Agriculture, Ecosystems and Environment 132 (2009) 267–275

Contents lists available at ScienceDirect

Agriculture, Ecosystems and Environment

journal homepage: www.elsevier.com/locate/agee

No effects of elevated CO_2 on the population relationship between cotton bollworm, *Helicoverpa armigera* Hübner (Lepidoptera: Noctuidae), and its parasitoid, *Microplitis mediator* Haliday (Hymenoptera: Braconidae)

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ARTICLE INFO

Article history:
Received 30 December 2008
Received in revised form 10 April 2009
Accepted 16 April 2009
Available online 17 May 2009

Keywords:
Elevated CO_2
Helicoverpa armigera
Microplitis mediator
Parasitism rate
Population consumption
Spring wheat

ABSTRACT

Estimating the population consumption of an insect population under elevated CO_2 is an important step in understanding the effects of elevated CO_2 on herbivore–crop interactions. Two successive generations of cotton bollworm, *Helicoverpa armigera* Hübner, were reared on milky grains of spring wheat (*Triticum aestivum* L.) grown in open-top chambers under increased carbon dioxide (CO_2) concentration. *H. armigera* development, wheat consumption, and parasitism by *Microplitis mediator* Haliday were examined, as were the effects of elevated CO_2 on the wheat itself. We experimentally tested the hypotheses that, by quantifying the population consumption of *H. armigera*, elevated CO_2 enhanced the pest-control ability of *M. mediator* again *H. armigera*. Decreases in protein, total amino acid, and nitrogen (N) content were noted in spring wheat when grown in an elevated-CO_2 environment, as were increases in total non-structure carbohydrates (TNCs) and in the ratio of TNC to N. In the first generation of *H. armigera* reared under elevated CO_2, no significant changes were observed in population generation time (T) or in the intrinsic rate of increase (r_m) between CO_2 treatments. However, in the second treatment generation, longer generation time resulted in a lower r_m value. Elevated-CO_2 levels caused no significant changes in the *H. armigera* population's total wheat consumption. The rates of parasitism, cocooning, and emergence by *M. mediator* were also unaffected, as were its average weight and adult lifespan. As no significant changes in wheat consumption by *H. armigera* or in the parasitic rate of *M. mediator* were revealed, the results indicate that the population relationship between *H. armigera* and *M. mediator* is unlikely to vary due to future elevated atmospheric CO_2 concentrations.

1. Introduction

The global atmospheric concentration of CO_2 has increased from a pre-industrial value of about 280–379 ppm in 2005, with an annual rate of increase of 1.9 ppm for the last 10 years (IPCC, 2007). Levels of atmospheric CO_2 are anticipated to double by the end of the 21st century (Houghton et al., 2001; Veteli et al., 2002).

Elevated-CO_2 levels directly impact plant physiology. Among these effects is an increase in photosynthetic rate which alters growth, aboveground biomass, yield, carbon-to-nitrogen ratio (C:N), and the efficiency of water use in most plant species. Reduced N concentrations impact the production of plant nutrients and secondary metabolites, especially in C_3 plants (Cotrufo et al., 1998; Pritchard et al., 1999; Agrell et al., 2000; Hartley et al., 2000). Decreased foliar N concentration reduces leaf nutritional quality, diminishing the value of foliage as a resource for insect herbivores (Mattson, 1980; Johns and Hugher, 2002).

Most leaf-chewing insects exhibit compensatory increases in food consumption and/or development times (thereby increasing the herbivores' exposure to predators, parasitoids, and pathogens), reduced growth, survival rates, population density and fitness in elevated-CO_2 environments, presumably due to the increased foliar C:N ratios of host plants (Scriber, 1982; Ayres, 1993; Masters et al., 1998; Coviella et al., 2002). The grasshoppers (Johnson and Lincoln, 1990, 1991) and caterpillar larvae (Lindroth et al., 1993, 1995), for example, generally consume more leaf area when they feed upon plants grown in elevated-CO_2 environments. Thus, elevated-CO_2 conditions may amplify the crop damage caused by pests (Lincoln et al., 1984). Most published studies describe plant

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doi:10.1016/j.agee.2009.04.010

consumption by herbivorous insects "per individual" by developmental rate, by mortality, and by fecundity (Bezemer and Jones, 1998a; Chen et al., 2007). Few experiments (except for Wu et al. (2006)) have been carried out at the population levels, making it difficult to estimate an insect population's potential consumption of a crop growing in an elevated-CO_2 system. Wu et al. (2006) demonstrates that elevated CO_2 adversely affects grain quality, increasing the consumption per individual larva of *H. armigera*. However, in the Wu et al. (2006) study, the potential population consumption of cotton bollworm under elevated CO_2 was reduced in the two latter generations, due to increased mortality and reduced fecundity within the population (Wu et al., 2006). These results suggest that the net damage caused by cotton bollworm on wheat will be reduced under elevated CO_2. However, quantifying consumption at a population levels to assess the impact of elevated CO_2 on future agro-ecosystems is a major task.

Altered plant nutrition under elevated-CO_2 conditions may influence the third trophic levels (host plant – herbivorous insect – insect predator) through "bottom up" effects. Patterns of chemical allocation not only regulate the interactions between herbivorous insects and their host plants, but potentially also those between herbivores and their natural enemies (Ohgushi, 1995; Coley, 1998; Bezemer et al., 1998b; Stiling et al., 1999). Coll and Hughes (2008) suggested that the omnivorous predator *Oechalia schellenbergii* may impose greater pressure on its prey, *H. armigera*, at elevated-CO_2 levels because the prey became more vulnerable to predation under such conditions; possibly due to their consumption of lower-quality foliage during growth in an environment with elevated CO_2. Stacey and Fellows (2002), however, found that neither body size or food consumption or prey choice or prey number of ladybird *Hippodamia convergens* nor body size of parasitoid *Diaeretiella rapae* changed under elevated-CO_2 levels. Because of the complexity involved in discerning the effects of rising CO_2 on the third trophic levels by studying three levels food chains, further studies on these higher trophic levels are needed (Bezemer et al., 1998b; Stacey and Fellows, 2002; Hoover and Newman, 2004). Moreover, as natural enemies are considered to be one of the most efficient methods of pest control, their reactions to elevated environmental CO_2 levels deserve particular scrutiny (Chen et al., 2004).

In this study, we examine the effects of elevated-CO_2 levels on the three levels food chain between spring wheat, *H. armigera* and *M. mediator*. Spring wheat (*Triticum aestivum* L.), a C_3 plant, seems especially sensitive to elevated-CO_2 levels. Elevated CO_2 can increase growth, with the grain yield observed to increase by 35%, when the ambient-CO_2 levels are doubled (Cure and Aycock, 1986; Amthor, 2001; Chen et al., 2004).

One of the common pests affecting spring wheat is cotton bollworm *Helicoverpa armigera* Hübner, a cosmopolitan phytophagous chewing insect (Zalucki et al., 1986; Zalucki and Furlong, 2005). In North China, the first generation of cotton bollworm damages wheat, and alters their host between corn and cotton in their successive generation (Ge et al., 2003). The endoparasitoid larvae of wasps *Microplitis mediator* Haliday parasitize the second instar larvae of *H. armigera* (Wang et al., 1984; Liu et al., 2004). *M. mediator* is widely used as a biocontrol agent against *H. armigera* in the wheat agro-ecosystem (Li, 2005). However, the effects of *H. armigera* on spring wheat in the presence of both *M. mediator* and elevated carbon dioxide levels are currently unclear.

In this study, *H. armigera* were reared using milky grains of spring wheat grown under elevated-CO_2 conditions as a food source. The growth, development, and consumption of two successive generations of *H. armigera* were examined, as well as their parasitism by two successive generations of *M. mediator*. Our specific objectives were to quantify: (1) the parasitism rates of two successive generations of *M. mediator* on an *H. armigera* population reared on a food source grown under elevated CO_2, (2) the development, survival rate, and population parameters of two successive generations of *H. armigera* in an elevated-CO_2 environment when parasitized by *M. mediator*, and when unparasitized, and (3) the population's total consumption of two successive generations of *H. armigera* under the aforementioned conditions.

2. Materials and methods

2.1. CO_2 concentration

2.1.1. Open-top chamber

This experiment was carried out using six octagonal open-top chambers (OTC), each 4.2 m in diameter, located at the Observation Station of the global change biology group, Institute of Zoology, Chinese Academy of Science (CAS) in Xiaotangshan County, Beijing, China (40°11′N, 116°24′E). The atmospheric CO_2 concentration treatments were: (1) current ambient-CO_2 levels (375 μl/L) ("ambient CO_2") and (2) double the current ambient-CO_2 levels (750 μl/L) ("elevated CO_2") (Chen et al., 2004). Three OTCs were used for each CO_2 concentration treatment. During the period from seedling emergence to harvesting for wheat, CO_2 concentrations were monitored continuously and were adjusted using an infrared CO_2 analyzer (Ventostat 8102, Telaire Company, USA) once every 20 min to maintain the assigned CO_2 concentrations. The automatic-control system for adjusting the levels of CO_2 concentration as well as specifications for the open-top chambers is detailed in Chen et al. (2005a, 2005b, 2005c).

2.1.2. Closed-dynamics CO_2 chamber

Insects were reared in a growth chamber (HPG280H; Orient Electronic, Haerbin, China). Growth chamber conditions were maintained at 25 ± 1 °C, 60–70% relative humidity, a photoperiodic ratio of 14:10 (hours of light:hours of dark), and active radiation measuring 9000 lux (supplied by 1260 W fluorescent lamps in each chamber). Two atmospheric CO_2 concentrations consisting of the current ambient-CO_2 levels (375 μl/L) and double the current ambient-CO_2 levels (750 μl/L), were maintained to match the OTCs used for wheat growth. Three chambers were used for each CO_2 treatment. As previously mentioned, CO_2 concentrations were automatically monitored and adjusted with an infrared CO_2 analyzer (Ventostat 8102; Telaire, Goleta, CA, USA). A detailed explanation of the methodology employed by the automatic-control system for maintaining and adjusting the CO_2 concentrations is described in Chen and Ge (2004).

2.2. Wheat variety and growth conditions

Spring wheat (Longfu174379 variety) seeds were sown on 10 March 2007 in plastic pots (height: 35 cm, diameter: 45 cm), in the six open-top chambers previously mentioned with a seeding rate of 150 seeds per pot. 35 pots were placed in each OTC. Pot placement was re-randomized in each OTC weekly.

On 19 April 2007, the crop was thinned to 100 plants per pot. Pure CO_2 was mixed with ambient air and supplied to each chamber throughout wheat development. The crop was irrigated sufficiently every other day using tap water. During the milky-grain stage of spring wheat, ears and grains were harvested from all six OTCs, and then refrigerated at −20 °C until supplied to *H. armigera* as food.

2.3. Insect stocks

2.3.1. *H. armigera*

Egg masses were obtained from a laboratory colony maintained by the Insect Physiology Laboratory, Institute of Zoology at CAS,