Far Eastern Entomologist

Number 351: 17-26 ISSN 1026-051X February 2018

https://doi.org/10.25221/fee.351.2
http/urn:lsid:zoobank.org:pub:75D36DAF-303B-4C97-9382-B0F9E83E29E1

IMPACT OF ENRICHED CO_2 FUMIGATION EFFECTS ON PLANT-INSECT INTERACTION: FEEDING BEHAVIOUR AND GROWTH OF EARLY AND LATE INSTAR LARVAE OF THE COTTON LEAF WORM *SPODOPTERA LITTORALIS* (LEPIDOPTERA: NOCTUIDAE)

S. A. Abu ElEla*, W. M. ElSayed

Department of Entomology, Faculty of Science, Cairo University, Giza 12513, Egypt.
**Corresponding author, E-mail: shosho_ali76@yahoo.com*

Summary. The effect of enriched CO_2 environments on natural plant-insect herbivore interactions is under attention. To understand such effects on insect growth and consumption, early and late instar larvae of the cotton leaf worm, *Spodoptera littoralis* (Lepidoptera: Noctuidae) reared on the cotton plant leaves *Gossypium barbadens* (Malvacae) grown under either ambient (350 PPM) or high (700 PPM) CO_2 atmospheres. Despite consuming more foliage, the mean larval fresh weight of the early (2nd) and late (4th) instar larvae increased insignificantly with age when fed cotton plant leaves from both ambient and enriched CO_2 regimes. Early and late *Spodoptera littoralis* larvae reared on high CO_2-grown *Gossypium barbadens* consumed 32.87%, 44.98% respectively more foliage than larvae reared on low CO_2-grown cotton plant. Larval duration for early and late larvae reared on high CO_2-grown plants was longer compared with ambient treatments. The Consumption rate (CR) was decreased through the studied instars, with a high significant difference only between the 2nd instars. There was a tendency for ECI and ECD to decrease with age for larvae fed leaves from enriched CO_2 treatment. Differences in growth responses of early and late instar larvae to lower nitrogen and high-CO_2 grown foliage may be due to the inability of early instar larvae to efficiently process the increased flow of food through the gut caused by additional consumption of high CO_2 foliage. Under enriched CO_2 regime cotton plant shoot and root are significantly stimulate length, fresh and dry weights compared with ambient regime.

Key words: *Spodoptera littoralis*, Nutritional indices, *Gossypium barbadens*, CO_2 enrichment, no choice experiment.

С. А. Абу-Эльэля, В. М. Эльсаид. Влияние эффекта обогащенного CO_2 окуривания на взаимодействие растение–насекомое: питание и рост гусениц ранних и поздних возрастов египетской хлопковой совки *Spodoptera littoralis* (Lepidoptera: Noctuidae) // Дальневосточный энтомолог. 2018. N 351. С. 17-26.

Резюме. Обсуждается влияние повышения концентрации углекислого газа на взаимодействие растений и растительноядных насекомых. Для этого гусеницы египетской хлопковой совки *Spodoptera littoralis* (Lepidoptera: Noctuidae) разводились на листьях хлопчатника *Gossypium barbadens* (Malvacae), выращенных в атмосфере CO_2 при низком и высоком давлении (соответственно, 350 и 700 мм. рт. ст.). Гусеницы совки младших и старших возрастов потребляли листьев хлопчатника, выращенного при повышенной концентрации CO_2, на 32.87% и 44.98% соответственно больше, по сравнению с выращенными при нормальном содержании углекислого газа растениями. Развитие гусениц младших и старших возрастов занимало больше времени при потреблении листьев растений, выращенных при повышенном содержании CO_2. Норма потребления пищи (CR) уменьшалась у гусениц с возрастом, причем наиболее значительные различия отмечены у гусениц 2-го возраста. Отличия в росте гусениц ранних и поздних возрастов, питающихся выращенным при разной концентрации CO_2 хлопчатником, вероятно, обусловлено неспособностью гусениц младших возрастов эффективно переваривать листья кормового растения, выращенные при высокой концентрации углекислого газа.

INTRODUCTION

Research on the possible impact of enriched CO_2 has increased as more reliable scenarios for climate change, according to Watt *et al.* (1995) the present atmospheric levels of CO_2 are about 355 ppm to be double its current level by the end of 21st century, as a result of fossil fuel consumption and land-use change (Houghton, 1992; Leakey *et al.*, 2009; Goufo *et al.*, 2014). The rate of change of CO_2 concentration has accelerated with models predicting that the CO_2 concentration will increase to 550 ml L^{-1} by the middle of this century and climb up to 800 ml L^{-1} by the end of this century (Long & Ort, 2010; Feng & Cheng, 2014). Interactions between herbivorous insects and their host plants are expected to be altered significantly as atmospheric CO_2 concentrations continue to rise (Fajer, 1989; Bazzaz, 1990; Lincoln *et al*., 1993). In Egypt, the most important fiber crop is the cotton *Gossypium barbadens* (C3 plant) which have extra arid fibers which belongs to family Malvaceae and because of its economic importance, the phytophagous insect *Spodoptera littoralis* (Lepidoptera: Noctuidae) larvae is considered as a major and injurious pest of cotton in Egypt (Adham *et al.*, 2005a, b). Thus, an important consideration here is that enriched CO_2 will generally increase the C allocations to roots in the cotton plant and the increase in root C will stimulate root growth (Rogers *et al.*, 1992, 1994; Li, 2012). In general, the growth response to enriched CO_2 is greater in C3 species than C4 species (Wand *et al.*, 1999; Lee, 2011). For example, the yield of wheat (C3) increased by 31 % with enriched CO_2 at 500–700 mL L^{-1} in a Free Air CO_2 Enrichment (FACE) facility (Mauney *et al.*, 1994; Amthor, 2001; Jablonski *et al.*, 2002), whereas sorghum (C4) yield was not increased in the same environment (Ottman *et al.*, 2001). Lower foliar N content due to elevated CO2 causes an increase in food consumption by herbivores by up to 40% (Hunter, 2001). Many species of herbivorous insects will confront less nutritious host plants under elevated CO_2, which may induce both lengthened larval developmental times and greater larval mortality (Coviella & Trumble, 1999). Increased levels of CO_2 will enhance plant growth, but may also increase the damage caused by some phytophagous insects (Gregory *et al.*, 2009). However, when plants were exposed to enriched CO_2, the growth rate of the shoots increased together with an increase in the carbon allocation to roots, and this generally increased the root-to-shoot C ratio (Ainsworth *et al.*, 2003; Jin *et al.*, 2012). The main aims of the current study were: i) the prediction that plants grown in enriched CO_2 environments are better able to compensate for biomass lost to herbivores choice behavior than plants grown in ambient CO_2 environments. ii) to determine whether enriched CO_2 should affect the larval feeding preference of a generalist insect, the cotton leaf worm (*Spodoptera littoralis* Boisd.) and iii) whether the larval response including growth and nutritional indices and leaf preference could be explained by the observed changes in the leaf character and morphology.

MATERIALS AND METHODS

Study site and plant materials

The study was conducted at Department of Entomology experimental site, Cairo University, Egypt 30°14′36″ N, 31°12′36.5″ E. The mean weakly maximum and minimum relative humidity ranged between 65-76%, respectively. The mean monthly precipitation was zero and the photoperiod was 14D : 10L. Cotton seeds of *Gossypium barbadens* (Giza 85) obtained from Faculty of Agriculture, Cairo University and were germinated, 5 seeds/4 liter soil, in plastic box containing sand and clay through summer season from May till September during summer season. Fifteen days after germination, plants were randomly divided into 2 treatments, 20 replicate each, one for ambient (control) CO_2 regime (350 ppm) and the other for the enriched treatment (700 ppm).

The first is the ambient CO_2 regime treatment where the plastic pots were placed in the garden of the Department of Entomology, Faculty of Science, Cairo University. A certain distance was observed between successive planting pots to avoid overlapping of green shoot and to reduce mutual shading. A large muslin cloth net was set to cover most of the field area to avoid severe damage to cotton by insect pests specially aphids. The harvested plants were separated into root and shoot organs to measure their lengths. Roots were washed with water to remove soil particles, and then blotted dry to measure the fresh weights.

The experimental design

Saplings of cotton plant pots were placed in a cuboid (80 *l* x 80 *w* x 80 *h* cm) specially designed glass house which was built for enriched CO_2 regime. Natural lightning was ranged from 600 µ $mol^{-2}s^{-1}$ to 2000 µ $mol^{-2}s^{-1}$ was primarily used. Although a white fluorescent Philips® lamps, programmed to maintain a 12D: 12L light regime, added additional light at 1000 $\mu mol^{-2}s^{-1}$ when light levels fell below 600 $\mu mol^{-2}s^{-1}$ (Carlson & Bazzaz, 1980), The temperature inside the glass house ranged between (35-38 °C) and it was controlled automatically by a thermostat using a Traceable® Digital Thermometer (± 1 °C accuracy, 1 digit resolution). Relative humidity fluctuate between 70-85 %, CO_2 cylinders were used as a source of CO_2 to maintain the concentration inside the glass house at 700 ppm. The flow rate of inlet air stream of CO_2 was 0.1 l/min. no natural or artificial fertilizers were added to the soil. Growing cotton plants were watered with tap water every 3 days and rotated within the glass house within CO_2 treatment every week in order to minimize pseudo-replication and glass houses effects. Cotton plant leaves were obtained from 45-75 day old cotton plants from both ambient (350 ppm) (control) and enriched (700 ppm) CO_2 regimes and supplied daily to the larvae during feeding experiments.

Monitoring of herbivore consumption

Newly 2nd and penultimate 4th instar larvae of *S. littoralis* were used to form colonies. Each CO_2 treatment had 5 replicates of 10 larvae/ plastic box (12 *w* x 6 *h* x 18 *l* cm) and each replicate was treated as a single unit. Larval crowding was avoided since it may affect the rates of feeding and growth. Clear and fresh cotton leaves from the two CO_2 regimes were supplied every 24 hr. to the larvae. Uneaten leaves were removed and newly fresh ones were provided. The initial weight of the leaves offered to the larvae was measured. The tested 2nd (early) and 4th (late) instar larvae in each replicate were weighed daily as a group. The initial and final fresh weights, fresh weight of feces, fresh weight of food ingested and the weight gained were determined by using Mettler® analytical digital balance. The nutritional indices served as a means to detect more subtle effects in terms of larval feeding and food conversion to biomass. No choice experiments were performed to determine consumption and food utilization, the consumption rate (CR) and the efficiency of conversion of ingested food to body substance (ECI), the efficiency of conversion of digested food to body substance (ECD) and the approximate digestibility of food (AD) were determined. Whereas the (ECI) is an overall measure of an insect's ability to utilize the food ingested for growth. ECI varies with both the digestibility of the food and the proportion of digestible food that is converted to body substance and energy. The ECD provides more information about the use of food for energy. The AD finally provides information about the digestibility of the food offered (Waldbauer, 1968). Exuviae were measured with faeces since they are not a part of the insect at the end of the experiment (Reese & Beck, 1976).

Statistical analysis

Data were analyzed using one way analysis of variance (ANOVA) and Duncan's multiple range test and were presented as mean ± SE. Statistical computations were performed using SAS program (Anonymous, 2000).

RESULTS AND DISCUSSION

Growth responses of early and late instar larvae

Data presented in Table 1 showed that the mean larval fresh weight of the early (2^{nd}) and late (4^{th}) instar larvae increased insignificantly with age when fed cotton leaves cotton plant leaves from both ambient and enriched CO_2 regimes. The mean fresh weight of the 2^{nd} instar larvae was 26.67% ($P < 0.05$) lower than that of larvae fed cotton leaves at ambient CO_2 treatment. However, fresh weight of the late (4^{th}) instar larvae was higher by 15.6% when fed cotton leaves grown under enriched CO_2 treatment compared with ambient treatment (Table 1).

Early and late instar *S. littoralis* larvae reared on high CO_2-grown *Gossypium barbadens* consumed 32.87%, 44.98% respectively more foliage than larvae reared on low CO_2-grown cotton plant (Table 1).

Despite insignificant difference in larval duration between ambient and enriched CO_2 treatments, larval duration for early and late larvae reared on high CO_2-grown plants was longer compared with ambient treatments (Table 1). Plant quality are important in understanding plant-insect herbivore interactions under enriched CO_2 environments because insect feeding and growth are a function of both the variation in nutrition between plants and the variation in response to plant quality by insects. Fajer (1989) stated that foliar nitrogen concentrations probably responsible for the changes in the feeding behavior of the early and late instar buckeye larvae reared on high CO_2-grown foliage and "high quality" food may be even less available under enriched CO_2 environment. Although late *S. littoralis* larvae consumed additional high CO_2-grown leaves, they showed slower growth with longer larval duration (Table 1). Reduced growth of late instar larvae on a high CO_2-grown diet probably resulted from their inability to fully compensate for the diet's reduced nitrogen; they were forced to metabolize food at higher flow rates, such as when they consumed additional high CO grown foliage, they could not process enough food effectively to compensate for lower nitrogen concentrations (Rogers *et al.*, 1994; Davis & Potter, 1989).

Table 1. Growth response of the 2nd and 4th instar larvae of cotton leaf worm *Spodoptera littoralis* fed cotton plant leaves grown under ambient (350 ppm) and enriched (700 ppm) CO_2 regimes

Treatment (ppm) / Larval instar	CO_2 Regime (Mean ± SE)		P value*
	Ambient (350 ppm)	Enriched (700 ppm)	
2nd instar			
Duration (days)	4 ± 0.158^{a}	4.05 ± 0.166^{a}	N
Fresh weight (gm)	0.033 ± 0.002^{a}	0.045 ± 0.004^{b}	S
Weight gain (gm)	0.041 ± 0.003^{a}	0.044 ± 0.006^{a}	N
Fresh weight of feces (gm)	0.008 ± 0.001^{a}	0.009 ± 0.001^{a}	N
Fresh weight of food ingested (gm)	0.073 ± 0.001^{a}	0.049 ± 0.002^{b}	HS
4th instar			
Duration (days)	4.4 ± 0.187^{a}	4.8 ± 0.2^{a}	N
Fresh weight (gm)	0.891 ± 0.103^{a}	0.771 ± 0.101^{a}	N
Weight gain (gm)	0.913 ± 0.126^{a}	0.771 ± 0.095^{a}	N
Fresh weight of feces (gm)	0.364 ± 0.013^{a}	0.207 ± 0.012^{b}	HS
Fresh weight of food ingested (gm)	1.296 ± 0.092^{a}	0.713 ± 0.156^{b}	HS

* HS – highly significant ($P < 0.01$); S – significant ($P < 0.05$); N – insignificant ($P \geq 0.05$).

Table 2. Nutritional indices of the early (2nd) and late (4th) instar larvae of the cotton leaf worm *Spodoptera littoralis* fed cotton plant leaves from ambient and enriched regimes in no-choice feeding assays

Treatment (ppm) / Larval instar	CO_2 Regime (Mean ± SE)		P value*
	Ambient (350 ppm)	Enriched (700 ppm)	
2nd instar			
CR (mg/ day)	0.559 ± 0.045^{a}	0.283 ± 0.03^{b}	HS
GR(mg /day)	0.312 ± 0.005^{a}	0.244 ± 0.011^{b}	S
ECI (%)	56.154 ± 4.712^{a}	90.965 ± 9.696^{b}	HS
ECD(%)	63.571 ± 4.801^{a}	112.646 ± 8.834^{b}	HS
AD(%	89.886 ± 0.872^{a}	81.687 ± 1.053^{a}	N
4th instar			
CR (mg /day)	0.344 ± 0.033^{a}	0.256 ± 0.03^{a}	N
GR(mg/ day)	0.232 ± 0.004^{a}	0.202 ± 0.009^{b}	N
ECI(%)	70.334 ± 8.145^{a}	85.76 ± 8.214^{a}	S
ECD(%)	98.697 ± 11.495^{a}	112.151 ± 9.625^{a}	S
AD(%)	71.545 ± 1.896^{a}	76.4 ± 2.487^{a}	N

* HS – highly significant ($P < 0.01$); S – significant ($P < 0.05$); N – insignificant ($P \geq 0.05$).

Table 3. Growth criteria of cotton plant shoot *Gossypium barbadens* (Malvaveae) grown under ambient (350 ppm) and enriched (700 ppm) CO_2 regimes

Treatment (ppm) / Time of Harvest (days)	CO_2 Regime (Mean ± SE)		P value*
	Ambient (350 ppm)	Enriched (700 ppm)	
Shoot length (cm)			
15	9.133 ± 0.318^{a}	13.8 ± 0.173^{b}	HS
30	14.233 ± 0.549^{a}	22.66 ± 1.244^{b}	S
45	27.933 ± 0.821^{a}	35.133 ± 0.809^{b}	S
60	37.767 ± 0.636^{a}	47.567 ± 0.968^{b}	HS
75	43.966 ± 1.651^{a}	67.233 ± 2.794^{b}	HS
Shoot fresh weight (gm)			
15	2.311 ± 0.059^{a}	4.633 ± 0.101^{b}	HS
30	8.25 ± 0.561^{a}	11.303 ± 0.712^{b}	S
45	39.052 ± 3.517^{a}	62.976 ± 5.402^{b}	HS
60	72.904 ± 3.281^{a}	110.656 ± 9.425^{b}	S
75	194.949 ± 5.67^{a}	279.279 ± 8.79^{b}	HS
Shoot dry weight (gm)			
15	0.226 ± 0.003^{a}	0.709 ± 0.027^{b}	HS
30	1.661 ± 0.084^{a}	2.136 ± 0.138^{b}	S
45	8.771 ± 0.416^{a}	12.871 ± 0.987^{b}	S
60	17.183 ± 0.936^{a}	22.634 ± 2.445^{a}	S
75	35.588 ± 1.328^{a}	59.254 ± 2.758^{b}	HS

***** HS – highly significant ($P < 0.01$); S – significant ($P < 0.05$).

Larval performance and nutritional indices

The consumption rate (CR) of 2nd and 4th instar larvae were significantly ($P < 0.05$) lower than those reared on ambient CO_2 treated leaves and consumed, on average, an additional 49.4%, 25.6% respectively. Growth rates (GR) of 4th instar larvae were lower when fed foliage from the two CO_2 regimes (Table 2). Reduced larval growth rates, such as those induced by the high CO_2-grown diets in this study, may prevent larvae from completing development in climatically limited environments with short growing seasons (Watt *et al.*, 1995; Davis & Potter, 1989). Reduced growth rates of the larvae fed enriched CO_2-grown leaves may also increase their exposure to predators and parasitoids (Ottman *et al.*, 2001; Carlson & Bazzaz, 1980; Davis & Potter, 1989).

From the results obtained it appeared that there was a tendency for food conversion efficiency (ECI and ECI) to decrease with age for larvae fed leaves from enriched CO_2 treatment. Our result was confirmed with that of Lindroth *et al.* (1993) in which they stated that low efficiency of conversion of digested food may result from a requirement of these insects to metabolize digested food in order to produce water. In contrast with early instar larvae insignificant differences in (ECI) and (ECD) were observed when 4th instar larvae fed foliage from the two CO_2 regimes. Other nutritional indices, approximate digestibility (AD), decreased insignificantly with age for both early and late instars fed cotton plant leaves from ambient and enriched CO_2 regimes (Table 2).

Table 4. Growth criteria of cotton plant root *Gossypium barbadens* (Malvaveae) grown under ambient (350 ppm) and enriched (700 ppm) CO_2 regimes

Treatment (ppm) / Time of Harvest (days)	CO_2 Regime (Mean ± SE)		P value*
	Ambient (350 ppm)	Enriched (700 ppm)	
Root length (cm)			
15	5.7 ± 0.451^{a}	7.233 ± 0.921^{a}	N
30	6.766 ± 0.669^{a}	11.133 ± 0.088^{b}	HS
45	7.267 ± 0.895^{a}	15.033 ± 1.615^{b}	S
60	12.233 ± 0.677^{a}	18.667 ± 1.424^{b}	S
75	16.966 ± 0.705^{a}	23.833 ± 0.727^{b}	HS
Root fresh weight (gm)			
15	0.357 ± 0.026^{a}	0.397 ± 0.016^{a}	N
30	0.9 ± 0.023^{a}	1.429 ± 0.089^{b}	S
45	4.612 ± 0.506^{a}	8.018 ± 0.943^{b}	S
60	9.393 ± 0.255^{a}	14.678 ± 0.741^{b}	HS
75	23.002 ± 0.963^{a}	40.776 ± 2.245^{b}	HS
Root dry weight (gm)			
15	0.038 ± 0.002^{a}	0.055 ± 0.002^{b}	HS
30	0.181 ± 0.01^{a}	0.312 ± 0.03^{b}	S
45	0.705 ± 0.039^{a}	1.727 ± 0.134^{b}	HS
60	1.924 ± 0.035^{a}	3.76 ± 0.145^{b}	HS
75	5.114 ± 0.4^{a}	11.112 ± 0.989^{b}	HS

***** HS – highly significant ($P < 0.01$); S – significant ($P < 0.05$); N – insignificant ($P \geq 0.05$).

Previous studies confirmed that most leaf-chewing insects exhibit compensatory increase in food consumption (Lee, 2011). Insects, when fed on elevated CO2 grown plants, were shown to increase their individual consumption due to the poor food quality of these plants (Coviella & Trumble, 1999; Houghton *et al.*, 1992).

Shoot and Root morphology traits under enriched CO_2

Treatment with enriched CO_2 regime caused a significant stimulation in the cotton plant shoot and root, which showed a rapid growth and significant increase with age from day 15 until day 75 in length , fresh and dry weights compared with that of ambient CO_2 (Tables 3, 4). These results are confirmed with that of Stitt & Krapp (1999) who stated that the photo-synthesis and growth of many plants are stimulated when plants are grown under elevated CO_2 condition and reduction in leaf N content in plants grown at elevated CO_2, due to faster growth of the plant. This leads to greater root and shoot dry weight and greater root length (Coviella *et al.*, 2000; Jin *et al.*, 2012) and occasionally to improved yields (Ainsworth *et al.*, 2003; Stitt & Krapp, 1999; Mauney *et al.*, 1994). Increased photosynthesis rates can result in more biomass accumulation and the potential compensatory response to insect feeding depend strongly on the availability of nutrients for plant growth (Williams *et al.*, 1981; Johnson & Lincoln, 1990; Mitchell *et al.*, 1993; Adham *et al.*, 2005b; Mauney *et al.*, 1994;

Sudderth *et al.*, 2005). Plants grown in enriched CO_2 environments had significantly greater shoot weights, leaf areas, and root weights, than plants grown in ambient CO_2 environments (Fajer, 1989). Increase in atmospheric levels of CO_2 can cause increases in plant growth rates, and changes in the physical and chemical composition of their tissues (Stockle, 1992).

REFERENCES

Adham F.K., Gabre, R.M., Abu El-Ela, S.A. & Hassan, M.M. 2005a. Growth and feeding efficiency of cotton leaf worm *Spodoptera littoralis* (Boisd.) (Lepidoptera: Noctuidae) on cotton plant *Gossypium barbadens* (Malvaceae) grown in enriched CO_2 atmosphere. *Bulletin of Entomological Society of Egypt*, 82: 187–196.

Adham F. K., Gabre, R.M. & Abu El-Ela, S.A. 2005b. The performance parameters of *Spodoptera littoralis* (Boisd.) (Lepidoptera: Noctuidae) fed on cotton leaves grown in enriched CO_2 atmosphere. *Bulletin of Entomological Society of Egypt*, 82: 197–205.

Ahmed, F.E., Hall, A.E. &Madore, M.A. 1993. Interactive effects of high temperature and elevated carbon dioxide concentration on cowpea [*Vigna unguiculata* (L.) Walp.]. *Plant Cell and Environment*, 16: 835–842.

Ainsworth, E.A., Rogers, A., Blum, H., Nösberger, J. & Long, S.P. 2003. Variation in acclimation of photosynthesis in Trifolium repens after eight years of exposure to Free Air CO_2 Enrichment (FACE). *Journal of Experimental Botany*, 393: 2769–2774.

Allen, L.H. Jr., Bisbal, E.C., Boote, K.J. & Jones, P.H. 1991. Soybean dry matter allocation under subambient and superambient levels of carbon dioxide. *Agronomy Journal*, 83: 875–883.

Amthor, J.S. 2001. Effects of atmospheric CO_2 concentration on wheat yield: review of results from experiments using various approaches to control CO_2 concentration. *Field Crops Research*, 73: 1–34.

Anonymous. 2000. SAS program version release 6.12 (SAS institute Incorporation, Cary, New York).

Bazzaz, F.A. 1990. The response of natural ecosystems to the rising global carbon dioxide levels. *Annual Review of Ecology and Systematics*, 21: 167–196.

Carlson, R.W. & Bazzaz, F.A. 1980. The effects of elevated CO_2 concentration on growth, hotosynthesis, transpiration and water efficiency of plants. In: Singh, J.J. & Deepark, A. (Eds.). *Environmental and climatic impact of coal utilization*. New York.

Clancy, K.M. & Price, P.W. 1987. Rapid herbivore growth enhances enemy attack: sublethal plant defenses remain a paradox. *Ecology*, 68: 736–738.

Coviella, C.E. & Trumble, J.T. 1999. Effects of elevated atmospheric carbon dioxide on insect-plant interactions. *Conservation Biology*, 13: 700–712.

Coviella, C.E., Stipanovic, R.D. & Trumble, J.T. 2000. Plant allocation to defensive compounds: interactions between elevated CO_2 and nitrogen in transgenic cotton plants. *Journal of Experimental Botany*, 53(367): 323–331.

Davis, T.D. & Potter, J.R. 1989. Relations between carbohydrate, water status and adventitious root formation in leafy pea cuttings rooted under various levels of atmospheric CO_2 and relative humidity. *Physiologia Plantarum*, 77(2): 185–90.

Fajer, E.D. 1989. The effects of enriched carbon dioxide atmospheres on plant-insect herbivore interactions: growth responses of larvae of the specialist butterfly, *Junonia coenia* (Lepidoptera: Nymphalidae). *Oecologia* (Berlin), 81: 514–520.

Fajer, E.D., Bowers, M.D. & Bazzaz, F.A. 1991. The effects of enriched CO_2 atmospheres on the buckeye butterfly *Junonia coenia*. *Ecology*. 72: 751–754.

Feng, G.Q., Li Y., & Cheng, Z.M. 2014. Plant molecular and genomic responses to stresses in projected future CO_2 environment. *Critical Reviews in Plant Sciences*, 33: 238–249.
Goufo, P., Pereira, J., Moutinho-Pereira, J., Correia, C.M., Figueiredoc, N., Carrancac, C., Rosaa, E.A.S.& Trindadea, H. 2014. Rice (*Oryza sativa* L.) phenolic compounds under elevated carbon dioxide (CO_2) concentration. *Environmental and Experimental Botany*, 99: 28–37.
Gregory, P.J., Johnson, S.N., Newton, A.C. & Ingram, J.S.I. 2009. Integrating pests and pathogens into the climate change/food security debate. *Journal of Experimental Botany*, 60: 2827–2838.
Houghton, J.T., Callander, B.A. & Varney, S.K. 1992. *Climate change 1992. The supplementary report to the intergovernmental panel on climate change scientific assessment.* Cambridge University Press, Cambridge, United Kingdom.
Hunter, M.D. 2001. Effects of elevated atmospheric carbon dioxide on insect-plant interactions. *Agricultural Forest Entomology*, 3: 153–159.
Jablonski, L.M., Wang, X.Z. & Curtis, P.S. 2002. Plant reproduction under elevated CO_2 conditions: a meta-analysis of reports on 79 crop and wild species. *New Phytologist*, 156: 9–26.
Jin, J., Tang, C., Armstrong, R. & Sale, P. 2012. Phosphorus supply enhances the response of legumes to elevated CO_2 (FACE) in a phosphorus-deficient Vertisol. *Plant and Soil*, 358: 91–104.
Johnson, R.H. & Lincoln, D.E. 1990. Sagebrush and grasshopper responses to atmospheric carbon dioxide concentration. *Oecologia*, 84: 103–110.
Lawler, I R., Foley, W J., Woodrow, I E. & Cork, S.J. 1997. The effects of elevated CO_2 atmospheres on the nutritional quality of Eucalyptus foliage and its interaction with soil nutrient and light availability. *Oecologia,* 109:59–68.
Leakey, A D B., Ainsworth, E A., Bernacchi, C J., Rogers, A., Long, S P. , Ort, D.R. 2009. Elevated CO_2 effects on plant carbon, nitrogen, and water six important lessons from FACE. *Journal of Experimental Botany*, 60: 2859–2876.
Lee, J.S. 2011. Combined effect of elevated CO_2 and temperature on the growth and phenology of two annual C3 and C4 weedy species. Agriculture, *Ecosystems and Environment*, 140: 484–191.
Lee, K.,P., Behmer, S.T., Simpson, S.J. & Raubenheimer, D. 2002. A geometric analysis of nutrient regulation in the generalist caterpillar *Spodoptera littoralis* (Boisduval). *Journal of Insect Physiology*, 48: 655–665.
Li, T., Di, Z., Han, X., & Yang, X. 2012. Elevated CO_2 improves root growth and cadmium accumulation in the hypheraccumulator *Sedum alfredii*. *Plant and Soil*, 354: 325–334.
Lindroth, R.L., Kinney, K.K. & Platz, C.L. 1993. Responses of deciduous trees to elevated atmospheric CO2: Productivity, phytochemistry, and insect performance. *Ecology*, 74: 763–777
Lincoln, D.E., Fajer, E.D. & Johnson, R.H. 1993. Plant insect herbivore interactions in elevated CO_2 environments. *Trends in Ecology and Evolution*, 8: 64–68.
Long, S.P. & Ort, D.R. 2010. More than taking the heat: crops and global change. *Current Opinion in Plant Biology*, 13: 241–248.
Mauney, J.R., Kimball, B.A. & Pinter, P.J. 1994. Growth and yield of cotton in response to a free-air carbon-dioxide enrichment (FACE) environment. *Agricultural and Forest Meteorology*, 70: 49–67.
Mitchell, R.A. C., Mitchell, V.J., Dirscoll, S.P., Franklin, J. & Lawlor, D.W. 1993. Effects of increased carbon dioxide concentration and temperature on growth and yield of winter wheat at two levels of nitrogen application. *Plant Cell and Environment*, 16: 521–529.

Osbrink, W.L.A., Trumble, J.T. & Wagner, R.E. 1987. Host suitability of *Phaseolus lunatus* for *Trichoplusia ni* (Lepidoptera: Noctuidae) in controlled carbon dioxide atmospheres. *Environmental Entomology*, 16: 639–644.

Ottman, M.J., Kimball, B.A. & Pinter, P.J. 2001. Elevated CO_2 increases sorghum biomass under drought conditions. *New Phytologist*, 150: 261–273.

Price, P.W., Bouton, C.E., Gross, P., McPheron, B.A., Thompson, J.N. & Weis, A.E. 1980. Interactions Among Three Trophic Levels: Influence of Plants on Interactions Between Insect Herbivores and Natural Enemies. *Annual Review of Ecology and Systematics*, 11: 41–65.

Reese, J.C. & Beck, S.D. 1976. Effects of allelochemics on the black cut worm, *Agrotis ispilon*, effects of P-benzoquinone, hydroquinone, and duroquinone on larval growth, development, and utilization of food. *Annals of Entomological Society of America*, 69: 59–67.

Rogers, H.H., Prior, S.A. & Oneill, E.G. 1992. Cotton root and rhizosphere responses to free-air CO_2 enrichment. *Critical Reviews in Plant Sciences*, 11: 251–263.

Rogers, H.H., Runion, G.B. & Krupa, S.V. 1994. Plant responses to atmospheric CO_2 enrichment with emphasis on roots and the rhizosphere. *Environmental Pollution*, 83: 155–189.

Slansky, F. & Scriber, J.M. 1985. *Food consumption and utilization. Comprehensive insect Physiology, Biochemistry, and Pharmacology*. Kerkut, G.A. Gilbert, L.I. (eds.). Pergamon Press, Oxford.

Stitt, M. & Krapp, A. 1999. The interaction between elevated CO_2 and nitrogen nutrition: The physiological and molecular background. *Plant, Cell and Environment*, 22: 583–621.

Stockle, C.O., Williams, J.R., Rosenberg, N.J. & Jones, C.A. 1992. A method for estimating the direct and climatic effects of rising atmospheric carbon dioxide on growth and yield of crops. Part 1. Modification of the EPIC model for climate change analysis. *Agricultural Systems*, 38: 225–238.

Sudderth, E.A., Stinson, K.A. & Bazzaz, F.A. 2005. Host-specific aphid population responses to elevated CO_2 and increased N availability. *Global Change Biology*, 11: 1997–2008.

Trumble, J.T., Kolodny-Hirsch, D.M. & Ting, I.P. 1993. Plant compensation for arthropod herbivory. *Annual Review of Entomology*, 38: 93–119.

Waldbauer, G.P. 1968. The consumption and utilization of food by insects. *Advances in Insect Physiology*, 5: 229–288.

Wand, S.J.E., Midgley, G.F., Jones, M.H. & Curtis, P.S. 1999. Responses of wild C4 and C3 grass (Poaceae) species to elevated atmospheric CO_2 concentration: a meta-analytic test of current theories and perceptions. *Global Change Biology*, 5: 723–741.

Watt, A.D., Whittaker, J.B., Docherty, M., Brooks, G., Lindsay, E. & Salt, D.T. 1995. *The impact of elevated atmospheric CO_2 on insect herbivores*. P. 197–217. In: Harrington, R. & Stork, M.E. (eds.). *Insects in a changing environment*. Academic Press, San Diego, California.

Williams, L.E., Dejong, T.M. & Philips, D.A. 1981. Carbon and Nitrogen Limitations on Soybean Seedling Development. *Plant Physiology*, 68: 1206–1209.

Yelle, S., Beeson Jr., R.C., Trudel, M.J. & Gosselin, A. 1989. Acclimation of two tomato species to high atmospheric carbon dioxide. I. Sugar and starch concentrations. *Plant Physiology*, 90: 1465–1472.