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EFFECT OF CLIMATE CHANGE ON LONGEVITY AND REPRODUCTION OF *SIPHA FLAVA* (HEMIPTERA: APHIDIDAE)

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Abstract

This study examined effects of elevated CO_2 alone and in combination with elevated temperature on plant-aphid interactions. CO_2 levels in which the host plants were grown affected the durations of some nymphal stadia, but not the survivorship within each instar or of all nymphal instars. *Sipha flava* (Forbes) (Hemiptera: Aphididae) adults kept under a constant high CO_2 environment (500 ppm) and fed on plants grown under fluctuating CO_2 levels (avg. 440 ppm) in a greenhouse had significantly greater longevity and greater reproduction than aphids fed on plants grown either under a constant high CO_2 level (500 ppm) or under fluctuating CO_2 levels (avg. 368 ppm). Nevertheless, no significant differences were observed in these biological parameters of *S. flava* that were kept individually in a greenhouse, regardless of the CO_2 and temperatures under which the plants used to feed them were grown. However, populations of aphids kept and fed on plants grown in the greenhouse produced significantly more nymphs and adults than did those fed plants grown in a climate-controlled chamber under a constant high CO_2 level (500 ppm). The combination of elevated CO_2 and high temperature significantly decreased the duration of nymphal stadia, the longevity and reproductive success of *S. flava* but not nymphal survival. Adults produced fewer nymphs in an environment with elevated CO_2 and high temperature than an environment with elevated CO_2 and lower fluctuating temperatures. Based on these results, we concluded that *S. flava* populations will significantly decrease under future climatic conditions when both the concentration of atmospheric CO_2 and temperature are projected to increase.

Key Words: aphids, carbon dioxide, temperature, forage grass

Resumo

Neste estudo avaliou-se o efeito da alta concentração de CO_2 sozinho e em combinação com alta temperatura na interação planta-afídeo. O período ninfal e o período de cada ínstar foram afetados pelo nível de CO_2 e o ambiente que a planta foi mantida. O mesmo não foi observado para a sobrevivência do período ninfal e de cada instar de *Sipha flava* (Forbes) (Hemiptera: Aphididae). Foi observado na avaliação da performance individual e populacional do afídeo-praga, que adultos mantidos em ambientes com CO_2 constante (500 ppm) e alimentados de plantas proveniente de casa de vegetação (média de 440 ppm) tiveram a longevidade e a capacidade reprodutiva significativamente maior comparado aqueles alimentados de plantas advindas de ambientes com nível de CO_2 constante e flutuante (média de 368). Além disso, nenhuma diferença significativa nesses parâmetros biológicos individuais de adultos mantidos em casa de vegetação foi observada, independente do ambiente em que as plantas ofertadas se desenvolveram. No entanto, a performance populacional de afídeos mantidos e alimentados de plantas crescidas na casa-de-vegetação produziram significativamente mais ninfas e adultos que aqueles alimentados de plantas crescidas em câmara climatizada com CO_2 constante. A combinação de CO_2 e temperatura elevada reduziu significativamente a duração ninfal, longevidade e capacidade reprodutiva de *S. flava*, mas não afetou a sobrevivência das mesmas. Os adultos mantidos no ambiente com CO_2 e temperatura elevada produziram menos ninfas que adultos mantidos em ambiente com CO_2 elevado e temperatura baixa. Baseado nos resultados deste estudo, conclui-se que a população de *S. flava* decrescerá significativamente nas condições climáticas futuras, em que se espera o aumento da concentração do nível de CO_2 e temperatura.

The yellow sugarcane aphid, first named *Chaitophorus flavus* Forbes, but later *Sipha flava* (Forbes) (Hemiptera: Aphididae) (Davis 1909), is yellow, 1.3-2.0 mm long, and has numerous long bristle-like hairs with dusky transverse markings on the dorsum (Blackman & Eastop 2000). *Sipha flava* has an extensive geographic range that includes all the Americas and Hawaii (Medina-Gaud et al. 1965; Kindler & Dalrymple 1999; Blackman & Eastop 2000). *Sipha flava* is not only a serious pest of sugarcane (*Saccharum* spp.; Poales: Poaceae) , but it infests corn, sor-

ghum, wheat, and several other grasses (Webster 1990; Hentz & Nuessly 2004; Oliveira et al. 2010). Plant injury caused by this aphid is often severe and is associated with the release of an unidentified toxin followed by leaf chlorosis (Breen & Teetes 1986; Webster 1990).

In Brazil, elephant grass, *Pennisetum purpureum* (Schumach); Poales: Poaceae, is one of the most widely used grasses for dairy cattle forage, and is noted for high productivity and quality of forage (Xavier et al. 2001). However, production of this forage grass is being compromised by *S. flava* attack. Thus, studies on effects of *S. flava* on forage grasses such as *P. purpureum* are needed to develop effective management programs for the pest. Oliveira et al. (2009) evaluated effects of different temperatures on the development, survival, reproduction, life expectancy, and fertility tables of *S. flava* feeding on *P. purpureum,* and concluded that temperatures between 20 °C and 24 °C are most suitable for *S. flava* development and reproduction. Furthermore, this temperature range is appropriate for the insect to reach pest status in elephant grass. Increasing temperatures will directly affect development, survival, and abundance of aphids (Oliveira et al. 2009; Auad et al. 2009), and both elevated CO_2 and increased temperatures affect insect herbivores indirectly by influencing host plant physiology and phytochemistry (Flynn et al. 2006).

By 2100 the world is projected to experience an approximate doubling of atmospheric CO_2 concentrations to around 700 ppm accompanied by a 1.4-5.8 °C rise in mean global temperatures (Houghton et al. 2001), and CO_2 concentrations may reach 770 ppm (IPCC 2007). These climatic changes would greatly alter relationships between plants and insects in areas of important agricultural production and elsewhere (Theurillat & Guisan 2001).

The effects of such elevated CO_2 levels on plants, in turn, have been shown to affect the biology of herbivorous insects (Chen et al. 2005, 2007; Wu et al. 2006). Direct and indirect effects of elevated CO_2 on herbivores should therefore be studied to better understand interactions between host plants and phytophagous insects under the CO_2-enriched environments expected in the future (Yin et al. 2010).

Given the potentially large effect of *S. flava* on *P. purpureum* (Oliveira et al. 2010), it is important to understand how global climatic changes influences this aphid's ecology, and to determine whether future elevated CO_2 levels and temperatures could enhance the destructiveness of this pest. To our knowledge, there has been no previous investigation on the effects of global climatic changes on this pest. Hence, we investigated effects of elevated CO_2 alone and in combination with elevated temperature on the interactions of *S. flava* and one of its hosts, *P. purpureum*.

Materials and Methods

Aphids

The *Sipha flava* aphids used in all experiments were obtained from a colony maintained in a greenhouse at the EMBRAPA Dairy Cattle Research Station, Juiz de Fora, Minas Gerais, Brazil. Adults were transferred to petri dishes (8.5 cm × 2 cm) containing one foliar disc of *P. purpureum* (8.5 cm diam) placed on a 1.0 cm-thick layer of 1% agar in order to keep the leaf disc turgid. Each petri dish was covered with organza secured with rubber bands, and it was maintained in a chamber at 25 ± 1 °C, 70 ± 10% RH and 14:10 h L:D to facilitate aphid reproduction.

To study the biology of *S. flava* individuals, the nymphs were ≤24 h old and collected from these petri dishes with a fine-tipped paint brush. In each test the individual nymph was kept alone in a plastic container (2.5 × 2.5 cm) containing a foliar disc of *P. purpureum* placed on a layer of 1% agar, and the plastic container were covered with organza secured with a rubber band. The foliar disc was changed each 48 h to avoid degradation as a food resource. This technique was used because Oliveira et al. (2009) had successfully used it to study the biology of *S. flava.* To study *S. flava* population performance, 10 nymphs were placed on each *P. purpureum* plant (50 cm high) maintained in plastic cages (20 cm diam × 60 cm high) closed with a voile lid secured with a rubber band. In the present study, foliar discs and plants were obtained from environments with different CO_2 levels, either constant or fluctuating.

Plant Growth Conditions

The host plant in all tests was *P. purpureum*, 'Cameron de Piracicaba', because this genotype is very suitable for the development of *S. flava* (Oliveira et al. 2010). *P. purpureum* cuttings were each planted in a 1.0-L pot with a plant growth substrate of soil/manure at the ratio 2:1 and kept in the following 3 growth environments: 1) a greenhouse (avg. 440 ppm; min 384 ppm and max 924 ppm of CO_2), 2) a climate-controlled chamber with an almost constant CO_2 level, i.e., a range of 500-550 ppm; henceforth referred to as 500 ppm, and 3) climate-controlled chamber with fluctuating CO_2 levels (avg. 368 ppm; min 163 ppm and max 832 ppm of CO_2). Each climate-controlled growth chamber (2.5 × 2.20 × 2.80 m) was maintained at 25 ± 2 °C during the day, 20 ± 2 °C at night, 70 ± 10% RH and 14:10 h L:D. Conditions in the climate-controlled chamber with fluctuating CO_2 levels and in the greenhouse were recorded with a HOBO U12 Temperature/Relative Humidity/Light/External Data Logger - U12-012 (Onset Co., Pocasset, Massachusetts, USA). Conditions in the constant CO_2 chamber

were maintained with an automatic monitoring system, COEL HW 4200 (Manaus - Amazonas, Brazil) and an injection system using a CO_2 cylinder to maintain the desired CO_2 concentration. Fluctuating CO_2 levels were recorded with a data logger every 2 min and the data were transferred to a computer using HOBOware® software (Onset Co., Pocasset, Massachusetts, USA). Thus we were able to maintain the desired CO_2 concentration (avg. 368 ppm) during the experimental period. All plants were 74 d old when foliar discs were explanted. Despite the similar CO_2 concentrations in the greenhouse and in the climate chambers, other abiotic factors fluctuated in the greenhouse (temperature 18 ± 5 °C and RH 74 ± 10 %), but these were kept almost constant in the climate-controlled chambers.

The CO_2 concentrations used for the treatments with constant CO_2 levels were selected based on predicted CO_2 levels for the year 2100 by the Intergovernmental Panel on Climate Change (IPCC 2007), and treatments with fluctuating CO_2 levels were selected according to those recorded in the greenhouse.

Experiments

In all the experiments, both plants and insects were contained either in a greenhouse with fluctuating CO_2 concentrations, or in climate-controlled chambers either with relatively constant or variable CO_2 concentrations. Insects in a climate-controlled chamber were fed forage grown in the greenhouse, while insects in the greenhouse were fed on plants grown in a climate-controlled chamber with relatively constant CO_2.

Experiment 1: Effects of Different CO_2 Regimes on *Sipha flava* Individuals.

Experiment 1 had 2 parts. In Part I, 3 treatments were applied with 50 individual nymphs per treatment. In Treatment #1 nymphs and forage grass were maintained in a climate-controlled chamber under a constant high CO_2 level (500 ppm). In Treatment #2 both nymphs and forage grass were maintained in a climate-controlled chamber with fluctuating CO_2 levels (avg. 368 ppm). In Treatment #3 nymphs were kept under a climate-controlled chamber at a constant high CO_2 level (500 ppm), but were fed forage grass grown in the greenhouse with fluctuating CO_2 levels (avg. 440 ppm).

In Part II, 2 treatments were applied with 50 individual nymphs per treatment. In Treatment #1 nymphs and forage grass plants were maintained in a greenhouse under fluctuating CO_2 levels (avg. 440 ppm). In Treatment #2 nymphs were also maintained in a greenhouse under fluctuating CO_2 levels (avg. 440 ppm), and fed on *P. purpureum* derived from a climate-controlled chamber under a constant high CO_2 level (500 ppm).

The following parameters were evaluated and recorded daily for Experiment 1: the duration (days) of each nymphal stadium, percent survival of each nymphal instar, and the longevity (days) and reproductive capacity of adults.

Experiment 2: Effects of Different CO_2 Regimes on *Sipha flava* Populations

Experiment 2 also had 2 parts, with each treatment the same as in Experiment 1. There were 20 replications per treatment, and each treatment within a replication involved 10 nymphs per plant. After 30 days, numbers of nymphs and adults were recorded. This 30 day-period was sufficient for approximately 4 generations to occur, according to Oliveira et al. (2009).

Experiment 3: Effects of Elevated CO_2 and Temperature on *Sipha flava*

This experiment was conducted with a constant high CO_2 level (500 ppm) in both treatments, moderate diurnally fluctuating temperatures in one treatment, and an elevated constant temperature in second treatment. The objective was to determine the effects of these conditions on the development, reproduction and longevity of *S. flava*. For each treatment, 50 *S. flava* individual nymphs were each kept in a plastic container (2.5 × 2.5 cm) containing a foliar disc of *P. purpureum* placed on a 1% agar layer, and the plastic container was covered with organza secured with a rubber band. Foliar discs were explanted from plants grown in a greenhouse with fluctuating CO_2 levels (avg. 440 ppm), and the insects were maintained in a controlled-climate chamber with a constant high CO_2 level (500 ppm), 28 ± 2 °C, 70% ± 10% RH, and 14:10 h L:D. Data from this experiment were compared to data from Treatment 3 of Experiment 1 (a constant high CO_2 level (500 ppm), 25 ± 2 °C (day), and 20 ± 2 °C (night)). The following parameters were evaluated and recorded daily: duration of each nymphal stadium and of the entire nymphal phase, percent survival of each nymphal instar and of all nymphal instars, and longevity and reproductive capacity of the adults.

Statistical Analyses

The effects of CO_2 on the performances of *S. flava* individuals (Experiment 1) and *S. flava* populations (Experiment 2) when insects and/or plants were provided conditions in which only CO_2 concentration varied (climate-controlled chambers) or in which all abiotic factors varied (greenhouse), and effects of elevated temperature on individual performance of *S. flava* under elevated CO_2 levels (Experiment 3) were evaluated. In each experiment the data were subjected to

an analysis of variance (ANOVA), and the means were compared with Tukey's test using Sisvar 5.1 software (Lavras, Minas Gerais, Brazil).

Results

Experiment 1: Effects of Different CO_2 Regimes on *Sipha flava* Individuals.

In experiment 1 Part I (Table 1), when nymphs and the plants were held under a constant high CO_2 level (500 ppm) (Treatment 1), the duration of the third instar nymphs' development was prolonged compared to Treatment 2 (both nymphs and plants kept under fluctuating CO_2 levels (avg. 368 ppm)), and Treatment 3 (nymphs under a constant high CO_2 level (500 ppm), and plants under fluctuating CO_2 levels (avg. 440 ppm)). However the stadia of the second and fourth instars were not significantly different between the treatments. When both first instar nymphs and plants were kept under fluctuating CO_2 levels (avg. 368 ppm) (Treatment 2), the duration of the N1 stadium was shorter than when nymphs were kept under a constant high CO_2 level (500 ppm) were fed on plants kept under fluctuating CO_2 levels (avg. 440 ppm) (Treatment 3). Also when both nymphs and plants were kept under fluctuating CO_2 levels (avg. 368 ppm) (Treatment 2), the duration of total period of nymphal development was shorter than that of nymphs fed on plants under a constant high CO_2 level (500 ppm) (Treatment 1), or fed on plants under fluctuating CO_2 levels (avg. 440 ppm) (Treatment 3). No significant differences occurred in the percent survival of nymphs in all 3 treatments (Table 1).

Aphids kept under a constant high CO_2 level (500 ppm) environment (Fig. 1) and fed on plants from an environment with fluctuating CO_2 levels (avg. 440 ppm) (Treatment #3) lived significantly longer and displayed a significantly greater reproductive capacity than aphids in a constant high CO_2 level (500 ppm) environment and fed on plants also grown under a constant high CO_2 level (500 ppm) environment (Treatment #1), as well as significantly longer than insects kept along with their food plants in an environment with fluctuating CO_2 levels (avg. 368 ppm) (Treatment #2) ($F = 26.19$; $P = 0.0000$). Hence, the results show that aphids fed on plants derived from a constant high CO_2 level (500 ppm) environment and fluctuating CO_2 levels (avg. 368 ppm) environment produced about half as many progeny as did the aphids kept in a constant high CO_2 level (500 ppm) environment and fed on

Table 1. Experiment 1, part I: duration of each *Sipha flava* nymphal stadium and survival of each nymphal instar when (1) nymphs and forage grass were maintained in a climate-controlled chamber with constant 500 ppm CO_2 (treatment 1); (2) nymphs and forage grass were maintained in a climate-controlled chamber with fluctuating CO_2 levels - avg. 368 ppm (treatment 2), and (3) nymphs were maintained in a climate-controlled chamber with constant 500 ppm CO_2, but fed forage grass grown in a greenhouse with fluctuating CO_2 levels - avg. 440 ppm (treatment 3).

	Treatments			Analyzed by ANOVA
Instar	1	2	3	P
		Duration (days)		
N1	2.46 ± 0.09 ab n = 47	2.43 ± 0.07 b n = 48	2.73 ± 0.09 a n = 46	0.032
N2	2.23 ± 0.07 a n = 46	2.06 ± 0.04 a n = 46	2.23 ± 0.06 a n = 46	0.073
N3	2.43 ± 0.08 a n = 46	2.09 ± 0.07 b n = 44	2.13 ± 0.05 b n = 45	0.001
N4	2.93 ± 0.09 a n = 45	2.69 ± 0.07 a n = 42	2.70 ± 0.08 a n = 44	0.080
Total	10.04 ± 0.14 a n = 45	9.32 ± 0.10 b n = 43	9.79 ± 0.12 a n = 44	0.00
		Nymphal survival (%)		
N1	94.0 ± 02.44 a n = 50	96.00 ± 2.44 a n = 50	92.00 ± 3.74 a n = 50	0.641
N2	95.8 ± 02.59 a n = 47	95.80 ± 2.59 a n = 48	100.00 ± 0.00 a n = 46	0.301
N3	98.00 ± 2.00 a n = 46	98.00 ± 2.00 a n = 46	98.00 ± 2.00 a n = 46	1.000
N4	97.80 ± 2.22 a n = 46	93.60 ± 2.63 a n = 45	97.60 ± 2.50 a n = 45	0.408
Total	90.00 ± 4.47 a n = 45	84.00 ± 2.44 a n = 43	88.00 ± 4.89 a n = 44	0.585

Mean values followed by the same letter in the same row were not significantly different as determined by ANOVA and Tukey's test.

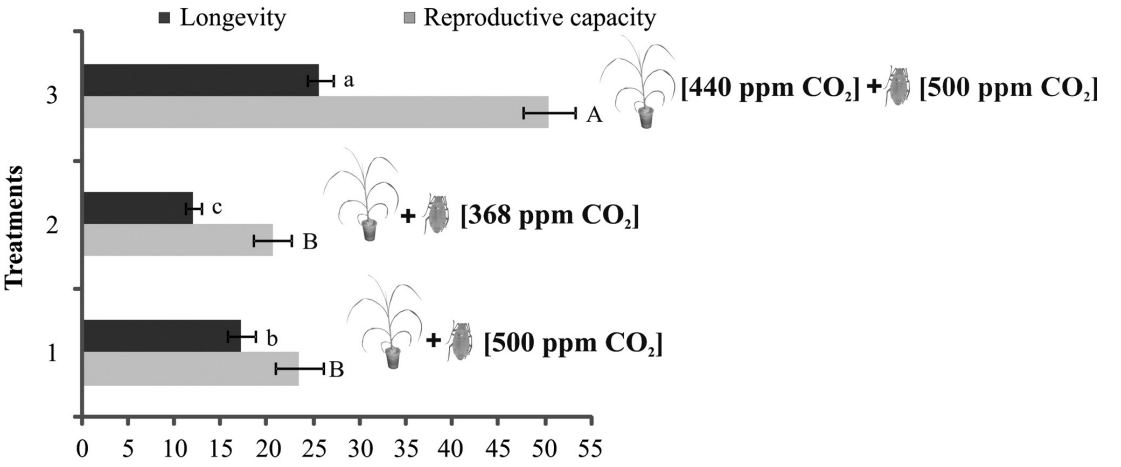

Fig. 1. Effects of forage grown either under a constant high (500 ppm) CO_2 level, or under lower but fluctuating CO_2 levels on longevity (days) and reproductive capacity (number of nymphs) of *Sipha flava* held under the same CO_2 regimes. Treatment 1: Both *S. flava* and forage grass were maintained in a climate-controlled chamber with constant high 500 ppm CO_2 level. Treatment 2: Both *S. flava* and forage grass were maintained in a climate-controlled chamber with fluctuating CO_2 levels - avg. 368 ppm. Treatment 3: *S. flava* were maintained in a climate-controlled chamber with constant 500 ppm of CO_2, but the forage grass fed to them was grown in a greenhouse with fluctuating CO_2 levels - avg. 440 ppm. Mean longevity values followed by different lower case letters were significantly different, as were mean values for reproductive capacity followed by different upper case letters based on ANOVA followed by the Tukey test.

plants grown with fluctuating CO_2 levels (avg. 440 ppm) ($F = 42.48$; $P = 0.0000$) (Fig. 1).

In Experiment 1, Part II (Table 2), the duration of the second nymphal stadium was significantly shorter when the aphids were kept under fluctuating CO_2 levels (avg. 440 ppm) and fed on plants derived from a constant high CO_2 level (500 ppm) environment (Treatment #2) than when both the aphids and their food plants were kept under fluctuating CO_2 levels (avg. 440 ppm, Treatment 1). However, durations of the first, third and fourth instars, the overall nymphal period, and the survival of *S. flava* were not significantly affected regardless of the environment in which the plants were grown (Table 2). Moreover, no significant differences in longevity ($F = 0.54$; $P = 0.463$) or reproductive capacity ($F = 2.95$; $P = 0.089$) of *S. flava* occurred when the aphids were kept under fluctuating CO_2 levels (avg. 440 ppm) regardless of the environment in which plants consumed by the insects were grown (Fig. 2).

Experiment 2: Effects of Different CO_2 Regimes on *Sipha flava* Populations

The aphids kept under a constant high CO_2 level (500 ppm) and fed on plants grown under fluctuating CO_2 levels (avg. 440 ppm) (Treatment 3) produced significantly more nymphs ($F = 5.23$; $P = 0.008$) (Fig. 3A) and adults ($F = 5.55$; $P = 0.006$) (Fig. 3B) than did aphids kept together with their host plants under a constant high CO_2 level (500 ppm) (Treatment 1), or when both aphids and host plants were kept under fluctuating CO_2 levels (avg. 368 ppm) (Treatment 2).

Also aphids kept in the greenhouse and fed on plants grown in the greenhouse under fluctuating CO_2 levels (avg. 440 ppm) produced significantly more nymphs ($F = 10.78$; $P = 0.002$) (Fig. 4A) and adults ($F = 4.89$; $P = 0.03$) (Fig. 4B) than did aphids also kept in a greenhouse but fed plants grown under a constant high CO_2 level (500 ppm).

Experiment 3: Effects of Elevated CO_2 and Temperature on *Sipha flava*

As shown in Table 3, the combination of a high temperature and a constant high CO_2 level (500 ppm) significantly decreased the duration of the overall nymphal period, but not decrease nymphal survival. The durations of all of the nymphal stadia in an environment with a constant high CO_2 level (500 ppm) and high temperature (28 ± 1 °C) were shorter than those in an environment with the same CO_2 environment but lower diurnally fluctuating temperatures (25 ± 1 °C/20 ± 1 °C, day/night). Moreover, this combination of conditions drastically affected the longevity and reproductive capacity of *S. flava* (Fig. 5). Aphids exhibited shorter longevity when kept in an environment with elevated CO_2 and elevated temperature (28 ± 1 °C) (Treatment 2) than when kept in the same CO_2 environment but lower fluctuating temperatures (25 ± 1 °C/20 ± 1 °C, day/night) (Treatment 1) ($F = 101.2$; $P = 0.000$) (Fig. 5). These

TABLE 2. EXPERIMENT 1, PART II: DURATION OF EACH *SIPHA FLAVA* NYMPHAL STADIUM AND SURVIVAL OF EACH NYMPHAL INSTAR WHEN (1) NYMPHS AND FORAGE GRASS PLANTS WERE MAINTAINED IN A GREENHOUSE WITH FLUCTUATING CO_2 LEVELS - AVG. OF 440 PPM (TREATMENT 1), AND (2) NYMPHS WERE MAINTAINED IN A GREENHOUSE WITH FLUCTUATING CO_2 LEVELS - AVG. OF 440 PPM, BUT FED ON *P. PURPUREUM* DERIVED FROM A CLIMATE-CONTROLLED CHAMBER WITH CONSTANT 500 PPM CO_2 (TREATMENT 2).

	Treatments		Analyzed by ANOVA
Instar	1	2	*P*
		Duration (days)	
N1	3.47 ± 0.09 a n = 48	3.34 ± 0.09 a n = 49	0.324
N2	3.53 ± 0.09 a n = 45	3.11 ± 0.09 b n = 47	0.001
N3	3.37 ± 0.09 a n = 45	3.52 ± 010 a n = 46	0.296
N4	3.95 ± 0.13 a n = 44	3.71 ± 0.13 a n = 45	0.201
Total	13.88 ± 0.16 a n = 43	14.13 ± 0.18 a n = 45	0.307
		Nymphal survival (%)	
N1	96.00 ± 2.44 a n = 50	98.00 ± 2.00 a n = 50	0.544
N2	96.60 ± 2.63 a n = 48	96.00 ± 2.44 a n = 49	0.516
N3	100.00 ± 0.00 a n = 45	97.80 ± 2.22 a n = 47	0.346
N4	95.50 ± 2.78 a n = 45	98.00 ± 2.00 a n = 46	0.486
Total	88.00 ± 3.74 a n = 43	90.00 ± 3.16 a n = 45	0.693

Mean values followed by the same letter in the same row were not significantly different as determined by ANOVA and Tukey's test.

longevity results directly correlated with the reproductive capacity results in that aphids kept under a high CO_2 environment (500 ppm) and a high temperature (28 ± 1 °C) produced far fewer nymphs than those kept in an environment with the same CO_2 environment but lower diurnally fluctuating temperatures (25 ± 1 °C/20 ± 1°C, day/night) (F = 135.6; P = 0.000) (Fig. 5).

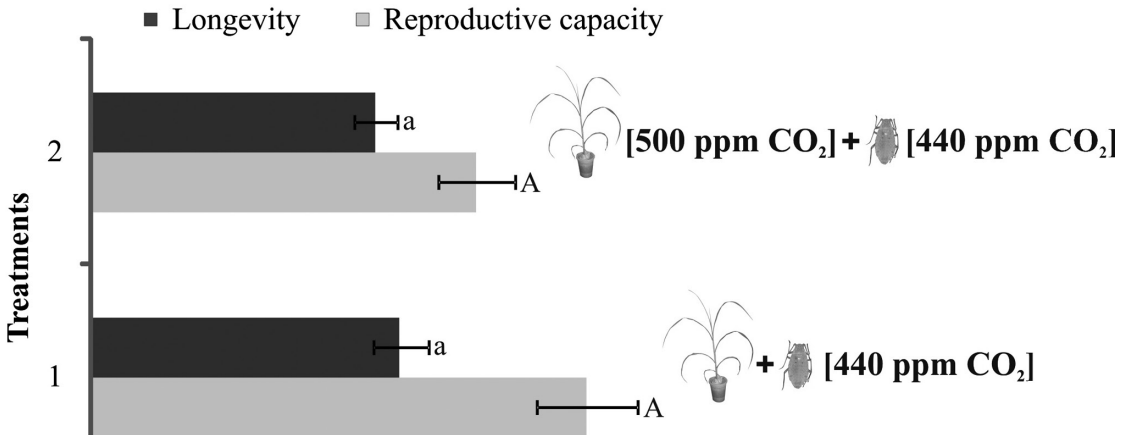

Fig. 2. Effects of forage grass grown either under a constant high (500 ppm) CO_2 level, or under fluctuating CO_2 levels - avg. 440 ppm on longevity (days) and reproductive capacity (number of nymphs) of *Sipha flava* under artificial conditions. Treatment 1: *S. flava* and forage grass were under fluctuating CO_2 levels - avg. 440 ppm (greenhouse). Treatment 2: *S. flava* were maintained under fluctuating CO_2 levels - avg. 440 ppm (greenhouse), but fed forage grass under a constant high (500 ppm) CO_2 level (climate-controlled chamber). Mean longevity values followed by the same lower case letters were not significantly different, and neither were mean reproductive capacity values followed by the same upper case letters based on ANOVA and Tukey test.

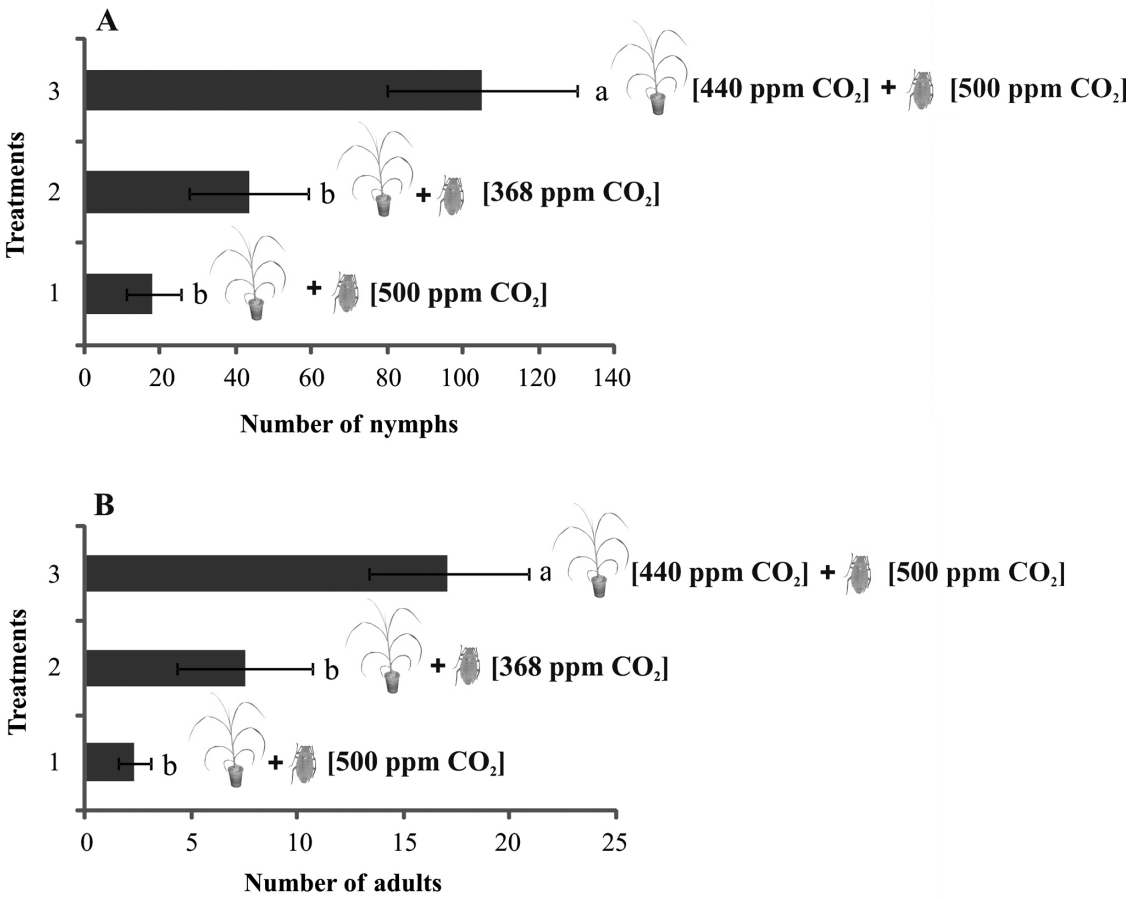

Fig. 3. Reproductive performance of *Sipha flava* kept under constant and fluctuating CO_2 environments. A) Upper panel - number of nymphs and B) Lower panel - number of adults. In Treatment 1, both *S. flava* and forage grass were kept under a constant high CO_2 level (500 ppm) (climate-controlled chamber). In Treatment 2, both *Sipha flava* and forage grass were maintained under fluctuating CO_2 levels (avg. 368 ppm) (climate-controlled chamber). In Treatment 3, *S. flava* were kept under a constant high CO_2 level (500 ppm) (climate-controlled chamber), but fed forage grass grown under fluctuating CO_2 levels (avg. 440 ppm) (greenhouse). Mean numbers of nymphs followed by the same lower case letter were not significantly different based on ANOVAS and Tukey tests; and likewise for mean numbers of adults.

Discussion

The effects of climate change on animal populations are of critical concern (Fleming & Volney 1995; Thomas et al. 2004). However, researchers are only beginning to investigate how insects respond to such changes (Mondor et al. 2005; Balanyá et al. 2006). Global climate change may alter ecosystem functioning and species interactions by promoting a shift in the geographical range of herbivores (Jepsen et al. 2008), by facilitating the spread new adventive and invasive species (e.g., Crow et al. 2008), and by altering the natural climatic control of herbivorous species (Jepsen et al. 2008).

Our results suggest that effects of elevated CO_2 on *S. flava* mediated through one of its food plants may affect the fitness of this insect pest. We found that aphids kept either in a constant CO_2 environment and fed plants grown in a greenhouse (fluctuating CO_2 levels) had significantly greater longevity than aphids fed either plants kept under constant (500 ppm) CO_2 or in a climate-controlled chamber with a fluctuating CO_2 environment with a lower avg. CO_2 concentration. However, no significant differences in the longevity or reproductive aspects of *S. flava* adults kept in a greenhouse were observed, regardless of the environment in which the plants were grown, hence other abiotic factors in the greenhouse such as higher light intensity may favor development of the insect. However, regarding reproduction in *S. flava* populations, aphids maintained in a greenhouse and fed on plants grown in a greenhouse produced significantly more progeny than did aphids consuming plants grown in a climate-controlled chamber with constant high (500 ppm)

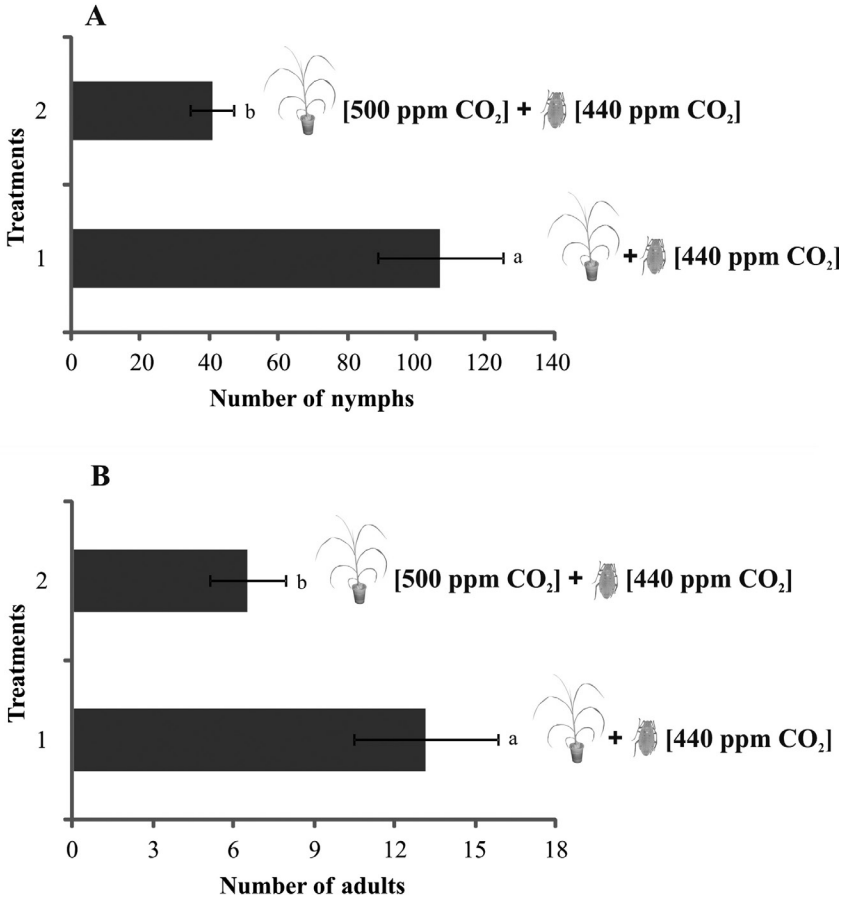

Fig. 4. Effects of forage grown either under a constant high CO_2 level (500 ppm), or under fluctuating CO_2 levels (avg. 440 ppm) on the reproductive success of *Sipha flava* held under fluctuating CO_2 levels (avg. 440 ppm). A) Upper panel - number of nymphs and B) Lower panel - number of adults. In Treatment 1, both *S. fava* and forage grass were maintained under fluctuating CO_2 levels (avg. 440 ppm) (greenhouse). In Treatment 2, *S. flava* were maintained under fluctuating CO_2 levels (avg. 440 ppm) (greenhouse), but the forage grass was grown under a constant high CO_2 level (500 ppm) (climate-controlled chamber). Mean numbers of nymphs followed by the same lower case letter were not significantly different based on ANOVA and Tukey test; and likewise for mean numbers of adults.

CO_2. These results suggest that our artificial CO_2 regime changed the physiology of the plants, thereby affecting longevity and fecundity of *S. flava* feeding on these plants.

Plant tissues changes under altered climate-controlled conditions affect food quality for herbivores and may in consequence alter the performance of herbivorous insects species (Zvereva & Kozlov 2006; Valkama et al. 2007). An explanation for this effect is that elevated CO_2 tends to increase photosynthesis and plant biomass (Will & Ceuleman 1997), while it reduces host plant quality for herbivores because of increased foliar carbon and secondary organic compounds (Zvereva & Kozlov 2006; Stiling & Cornelissen 2007) and decreased availability of nitrogen (Lawler et al. 1997; Norby et al. 1999).

Many studies have investigated alterations in plant responses to elevated CO_2 with respect to aphids (Hughes & Bazzaz 2001; Hunter 2001; Stacey & Fellowes 2002; Newman et al. 2003; Chen et al. 2004; Dermody et al. 2008; Mondor et al. 2010; Fu et al. 2010). Elevated CO_2 results in larger, more architecturally complex *Brassica oleracea* L. (Brassicales: Brassicaceae) plants with a higher tissue carbon-to-nitrogen ratio. The aphids, *Brevicoryne brassicae* (L.) and *Myzus persicae* (Sulzer) (Aphididae), exhibited different responses to these changes. *Brevicoryne brassicae* reared on plants grown in elevated CO_2 were larger and accumulated more fat, whereas the corresponding traits of *M. persicae* do not change (Stacey & Fellowes 2002). Populations of corn rootworm (*Diabrotica virgifera* Leconte) (Chrysomelidae)

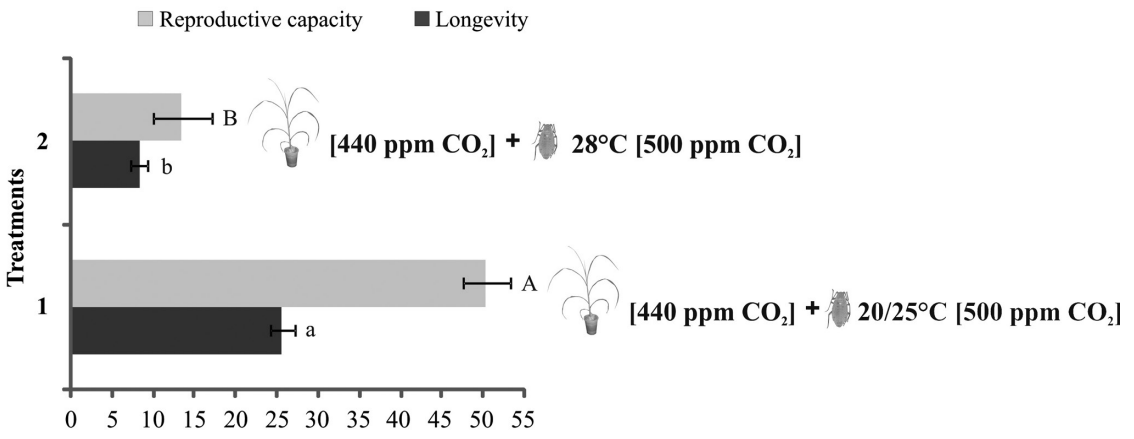

Fig. 5. Effects of temperature on longevity (days) and reproductive capacity (number of progeny) of *Sipha flava*. Both in Treatments 1 and 2, the forage grass used to feed the aphids was grown in a greenhouse under fluctuating CO_2 levels (avg. 440 ppm). However, in Treatment 1, the aphids were kept under a constant CO_2 level (500 ppm) (climate-controlled chamber) and 25 ± 2 °C during the day and 20 ± 2 °C at night. In Treatment 2, the aphids were kept under a constant 28 ± 2 °C both day and night. Mean longevity values (days) followed by different lower case letters were significantly different as were the reproductive capacity values (numbers of progeny) followed by different upper case letters based on ANOVA and Tukey test.

adults and soybean aphids (*Aphis glycines* Matsumura) (Aphididae) increased on soybeans grown under elevated CO_2 conditions (Dermody et al. 2008). Hughes et al. (2001) suggested that under future CO_2 levels, the population of *M. persicae* will increase, populations of *Acyrthosiphon pisum* Harris (Aphididae) will decrease; and populations of *Aphis nerii* Boyer de Fonscolombe, *Aphis oenotherae* Oestlund, and *Aulacorthum solani* (Kaltenbach) (Hemiptera: Aphididae) will not be affected. O'Neill et al. (2010) predicted that an increase in the production of volatiles in soybeans grown under elevated CO_2 will lead to larger herbivore outbreaks in the future.

Differences in the population densities of aphids, especially in relation to CO_2 elevation, vary with specific populations within a species; some populations will increase, decrease, or remain the same (Flynn et al. 2006). In our study, *S. flava* populations decreased when they were kept in a greenhouse and fed plants grown in either in a constant high (500 ppm) CO_2 environment or in fluctuating (avg. 368 ppm) CO_2 environments. *Sipha flava* populations also decreased when plants and insects were kept under a constant high (500 ppm) CO_2 concentration at 28 °C. The longevity and fertility of *S. flava* adults were lower when they were kept in a high (500 ppm) CO_2 concentration and a high temperature (28 °C) than when they were kept under the identical CO_2 concentration but lower diurnally fluctuating temperatures (25 °C/20 °C, day/night). These simultaneous effects of elevated CO_2 and temperature on aphids performance could also be a reflection of changes in plant chemistry.

Temperature elevation should not be overlooked when predicting the effects of climate change on plant - herbivore interactions (Newman 2004). Some authors concluded that temperature does not influence plant and herbivore responses to CO_2 elevation (Williams et al. 2000), whereas others have shown strong interactive effects between CO_2 and temperature (Johns & Hughes 2002; Johns et al. 2003). Flynn et al. (2006) showed that modifications of plant physiology under altered CO_2 and temperature do not impair and may actually enhance *Macrosiphum euphorbiae* Thomas aphid populations.

Although the population of *S. flava* decreased under elevated CO_2 and temperature conditions, additional studies should be performed to assess whether insects will increase consumption because of the poor food quality in an elevated CO_2 - high temperature environment. According to Coviella et al. (2000) and Hunter (2001), insects consuming plants grown under elevated CO_2 conditions exhibit increased consumption because of poor food quality of these plants.

Our results show that the population of *S. flava* decreased when fed on plants grown under the elevated CO_2 conditions alone and in combination with high temperature. This result may be used to predict the future populations of this insect as the concentration of atmospheric CO_2 continues to build.

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Table 3. Experiment 3: Duration of each nymphal stadium and survival of each nymphal instar when cohorts of 50 nymphs were kept in climate-controlled chambers with a constant $C0_2$ level of 500 PPM and 2 different temperature regimes. These nymphs were fed forage grass grown in a greenhouse with fluctuating $C0_2$ levels—avg. of 440 PPM. One climate-controlled chamber was maintained 25 ± 1 °C during the day and 20 ± 1 °C during the night (treatment 1), while another was maintained at 28 ± 1 °C both day and night (treatment 2).

	Treatments		Analyzed by ANOVA
Instar	1	2	*P*
		Duration (days)	
N1	2.47 ± 0.09 a n = 47	1.96 ± 0 0.07 b n = 48	0.000
N2	2.24 ± 0 0.06 a n = 46	1.98 ± 0 0.05 b n = 48	0.001
N3	2.13 ± 0 0.05 a n = 46	1.38 ± 0 0.08 b n = 47	0.000
N4	2.70 ± 0 0.08 a n = 45	1.81 ± 0 0.08 b n = 43	0.000
Total	9.80 ± 0 0.12 a n = 45	7.07 ± 0 0.08 b n = 43	0.000
		Nymphal survival (%)	
N1	92.00 ± 3.74 a n = 50	98.00 ± 2.00 a n = 50	0.195
N2	98.00 ± 2.00 a n = 47	97.60 ± 2.40 a n = 48	0.901
N3	97.77 ± 2.22 a n = 46	98.00 ± 2.00 a n = 48	0.943
N4	96.00 ± 2.45 a n = 46	97.00 ± 2.50 a n = 47	0.679
Total	88.00 ± 4.89 a n = 50	92.00 ± 3.74 a n = 50	0.534

Mean values followed by the same letter in the same row were not significantly different as determined by ANOVA and Tukey's test.

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