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Cover: Watercolour illustrations—Striped Tiger *Danaus genutia*, Common Silverline *Cigaritis vulcanus*, Tamil Lacewing *Cethosia mahratta*. © Mayur Nandikar.

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COMMUNICATION

A short-term impact of enriched CO_2 [eCO_2] on select growth performance of *Spodoptera littoralis* (Boisd.) (Lepidoptera: Noctuidae) and its host plant *Gossypium barbadense* L. (Malvaceae)

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Abstract: Natural interactions between herbivorous insect pests and their host plants are expected to be altered significantly as atmospheric CO_2 concentrations (aCO_2) continue to rise according to climate change scenario. The possible effect of enriched CO_2 (eCO_2) environments on these interactions is under attention. To better understand such effects on select insect growth parameters; early (3rd) and penultimate (6th) instar larvae of the Cotton Leaf Worm *Spodoptera littoralis* (Boisd.) (Lepidoptera: Noctuidae), reared on the cotton plant leaves *Gossypium barbadense* L. (Malvacae) grown under either ambient (aCO_2 = 350 ppm) or enriched (eCO_2 = 700 ppm) atmospheres were investigated.

Keywords: Ambient CO_2, CO_2-enriched atmosphere, growth parameters.

Japanese: 気候変動シナリオに従って大気中の二酸化炭素濃度（aCO_2）が上昇するにつれて、草食性害虫と被食植物の間の自然な相互作用は大きく変化すると予測されます。高濃度のCO_2（eCO_2）環境がこれらの相互作用に及ぼす影響が注目されています。そのような効果が昆虫の成長に与える影響を調べるために、鱗翅目ヤガ科の*Spodoptera littlralis*（Boisd）の初期幼虫（3齢）と終齢幼虫（6齢）を、通常の二酸化炭素濃度（aCO_2=350ppm）条件下と高濃度の二酸化炭素濃度（eCO_2=700ppm）で栽培した綿植物*Gossypium barbadense* L.（ アオイ科）で飼育して、成長を比較しました。

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Author contributions: All the authors contributed in the field study; AA Shahenda conceived and designed the study; AA conducted the measurements and collected the data; AA Shahenda and ElSayed M. Wael wrote the manuscript draft; ElSayed Wael conducted statistical analysis, reviewed and edited the manuscript drafts; all authors approved the final draft and contributed significantly.

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INTRODUCTION

The ever-increasing combustion of fossil fuels, such as energy generation in coal-fired power plants, cement plants, oil refineries, and land-use changes has contributed towards the increase of atmospheric CO_2 concentration (aCO_2) (Houghton et al. 1992; Leakey et al. 2009; Goufo et al. 2014). The aCO_2 level has gone from the pre-industrial value of 280 ppm to a current level of 418 ppm (December 2022) where a high aCO_2 concentration is a big risk to human health, for example, it can trigger respiratory illnesses when the aCO_2 concentration is over 600 ppm (NOAA 2022; Åhlén et al. 2023).

The rate of change of aCO_2 levels has accelerated with models predicting that by the middle of this century; the aCO_2 levels will escalate to 550 ml L^{-1} and expected to rise to about 800 ml L^{-1} by the end of this century (Long & Ort 2010; Feng & Cheng 2014).

Increasing amount of CO_2 in the atmosphere affects the global climate temperature, which can have an adverse effect on all life forms on this planet (Bazzaz 1990; Abu ElELa & ElSayed 2018; Ashok et al. 2022). Thus, numerous studies have focused on understanding the CO_2 effects on various aspects of plant growth, productivity, and survival in crops. Only a few studies have dealt with the nutritional quality of food crops and even fewer studies on the health-promoting phytochemicals in food crops (Rajashekar 2018).

Little is known about the effects of the eCO_2 environments, which are anticipated to exist in the next century, on natural plant-insect herbivore interactions. Because of the crucial role of CO_2 in photosynthesis, the expected increase in global aCO_2 levels will exert a significant influence on the biological systems.

Climate change has a marked impact on the biology and population ecology of insect pests with direct impact on the physiology and behavior of the insect (Berrigan 2000). Insect life cycle is influenced by climate, this includes total duration of life span, fecundity, mortality, and genetic adaptation (Helmuth et al. 2002; Hoffmann et al. 2003; Stillman 2003; Abu ElEla & ElSayed 2018). Moreover, the indirect effects could be observed through the impact on host plant, parasitoids, and predators of insect pests (Manimanjari & Rao 2022). In addition to this, eCO_2 will affect the quality of foliage and in turn influence the potential herbivorous behavior of the insect pest.

Often, plant species grown in eCO_2 environments have a higher foliar water content than those grown under aCO_2 conditions (Wong 1979; Fajer et al. 1991; Lincoln et al. 1993), potentially enhancing insect herbivore performance (Scriber 1977, 1979). However, plant species reared in eCO_2 environments also showed comparatively reduced nitrogen concentrations in leaves (Wong 1979; Williams et al. 1981; Fajer et al. 1991; Lincoln et al. 1993).

Studies dealing with lepidopteran larvae have revealed that insect herbivores consistently respond to changes in plant foliar quality induced by eCO_2 environments by consuming more foliage (Osbrink et al. 1987; Johnson & Lincoln 1990; Fajer et al. 1991, Abu ElEla & ElSayed 2018). It is assumed that insects consume more foliage to compensate for reduced foliar nitrogen concentrations (Slansky & Feeny 1977). Some species showed a lower rate of larval development or even incomplete development of larvae; decreased fecundity , and increased mortality (Osbrink et al. 1987; Fajer 1989; Fajer et al. 1991).

In Egypt, one of the most important fiber crops is the cotton, *Gossypium barbadense* L. (Malvaceae), and because of its economic importance; the phytophagous insect *Spodoptera littoralis* (Boisd.) (Lepidoptera: Noctuidae) larva is considered as one of the major and injurious noctuid predator of cotton in Egypt (Abu ElEla & ElSayed 2018).

Laboratory feeding studies and growth chamber experiments have provided useful information about the responses of insect herbivores to specific foliage or plant species grown under aCO_2 and eCO_2 conditions (Caulfield & Bunce 1994; Abu ElEla & El Sayed 2018; Rao et al. 2012; Manimanjari & Rao 2022).

Indeed, there is a shortage of knowledge and the information pertaining to the possible influence of eCO_2 regime on natural interactions between the noctuid pest, *S. littoralis* (Boisd.), and its host plants especially those of economic importance (such as *G. barbadense* L.) are fragmentary. Thus, the aim of this research work is to focus some light on some select biological and life cycle parameters of *S. littoralis* (Boisd.) fed with cotton plant leaves, *G. barbadense* L. var. Super Giza 85, grown under both aCO_2 (350 ppm) & eCO_2 (700 ppm).

MATERIALS AND METHODS

The study was conducted at the Laboratory of Applied Entomology, Cairo University, Egypt. Cotton seeds of *Gossypium barbadense* L. (var. Super Giza 85) were obtained from Seeds Bank at the Ministry of Agriculture, Cairo, Egypt. Five seeds/4-liter soil were germinated in plastic pots containing sand & clay through summer season from May to September and were irrigated regularly by tap water. These pots were placed inside designated cuboid open top chambers (80 *l* x 80 *w* x 80 *h* cm). Natural lighting, ranging from 600 µ mol-2s^{-1} to 2,000 µ mol-2s^{-1}, was primarily used. Although white fluorescent Philips® lamps, automatically programmed were used to maintain a 12D: 12L light regime, added additional light at 1,000 µmol-2s^{-1} were used when light levels fell below 600 µmol-2s^{-1} (Carlson & Bazzaz 1980). These chambers containing the *G. barbadense* L. var. Super Giza saplings were exposed to aCO_2 (350 ppm) and eCO_2 (700ppm) regimes. Plants were grown for 30 days before offering the foliage as a diet for the experimental insect.

Leaf nutritional quality

Leaf nutritional quality was measured at 30 days and 45 days by chemical analyses of contents for total nitrogen, total carbohydrates, and phenolic compounds. Chemical analysis was done for total amino acids according to the method described by Russell (1944), total carbohydrates according to Streeter & Jeffers (1979), and total phenolic compounds according to the method by Jindal & Singh (1975).

Growth conditions of *S. littoralis* (Boisd.)

Eggs were obtained from the females of *S. littoralis* (Boisd.) reared from standard laboratory colony maintained at the Department of Entomology, Cairo University since 2000s. Two groups of 50 eggs were placed in plastic petridishes (Ø 14 cm) with moist paper towel strips taped to the lid to maintain suitable air humidity. One group of hatched larvae was offered cotton plant leaves grown in aCO_2 regime while the other group was fed on leaves grown in eCO_2 regime.

Hatched larvae were kept in growth chambers with a 14 h day: 10 h night light regime and 25°C day: 20°C night temperature regime. Fresh leaves were provided every other day. Each CO_2 treatment had 20 replicates of 10 larvae per petridish. Larvae were reared & fed from the 1st instar till last instar and ceased feeding as they reached prepupal stage.

The 3rd (hereafter considered as the early instar) and the 6th (considered as the penultimate instar) (Image 1) were used as main larval instars in this experiment due to their potential herbivory (ElEla & ElSayed 2018). Usually, *S. littoralis* (Boisd.) shows six larval instars, however, we treated the 3rd larval instar as an early instar since the 1st and 2nd instars showed less herbivory attitude to cotton leaves (personal observations) and only nibbling of soft leaves could be observed. Also, the 6th instar showed strong voracious tendency to consume leaves until reaching the prepupal stage which showed unambiguous cessation of feeding.

The number and average fresh weights of newly formed prepupae were recorded. The prepupae were then placed in sieved, sterilized, and moistened wood dust to proceed in forming the pupal cases. Percentage pupation and mean pupal duration were recorded. By the emergence of adults, number of emerged adults, longevity, and sex ratio were recorded. The freshly emerged adults were fed on 10% sugary solution (sucrose solution) and were offered small fresh twigs bearing leaves of *Nerium oleander* L. to serve as ovipositional sites for adult females.

Statistical analysis

The effects of CO_2 regimes on the select larval parameters were evaluated by one-way Analysis of Variance (ANOVA). The differences between the mean values of treatments were determined by Duncan's multiple range test. Treatment means were compared and separated using least significant difference (LSD) at $p < 0.05$. All statistical analyses were computed by using SPSS version 16.0.

RESULTS AND DISCUSSION

Data depicted in Table 1 revealed insignificant difference ($p > 0.05$) between mean larval duration for the 3rd and 6th larval instars fed cotton plant leaves grown under aCO_2 and eCO_2 regimes. In general, the larval duration for either 3rd (early) and 6th (penultimate) larval instars were slightly greater for those fed cotton leaves grown in eCO_2 regime. However, significant difference ($p < 0.05$) in the percentage larval survival was observed between the two regimes (Table 1). The percentage larval survival was greater for larvae fed aCO_2 grown cotton leaves compared to those fed enriched-grown leaves (Table 1). It was clear that relatively greater number of larvae fed aCO_2 could successfully complete the larval duration when compared to those fed eCO_2-grown cotton leaves. Also, it seemed that larval mortality could be related to the nutritional deficiency that resulted from reduced foliar nitrogen levels in eCO_2 grown plants (Brooks & Whittaker 1999; Abu ElEla & ElSayed 2018).

Although we found that penultimate *S. littoralis* (Boisd.) larvae consumed additional eCO_2-grown cotton leaves (based on personal observations), they showed relatively slower growth rate with longer larval duration (Table 1). Moreover, these penultimate larvae produce

Table 1. Select parameters of larval stages of *Spodoptera littoralis* (Boisd.) fed the leaves of *Gossypium barbadense* L. grown in ambient (aCO2 = 350 ppm) and enriched (eCO2 = 700 ppm) CO2 regimes.
*** Results followed by different letters are significantly different (p <0.05)**

Insect parameters	CO_2 treatment	
	aCO_2 (350 ppm)	eCO_2 (700 ppm)
Larval stage		
Larval duration (day)		
3rd instar (early)	3.6 ± 0.116^{a*}	3.83 ± 0.27^{a}
6th instar (penultimate)	4.5 ± 0.27^{a}	4.83 ± 0.253^{a}
Percentage total larval survival (%)	90.83 ± 0.19^{a}	83 ±2.27^{b}
Prepupal stage		
Prepupal fresh weight (g.)	2.27 ± 0.158^{a}	1.27 ± 0.014^{b}
Pupal stage		
Percentage pupation (%)	90.53 ± 1.486^{a}	84.66 ± 4.83^{a}
Pupal fresh weight (g)	2.583 ± 0.036^{a}	1.87 ± 0.027^{b}
Pupal duration (day)	11.33 ± 0.026^{a}	7.66 ± 0.068^{b}
Adult stage		
Percentage adult emergence (%)	96.27 ± 2.21^{a}	82.24 ± 3.98^{b}
Sex ratio		
Male (%)	56.33 ± 3.82^{a}	58.33 ± 3.21^{a}
Female (%)	46.67 ± 4.38^{a}	44.33 ± 3.82^{a}

pupae with relatively lighter fresh weights compared to those produced from the penultimate instars fed aCO_2-grown leaves (Table 1). This could be attributed to their inability to fully compensate for the diet which is relatively poor in nitrogen as they were forced to metabolize food at higher flow rates, such as when they consumed additional eCO_2-grown leaves, they could not effectively process enough food for the compensation of relatively lower nitrogen concentrations (Rogers et al. 1994; Davis & Potter 1989; Abu ElEla & ElSayed 2018). However, it is far from precise to generalize this finding among other insect pest species since Hughes & Bazzaz (1997) reported no effect on populations of *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae) fed with *Ascelpias syriaca* L. (Asclepiadaceae) grown in eCO_2 atmosphere.

Prolonged larval duration, such as those induced by the eCO_2-grown diets in this study, may prevent larvae from completing development in climatically limited environments with short growing seasons (Davis & Potter 1989; Watt et al. 1995). Reduced growth rates and increased larval duration of the larvae fed eCO_2-grown leaves may also increase their exposure to predators & parasitoids (Carlson & Bazzaz 1980; Davis & Potter 1989; Ottman et al. 2001).

As penultimate larvae reached the prepupal stage, the interruption of feeding was noticeable (Montezano et al. 2019). The prepupae started to build the pupal case which made it possible to observe metamorphosis and determine the end of the prepupal period which was relatively short duration (1–2 days) in both the CO_2 regime.

The recorded prepupal fresh weight showed significant difference ($p < 0.05$) between the aCO_2 and eCO_2 regimes (Table 1). Pre-pupae resulted from penultimate larvae fed cotton leaves grown in aCO_2 regime were remarkably heavier than those resulted from larvae fed eCO_2-grown leaves (Table 1).

Although the mean percentage pupation was found to be lower for larvae fed cotton leaves grown in eCO_2 regime (84.66 ± 4.83) rather than from aCO_2 regime (90.53 ± 1.486), insignificant difference ($p > 0.05$) was observed between the two regimes (Table 1). However, the mean pupal duration showed significant difference ($p < 0.05$) for pupae resulting from larvae fed on cotton leaves grown in aCO_2 regime (Table 1) where pupae of ambient condition showed relatively prolonged duration compared to pupae of enriched condition.

Moreover, significant difference ($p < 0.05$) was observed in the mean pupal fresh weight between the two CO_2 regimes where pupae resulted from larvae fed grown cotton leaves grown at aCO_2 regime showed greater fresh weight (2.583 ± 0.036) compared to those fed eCO_2-grown leaves (Table 1). Robinson et al. (2012) stated that growth rates when consuming high CO_2 foliage are reduced, and duration increased, resulting in lower prepupal, pupal, and adult weights.

Adults emerged from larvae reared on ambient grown cotton leaves showed a significant ($p < 0.05$) greater mean percentage emergence compared to those fed eCO_2-grown cotton leaves (Table 1). The mortality rate for adults resulted from larvae fed eCO_2-grown leaves was much greater (ca. 15%) compared to adults emerged from larvae fed aCO_2-grown leaves (Table 1).

More males emerged, but the Co_2 regimes did not influence the sex ratio as insignificant difference ($p > 0.05$) was observed between the CO_2regimes for both sexes (Table 1).

Measures of plant quality during the present study are thus of importance in understanding natural interactions between herbivorous insect and its host plant species under eCO_2 environment since insect feeding and growth is a function of both the variation since diverse plant species respond differently to atmospheric eCO_2 alterations in foliage quality composition (Rao et al. 2012; Abu ElEla & ElSayed 2018; Manimanjari & Rao 2022). Increase in aCO_2 levels can cause increases in plant growth rates, and changes in the physical and chemical composition of the plant tissues (Stockle 1992; Sudderth 2005; Abu ElEla & ElSayed 2018).

Treatment of cotton plants with eCO_2 regime caused a significant alteration in plant quality in term of chemical characteristics (Table 2). It was observed that nitrogen content was drastically reduced in cotton leaves grown in eCO$_2$ concentration to show 50% less nitrogen contents (0.281 ± 0.029 mg g^{-1}d.wt) compared to nitrogen contents in leaves grown at aCO$_2$ regime (Table 2). In accordance with this finding, other studies have also showed that many plant species grown under eCO$_2$ condition showed a reduction in leaf nitrogen content (Stitt & Krapp 1999; Rao et al. 2012; Manimanjari & Rao 2022).

Significant difference ($p < 0.05$) in total foliar carbohydrates was observed between the two CO$_2$ regimes (Table 2). In the present study, eCO$_2$ typically increases the concentration of foliar total carbohydrates (42.82 ± 0.381 mg g^{-1}d.wt) which showed 15% greater concentration than total carbohydrates concentration in foliar grown in aCO$_2$ (Table 2).

Results shown in Table 2 showed that the total concentration of phenolic contents were higher under eCO$_2$. A significant difference ($p < 0.05$) in the total phenolic contents was observed between the two CO$_2$ treatments (Table 2) where the total phenolic contents in cotton leaves increased by more than double its value under eCO$_2$ compared to the contents of phenolics in aCO$_2$-grown cotton leaves. This improvement in plant secondary metabolites could be attributed to increased total non-structural carbohydrates (TNC) as suggested by Ibrahim & Jafaar (2012). Phenolics are considered as one of the most important groups of secondary metabolites and bioactive compounds in plant species (Kim et al. 2005) and increased levels of CO$_2$ concentrations can influence the levels of total phenolics (Fine et al. 2006).

Table 2. Select nutritional quality of cotton plant leaves of *Gossypium barbadense* L. grown in ambient (aCO2 = 350 ppm) and enriched (eCO2 = 700 ppm) CO2 regimes.

Leaf nutritional quality(mg g^{-1}d.wt)	**CO$_2$ Treatment**	
	aCO$_2$ (350 ppm)	**eCO$_2$ (700 ppm)**
Total carbohydrates	36.49 ± 0.19^{a*}	42.82 ± 0.381^{b}
Total nitrogen	0.565 ± 0.046^{a}	0.281 ± 0.029^{b}
Phenolic compounds	0.645 ± 0.012^{a}	1.524 ± 0.016^{b}

* Results followed by different letters are significantly different ($p < 0.05$).

The eCO$_2$ exhibited a significant impact on cotton plant by altering the biochemical constituents of the foliage such as reduced nitrogen content, increased phenolics, increased carbon, C:N, and total carbohydrates. It was clear that eCO$_2$ amplified decreases in foliar total nitrogen, causing substantial increases in foliar C:N ratio (Zvereva & Kozlov, 2006) which in turn affect the growth & development of the phytophagous early & penultimate

Image 1. Larvae of *Sopdoptera littoralis* (Boisd.) feeding on cotton plant leaves *Gossypium barbadense* L.: a—3rd larval instar (early) | b—6th larval instar (penultimate) | c—cotton leaves | d—faeces of the larvae. © Wael M. ElSayed.

instars, and subsequent stages of *S. littoralis* (Boisd.).

Consuming more eCO_2-grown leaves is an unambiguous indicator that eCO_2 reduces insect growth rates by altering the chemical and physical properties of foliage. In our study, cotton leaves grown in eCO_2 regime possessed relatively high total carbohydrates and low nitrogen content (Table 2). Consequently, increasing C:N which causes apparent increase in the consumption of relatively low-quality food to meet critical nutrient limitations which is referred to as "compensatory feeding" and may portend greater herbivore damage to both managed & natural ecosystems as CO_2 continues to increase (Cornelissen 2011).

CONCLUSION

It was clear that the phytophagous pests respond in an immediate fashion to the leaves grown in eCO_2. Larvae fed aCO_2-grown cotton leaves showed shorter duration, comparatively heaviest prepupae & pupae, and greatest percentage of adult emergence. On the other hand, larvae fed eCO_2- grown cotton leaves showed relatively longer duration and lighter prepupae & pupae with smaller percentage adult emergence. Consequently, the population dynamics of *S. littoralis* (Boisd.) and the nutritional quality of the host plant, *G. barbadense* L., could be influenced by the future increase of aCO_2 levels.

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