Horticulture, Vancouver, BC, Canada) and watered every other day. Watering schedule and day length were the same for both treatments with watering every other morning and a combination of natural light and halogen lamps in the greenhouse with a day length of 14 h.

Air temperature was manipulated in the elevated CO₂ treatment to nullify the increased leaf temperature from reduced stomatal conductance that results from growth under elevated CO₂ conditions. Air temperature was maintained at 25°C in all chambers while plants were growing before the experiment started. To manipulate leaf temperature, all ambient CO₂ chambers were maintained at 27°C, for the duration of the experiment only, and all elevated CO₂ chambers were maintained at 25°C. Leaf temperatures were measured daily for each plant with a digital thermocouple (6400-04 leaf temperature thermocouple, Li-Cor, Lincoln, NE, USA, with HH506R thermometer, Omega Engineering, Inc., Stamford, CT, USA) attached to a data logger (21X micrologger; Campbell Scientific, Logan, UT, USA) to confirm that temperature ranges were equal in both atmospheric treatments. Individual chamber temperatures were raised or lowered if the range in that chamber deviated from the desired range. Twenty plants were grown under each atmospheric treatment, with five

plants in each of two chambers. Aphids were confined on plants at the R4 growth stage after 5 weeks of growth (McWilliams *et al.*, 2004). Fifty *A. glycines* were placed on one leaf on each plant and the same protocol used for measuring population growth at SoyFACE was followed. Populations were undisturbed for 1 week. At the end of the week, leaves with bags were cut and placed at -80°C, until aphids could be counted and differences in population growth counts (estimated the same as for the counts for aphids on the FACE plants) were analyzed by a one-way ANOVA with treatment as the independent variable. Again, results at the 0.05 level were considered significant, with the use of post-hoc tests considered unnecessary as there were only two treatments. Leaf temperatures were analyzed by a one-way ANOVA with treatment as the independent variable (SPSS 9.0).

Aphis glycines individuals for all experiments (field and growth chamber) were obtained from a campus laboratory colony. First instar nymphs were collected from Champaign County in Illinois and reared on the Williams 82 soybean cultivar in an environmental growth chamber (Wille & Hartman, 2009).

Results

Aphis glycines population growth on FACE plants

Aphid population growth in the field in the elevated CO₂ treatment was significantly greater than population growth in the ambient treatment (elevated CO₂ growth 805 ± 92 individuals; ambient CO₂ growth 464 ± 66 individuals; df = 1,75; *F* = 9.011; *P* = 0.004) (Fig. 1). Mean ± standard deviation (SD) air temperature for the week of the experiment was 23.9 ± 4.8°C. Mean ± SD mid-day (hours 12:00–2:00 PM when the sun is at its zenith) leaf temperatures for the week of the experiment were 31.0 ± 5.4°C for soybeans grown under elevated CO₂ conditions and 30.3 ± 4.9°C for soybeans grown under ambient levels of CO₂ (Bernacchi *et al.*, 2007).

Aphis glycines population growth under elevated CO₂ conditions and controlled temperatures

Mean leaf temperatures at the start of the experiment were 22.6 ± 1.7°C for ambient leaves and 24.8 ± 1.8°C for elevated CO₂ leaves when the air temperature was the same in the two treatments. Prior to putting aphids on leaves, air temperature in the ambient CO₂ chambers was raised and resulting leaf temperatures in the greenhouse chambers were not significantly different between the two CO₂ treatments (week

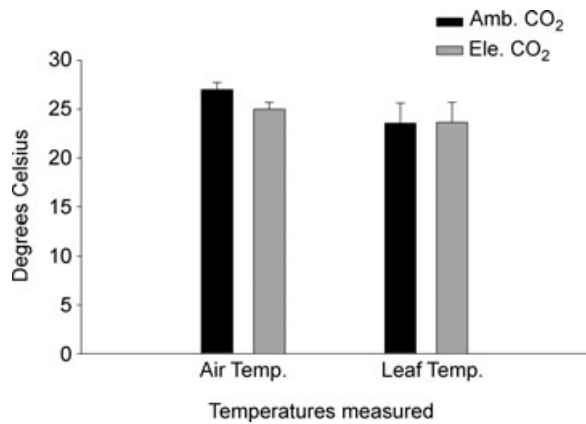


Fig. 2 Temperatures experienced by *Glycine max* grown under ambient and elevated levels of CO₂ and artificially controlled air temperatures. Air temperature is plotted on the left side of the graph (ANOVA, $df = 1,38$; $F = 3.626$; $P = 0.115$) while corresponding leaf temperature is plotted on the right side of the graph (ANOVA, $df = 1,38$; $F = 0.012$; $P = 0.914$). Black bars = chambers/plant grown under ambient levels of CO₂; grey bars = chambers/plants grown under elevated levels of CO₂.

mean leaf temperature in the ambient CO₂ chambers = $19.63 \pm 1.71^{\circ}\text{C}$; week mean leaf temperature in the elevated CO₂ chambers = $19.69 \pm 1.73^{\circ}\text{C}$; $df = 1,38$; $F = 0.012$, $P = 0.914$ (Fig. 2). While these temperatures were lower than we had intended, they are within the optimal temperature range for *A. glycines* (McCornack et al., 2004). Aphid population growth in the greenhouse chambers was not significantly different between the two treatments when the chambers were maintained at different air temperatures ($df = 1,38$; $F = 0.298$, $P = 0.589$) (Fig. 3).

Discussion

Population growth of *A. glycines* increased on soybeans grown under elevated CO₂ (Fig. 1). By removing the increase in leaf temperature from the other effects of elevated CO₂, we were able to reduce aphid population growth to the level seen on plants grown under ambient levels of CO₂ (Figs. 2 and 3). This finding suggests that the increase in aphid productivity seen on plants grown under elevated CO₂ is mainly the result of the increased leaf temperature of these plants, although other indirect effects of elevated CO₂, such as increased amounts of carbohydrates in the plant and effects directly on the insect may also be important.

Life history attributes of herbivores, such as longevity and fecundity, are extremely important in predicting fu-

ture impacts of global atmospheric change on agriculture. *Aphis glycines* on soybean plants reproduce clonally, producing apterae (wingless) and alatae (winged) nymphs, depending on the extent of crowding (Ragsdale et al., 2004). Individuals can live for roughly 1 month, maturing from a nymph to an adult capable of producing offspring within 1 week (Hong et al., 2010). This maturation process depends a great deal on ambient temperature, with even small temperature increases, such as the one degree difference measured at SoyFACE, speeding up development of *A. glycines* (Hirano et al., 1996). Populations can reproduce rapidly on soybean plants; 15 generations/season was measured in China and presumably growth is similar in the USA (Wang et al., 1962). This rapid population growth is facilitated by adults being able to produce two or three nymphs each day (Hong et al., 2010). While we only measured population growth after a 1-week interval, this period is sufficient for accurate population monitoring and is the period of time commonly used for assessing future population growth (Desneux et al., 2006; Costamagna et al., 2010). Population sizes of *A. glycines* on one leaf after this 1-week period may also cause significant crowding, leading to nutritional stress and increased production of winged alates and migration, both of which may give an inaccurate estimate of population dynamics and future growth (Hodgson et al., 2005). Increased population growth under elevated CO₂ conditions will potentially lead to higher herbivore loads on each plant, and increased dispersal throughout the field as larger

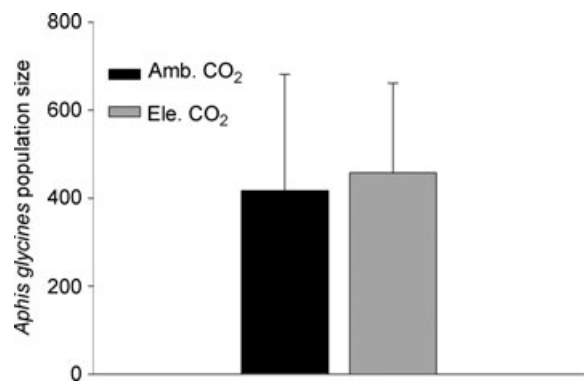


Fig. 3 *Aphis glycines* population growth on *Glycine max* grown under ambient and elevated levels of CO₂ under artificially controlled conditions (ANOVA, $df = 1,38$; $F = 0.298$; $P = 0.589$). Air temperature was maintained at 25°C for chambers with elevated levels of CO₂ and was maintained at 27°C for chambers with ambient levels of CO₂. Black bars = *A. glycines* population growth on *G. max* grown under ambient levels of CO₂; grey bars = *A. glycines* population growth on *G. max* grown under elevated levels of CO₂.

populations lead to crowding and increased production of alate nymphs (Ragsdale *et al.*, 2004).

Aphids are phloem feeders which are nitrogen-limited (Dixon, 1998). Levels of various nutrients in soybeans grown under elevated CO₂ have been previously measured at the SoyFACE site. Quercetin, a powerful flavonol antioxidant that may promote increased longevity, is significantly increased in foliage grown under elevated CO₂ during the time period of aphid peak population growth but is not significantly increased in the phloem (O'Neill *et al.*, 2010). Nitrogen is significantly decreased in foliage grown under elevated levels of CO₂, increasing the C : N in those plants (Dermody *et al.*, 2008), but more so in July than in August (Hamilton *et al.*, 2005). In fact, levels of the 17 amino acids available in soybean phloem are not significantly different in plants grown under ambient or elevated levels of CO₂ at SoyFACE during late July and early August (B.F. O'Neill, A.R. Zangerl, E.H. DeLucia, and M.R. Berenbaum, unpubl. data). As there are very few (or none depending on the year) significant differences in nutrient levels in soybean plants during peak aphid population growth, the increased temperature of soybean foliage grown under elevated levels of CO₂ is the most likely cause of increased aphid population growth during this period (Bernacchi *et al.*, 2007; Dermody *et al.*, 2008).

Aphids move into soybean fields fairly early in the summer and build slowly with increasing temperatures until their populations peak at the end of July and beginning of August (Ragsdale *et al.*, 2004). The increased temperature of plants grown under elevated CO₂ may allow aphid populations to build faster and peak earlier in the season. Aphids typically peak at the end of pod fill at the end of seed case development when the seeds themselves are starting to develop (Fehr *et al.*, 1971). Peaking earlier in the season with faster population growth rates, resulting from higher leaf temperatures, may lead to large faster-growing aphid populations at the start of pod fill instead of at the end, and a resulting increased period of potential economic injury (Ragsdale *et al.*, 2007). Even if these populations decrease rapidly, the earlier timing of the potential aphid infestation may damage soybean plants at a crucial point for yield determination (Myers *et al.*, 2005; Beckendorf *et al.*, 2008). This change will potentially affect soybean yield to an even greater extent than the yield reductions currently produced by aphids, as earlier large infestations may result in higher levels of yield loss in the USA (Catangui *et al.*, 2009).

Plants grown under elevated CO₂ conditions are no longer CO₂-limited during photosynthesis (Ainsworth & Long, 2005) and reducing water loss is a higher priority (Bernacchi *et al.*, 2007). Stomata will close more often,

increasing leaf temperature (Kana & Vass, 2008). Also under elevated CO₂ conditions, *A. glycines* population growth is enhanced, at least partially due to these elevated leaf temperatures. This enhancement of *A. glycines* population growth suggests that yield reduction of soybean resulting from *A. glycines* feeding may in the future become more severe as a consequence of global changes.

Acknowledgments

We thank Glen Hartman and Curt Hill for maintaining the *A. glycines* laboratory colony in the Department of Crop Sciences, UIUC. The SoyFACE experiment is supported by the Illinois Council for Food and Agricultural Research (C-FAR), Archer Daniels Midland Co., and USDA-ARS. This research was supported in part by grants from the U.S. Department of Energy (No. DE-FG02-04ER63489), and by USDA grant #2002-02723.

References

- Agrell, J., McDonald, E.P. and Lindroth, R.L. (2000) Effects of CO₂ and light on tree phytochemistry and insect performance. *Oikos*, 88, 259–272.
- Ainsworth, E.A. and Long, S.P. (2005) What have we learned from 15 years of free-air CO₂ enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO₂. *New Phytologist*, 165, 351–371.
- Ainsworth, E.A., Rogers, A., Leakey, A.D.B., Heady, L.E., Gibbon, Y., Stitt, M. and Schurr, U. (2007) Does elevated atmospheric [CO₂] alter diurnal C uptake and the balance of C and N metabolites in growing and fully expanded soybean leaves? *Journal of Experimental Botany*, 58, 579–591.
- Beckendorf, E.A., Catangui, M.A. and Riedell, W.E. (2008) Soybean aphid feeding injury and soybean yield, yield components, and seed composition. *Agronomy Journal*, 100, 237–246.
- Bernacchi, C.J., Kimball, B.A., Quarles, D.R., Long, S.P. and Ort, D.R. (2007) Decreases in stomatal conductance of soybean under open-air elevation of [CO₂] are closely coupled with decreases in ecosystem evapotranspiration. *Plant Physiology*, 143, 134–144.
- Catangui, M.A., Beckendorf, E.A. and Riedell, W.E. (2009) Soybean aphid population dynamics, soybean yield loss, and development of stage-specific economic injury levels. *Agronomy Journal*, 101, 1080–1092.
- Chen, F.J., Wu, G. and Ge, F. (2006) Responses of spring wheat to elevated CO₂ and their effects on *Sitobion avenae* aphid growth, development and reproduction. *Chinese Journal of Applied Ecology*, 17, 91–96.

- Chen, F.J., Wu, G. and Ge, F. (2004) Impacts of elevated CO₂ on the population abundance and reproductive activity of aphid *Sitobion avenae* Fabricius feeding on spring wheat. *Journal of Applied Entomology*, 128, 723–730.
- Costamagna, A.C., McCornack, B.P., Ragsdale, D.W. and Landis, D.A. (2010) Development and validation of node-based sample units for estimating soybean aphid (Hemiptera: Aphididae) densities in field cage experiments. *Journal of Economic Entomology*, 103, 1483–1492.
- Curtis, P.S. and Wang, X. (1998) A meta-analysis of elevated CO₂ effects of woody plant mass, form, and physiology. *Oecologia*, 113, 299–313.
- Dermody, O.C., O'Neill, B.F., Zangerl, A.R., Berenbaum, M.R. and DeLucia, E.H. (2008) Effects of elevated CO₂ and O₃ on leaf damage and insect abundance in a soybean agroecosystem. *Arthropod-Plant Interactions*, 2, 125–135.
- Desneux, N., O'Neil, R.J. and Yoo, H.J.S. (2006) Suppression of population growth of the soybean aphid, *Aphis glycines* Matsumura, by predators: The identification of a key predator and the effects of prey dispersion, predator abundance, and temperature. *Environmental Entomology*, 35, 1342–1349.
- Dixon, A.F.G. (1998) *Aphid Ecology*. Chapman & Hall, London. 300 pp.
- Ehhalt, D., Prather, M., Dentener, F., Derwent, R., Dlugokencky, E., Holland, E., Isaksen, I., Katima, J., Kirchhoff, V., Matson, P., Midgley, P., Wang, M., Berntsen, T., Bey, T., Brasseur, G., Buja, L., Collins, W.J., Daniel, J., DeMore, W.B., Derek, N., Dickerson, R., Etheridge, D., Feichter, J., Fraser, P., Friedl, R., Fuglestedt, J., Gauss, M., Grenfell, L., Grubler, A., Harris, N., Hauglustaine, D., Horowitz, L., Jackman, C., Jacob, D., Jaeglé, L., Jain, A., Kanakidou, M., Karlsdottir, S., Ko, M., Kurylo, M., Lawrence, M., Logan, J.A., Manning, M., Mauzerall, D., McConnell, J., Mickley, L., Montzka, S., Müller, J.F., Olivier, J., Pickering, K., Pitari, G., Roelofs, G.J., Rogers, H., Rognerud, B., Smith, S., Solomon, S., Staehelin, J., Steele, P., Stevenson, D., Sundet, J., Thompson, A., van Weele, M., von Kuhlmann, R., Wang, Y., Weisenstein, D., Wigley, T., Wild, O., Wuebbles, D. and Yantosca, R. (2001) Atmospheric chemistry and greenhouse gases. *Climate Change 2001: The Scientific Basis: Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change* (IPCC) (eds J.T. Houghton, Y. Ding, D.J. Griggs, M. Noguer, P.J. van der Linden, X. Dai, K. Maskell & C.A. Johnson), pp. 241–290. Cambridge University Press, Cambridge, United Kingdom.
- Fehr, W.R., Caviness, C.E., Burmood, D.T. and Pennington, J.S. (1971) Stage of development descriptions for soybeans, *Glycine max* (L) Merrill. *Crop Science*, 11, 929–931.
- Gang, W., Chen, F.J., Sun, Y.C. and Ge, F. (2007) Response of successive three generations of cotton bollworm, *Helicoverpa armigera* (Hübner), fed on cotton bolls und elevated CO₂. *Journal of Environmental Sciences*, 19, 1318–1325.
- Gao, F., Zhu, S.R., Sun, Y.C., Du, L., Parajulee, M., Kang, L. and Ge, F. (2008) Interactive effects of elevated CO₂ and cotton cultivar on tri-trophic interaction of *Gossypium hirsutum*, *Aphis gossypii*, and *Propylaea japonica*. *Environmental Entomology*, 37, 29–37.
- Hamilton, J.G., Dermody, O., Aldea, M., Zangerl, A.R., Rogers, A., Berenbaum, M.R. and DeLucia, E.H. (2005) Anthropogenic changes in tropospheric composition increase susceptibility of soybean to insect herbivory. *Environmental Entomology*, 34, 479–485.
- Hirano, K., Honda, K. and Miyai, S. (1996) Effects of temperature on development, longevity and reproduction of soybean aphid, *Aphis glycines* (Homoptera: Aphididae). *Applied Entomology and Zoology*, 31, 178–180.
- Hodgson, E.W., Venette, R.C., Abrahamson, M. and Ragsdale, D.W. (2005) Alate production of soybean aphid (Homoptera: Aphididae) in Minnesota. *Environmental Entomology*, 34, 1456–1463.
- Hong, S.C., Donaldson, J. and Gratton, C. (2010) Soybean cyst nematode effects on soybean aphid preference and performance in the laboratory. *Environmental Entomology*, 39, 1561–1569.
- Intergovernmental Panel on Climate Change (IPCC) (2007) *Fourth Assessment Report. Climate Change 2007*. Cambridge University Press, Cambridge, UK.
- Kana, R. and Vass, I. (2008) Thermoimaging as a tool for studying light-induced heating of leaves: Correlation of heat dissipation with the efficiency of photosystem II photochemistry and non-photochemical quenching. *Environmental and Experimental Botany*, 64, 90–96.
- Knepp, R.G., Hamilton, J.G., Zangerl, A.R., Berenbaum, M.R. and DeLucia, E.H. (2007) Foliage of oaks grown under elevated CO₂ reduces performance of *Antheraea polyphemus* (Lepidoptera: Saturniidae). *Environmental Entomology*, 36, 609–617.
- Long, S.P., Ainsworth, E.A., Rogers, A. and Ort, D.R. (2004) Rising atmospheric carbon dioxide: Plants face the future. *Annual Review of Plant Biology*, 55, 591–628.
- Maherali, H. and DeLucia, E.H. (2000) Interactive effects of elevated CO₂ and temperature on water transport in ponderosa pine. *American Journal of Botany*, 87, 243–249.
- McCornack, B.P., Ragsdale, D.W. and Venette, R.C. (2004) Demography of soybean aphid (Homoptera: Aphididae) at summer temperatures. *Journal of Economic Entomology*, 97, 854–861.
- McWilliams, D.A., Berglund, D.R. and Endres, G.J. (2004) *Soybean Growth and Management Quick Guide*. North Dakota State University, Fargo, ND, USA.
- Myers, S.W., Hogg, D.B. and Wedberg, J.L. (2005) Determining the optimal timing of foliar insecticide applications for control of soybean aphid (Hemiptera: Aphididae) on soybean. *Journal of Economic Entomology*, 98, 2006–2012.

- O'Neill, B.F., Zangerl, A.R., DeLucia, E.H. and Berenbaum, M.R. (2008) Longevity and fecundity of Japanese beetle (*Popillia japonica*) on foliage grown under elevated carbon dioxide. *Environmental Entomology*, 37, 601–607.
- O'Neill, B.F., Zangerl, A.R., Dermody, O., Bilgin, D.D., Casteel, C.L., Zavala, J.A., DeLucia, E.H. and Berenbaum, M.R. (2010) Impact of elevated levels of atmospheric CO₂ and herbivory on flavonoids of soybean (*Glycine max* Linnaeus). *Journal of Chemical Ecology*, 36, 35–45.
- Ragsdale, D.W., Voegtlin, D.J. and O'Neill, R.J. (2004) Soybean aphid biology in North America. *Annals of the Entomological Society of America*, 97, 204–208.
- Ragsdale, D.W., McCornack, B.P., Venette, R.C., Potter, B.D., MacRae, I.V., Hodgson, E.W., O'Neal, M.E., Johnson, K.D., O'Neil, R.J., DiFonzo, C.D., Hunt, T.E., Glogoza, P.A. and Cullen, E.M. (2007) Economic threshold for soybean aphid (Hemiptera: Aphididae). *Journal of Economic Entomology*, 100, 1258–1267.
- Reddy, G.V.P., Tossavainen, P., Nerg, A.M. and Holopainen, J.K. (2004) Elevated atmospheric CO₂ affects the chemical quality of *Brassica* plants and the growth rate of the specialist, *Plutella xylostella*, but not the generalist, *Spodoptera littoralis*. *Journal of Agricultural and Food Chemistry*, 52, 4185–4191.
- Venette, R.C. and Ragsdale, D.W. (2004) Assessing the invasion by soybean aphid (Homoptera: Aphididae): Where will it end? *Annals of the Entomological Society of America*, 97, 219–226.
- Wang, C.L., Siang, N.J., Chang, G.S. and Chu, H.F. (1962) Studies on the soybean aphid, *Aphis glycines* Matsumura. *Acta Entomologica Sinica*, 11, 31–44.
- Wille, B.D. and Hartman, G.L. (2009) Two species of symbiotic bacteria present in the soybean aphid (Hemiptera: Aphididae). *Environmental Entomology*, 38, 110–115.
- Xing, G., Zhang, J., Liu, J., Zhang, X., Wang, G. and Wang, Y. (2003) Impacts of atmospheric CO₂ concentrations and soil water on the population dynamics, fecundity and development of the bird cherry-oat aphid *Rhopalosiphum padi*. *Phytoparasitica*, 31, 499–514.

Accepted March 12, 2011