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Host plant-mediated effects of elevated CO_2 and temperature on growth and developmental parameters of *Zygogramma bicolorata* (Coleoptera: Chrysomelidae)

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Abstract

Mexican beetle, *Zygogramma bicolorata* Pallister (Coleptera: Chrysomelidae) is a potential weed control biocontrol agent in Australia, India and other countries. Its grubs and adults feed on the leaves of parthenium weed, *Parthenium hysterophorus* and check the further growth of the plant. Experiments were conducted to understand host plant-mediated effects of elevated temperature and elevated CO_2 on biocontrol agent *Z. bicolorata*. Food consumption, utilization, ecological efficiency and life-table parameters of *Z. bicolorata* were studied in grubs and adults stage up to diapause. Reduction of leaf nitrogen in parthenium weed foliage with a significant increase in carbon and C:N ratio was recorded at elevated CO_2. Elevated CO_2 and temperature had no effect on adult longevity before diapausing. Duration of egg's hatching, specific stages of grub and pupa of *Z. bicolorata* were significantly longer when beetles fed on leaves grown under elevated CO_2 but these parameters decreased significantly on leaves grown under elevated temperature. Significantly high consumption rates with low growth and digestion conversions were observed under elevated CO_2 and/or in coupled with elevated temperature. Elevated CO_2 and temperature-grown parthenium weed foliage also had a significant effect on *Z. bicolorata* intrinsic rate of increase (R), finite rate of increase (λ), mean generation time (T), and gross reproductive rate. Changed quality of parthenium weed leaves in elevated CO_2 and temperature levels resulted in the increase of consumption, slower food conversion rates, increase in developmental period with reduced reproduction efficiency of *Z. bicolorata*. Our results indicate that the reproduction efficiency of *Z. bicolorata* is likely to be reduced as the climate changes, despite increased feeding rates exhibited by grubs and adult beetles on parthenium weed foliage.

Introduction

The level of global atmospheric CO_2 concentration has increased from 284 to 397 ppm during the year 1832 to 2013 (Wheeler and von Braun, 2013). It has been estimated that CO_2 may increase from 600 to 1000 ppm by the end of 21st century (Stern and Taylor, 2007). The earth's global average surface temperature has increased by 0.78°C during the 20th century and it is expected to be increased from 1.8 to 4°C by the end of 21st century. However, the amount of increase is expected to be different across geographical locations (Choudhary *et al*., 2019). Increased CO_2 and temperature is likely to affect plants indirectly via climate change, and directly by producing changes not only in plant growth but also in plant's biochemical cycle (Kimball *et al*., 2002). High concentration of CO_2 may affect the eating habits of insect due to reduction in nutritional properties and self-defence of plants (Niziolek *et al*., 2013). An increasing proportion of carbon to nitrogen in plants leads to higher consumption of plant parts by insects (Bhumannavar and Balasubramanian, 1998; Hunter, 2001; Ainswort *et al*., 2007). Bezemer and Jones (1998) also reported more feeding by insects on plant foliage and stem parts because of 15% less content of nitrogen in the plant under elevated CO_2 conditions. Uptake of the high amount of CO_2 by plants increases photosynthesis rate, which ultimately produces very high amounts of sugar, ascorbic acid, phenols, starch, anthocyanins and flavonoids content in plants, therefore, more number of insects were attracted to them (Whittaker, 1999; Zavala *et al*., 2009; Niziolek *et al*., 2013). Adults of *Gratiana boliviana* (Coleoptera: Chrysomelidae) when reared at the high CO_2 level recorded low weight and smaller size (Diaz *et al*., 2012).

Parthenium or rag weed, *Parthenium hysterophorus* L. is a unique C_3-C_4 plant, which is an alien invasive herbaceous weed and has threatened agro-ecosystem and natural ecosystems of more than 30 countries in the world (Adkins and Shabbir, 2014). It also imposes big losses to grazing land productivity, livestock production and native biodiversity (Adkins and Navie, 2006). It has been categorized as one of the most noxious weeds in Australia (Dhileepan, 2012) and in India (Sushilkumar and Varshney, 2010; Sushilkumar, 2014). This weed has the capability to attack a wide range of environments due to its vigorous growth habit, high seed production and effective dispersal mechanisms (Bajwa *et al.*, 2016). Parthenium weed has spread in almost all the states of India and it is estimated to have invaded about 35 million hectares of land in India (Sushilkumar and Varsheny, 2010). Climatic factors also play a significant role in parthenium weed seed longevity in soil seed banks (Nguyen *et al.*, 2017). It has been found that if parthenium weed grown under elevated CO_2 (550 ppm) had a tremendous positive effect on the growth of root, stem, leaf, and flower (Nguyen *et al.*, 2017). Naidu (2013) also recorded a significant increase in growth of parthenium weed under elevated CO_2. Parthenium weed grown under elevated CO_2 concentration (700 ppm) reported high water usage, stomata conductance and the rate of transpiration (Pandey *et al.*, 2003). Increased plant height, biomass and seed production was also observed when parthenium weed was grown under elevated CO_2 (Navie *et al.*, 2005). Evidence strongly suggests that enhanced CO_2 and temperature, directly and indirectly, affect the distribution and ecosystem's structure and function of parthenium weed (Pandey *et al.*, 2003; Navie *et al.*, 2005; Naidu, 2013; Nguyen *et al.*, 2017).

An exotic biocontrol agent Mexican beetle, *Zygogramma bicolorata* Pallister (Coleptera: Chrysomelidae) is a parthenium weed leaf-feeding beetle. Its grubs and adults feed on the leaves of parthenium weed and cause heavy injury to the plant. The young grubs after hatching, congregate in the terminal and axillary buds causing heavy damage leading to stunted growth and reduced flower production. The high fertility, voracity and its host specificity towards parthenium weed made *Z. bicolorata* a good potential biocontrol agent (Jayanth and Nagarkatti, 1987; Sushilkumar, 2009). High food conversion potential of *Z. bicolorata* and its ability to eat the weed by both grub and adult stages can help increase the mass density of the insects and its effectiveness (Omkar and Uzma, 2011). Now it is well accepted that increased CO_2 concentration and temperature in the atmosphere will either directly or indirectly affect plant–insect interaction. Meager information is available on effects of these two factors either alone or in combination on development, emergence time and feeding capacity of insects, in general, and weeds eating biocontrol agents, in particular. No previous studies have been done on the effect of feeding potential and life cycle of *Z. bicolorata* reared on parthenium weed grown under elevated CO_2 either alone or interactive effect with temperature. In the present study, the effect of elevated CO_2 and temperature on growth and development of the *Z. bicolorata* feeding on parthenium weed foliage were examined using a factorial design. The complete life cycle of the weed controlling biocontrol agent reared on parthenium weed foliage in each of four $CO_2 \times$ temperature combinations was studied to determine the independent and interactive effect of elevated CO_2 and elevated temperature on the feeding, development and life table parameters of *Z. bicolorata*.

Materials and methods

Open-top chamber (OTC)

The present study was conducted at ICAR-Directorate of Weed Research, Jabalpur (23.90°N; 79.58°E), Madhya Pradesh, India in four OTCs, each having an area of 5.55 m^2. Four treatments included *e*Temp + *e*CO_2 [elevated temperature (ambient + 2°C) + elevated CO_2 (550 ± 50 ppm)], *a*Temp + *e*CO_2 [ambient temperature + elevated CO_2 (550 ± 50 ppm)], *e*Temp + *a*CO_2 [elevated temperature (ambient + 2°C) + ambient CO_2 (395 ppm)] and *a*Temp + *a*CO_2 [ambient temperature + ambient CO_2]. Elevated temperature was achieved through infrared heaters fitted inside the OTC chambers and precisely maintained with automatic control device through on/off mechanism by taking into account ambient temperature as a reference at a given time. The desired temperature was maintained round the clock throughout the experiment. Elevated CO_2 was achieved through the enrichment of CO_2 from an external source, which was continuously monitored and regulated based on the feedback from infrared gas analyzer (IRGA). Elevated CO_2 was maintained during sunshine only. Different treatments were imposed from 10 days after sowing (DAS) until the end of the experiment. The seeds of parthenium weed were sown in OTCs on 28 June 2017 by the broadcasting method and maintained.

Feeding trials

A hundred numbers of eggs of *Z. bicolorata* were brought into insect culture room having 26 ± 1°C temperature and 70 ± 10 RH from the stock culture at ICAR-Directorate of Weed Research, Jabalpur. Care was also taken to avoid mechanical injury during the transfer of eggs. These eggs were kept in one large plastic container (12×6 cm^2) for taking the grubs for experiments after hatching. Feeding trials of *Z. bicolorata* were initiated putting 1 g soft tender parthenium weed foliage (≈ 1 month old) plucked from four treatment OTCs, upon wet filter paper placed on the bottom of ten small size Petri-dishes for each treatment. The corresponding 1 g leaves were put into the oven at 40°C temperature for taking the dry weight. In each Petri-dish, one freshly hatched grub was transferred from the stocked plastic container. Thus, each Petri-dish was considered as one replication for each of the four treatments. From next day onward at one fixed time, each grub was removed from Petri-dish and weighed and averaged. The leftover leaves with faecal matter were removed from Petri-dish and put in-to oven at 40°C temperature for taking the dry weight. After cleaning the Petri-dishes, again 1 g weighed fresh leaves of parthenium weed were provided to grub in each Petri-dish. The procedure was repeated daily till the grubs went for pupation. Weight of each of the 10 grubs of different treatments was averaged. In the same way, mean leaf weight consumed by per grub and faecal matter per grub were calculated. Statistical analysis was performed using these means.

Fourth instar grubs showing discontinue feeding symptoms were removed from the Perti-dish and transferred into separate plastic container having 4 cm soil layer, to enable them for pupation. Newly emerged adults from pupation were put in pair (male and female) in new containers. Male and female adults were differentiated based on their morphological characteristics i.e. serrated and faint depression at the last abdominal ventrite in male with the smaller size as compared to female. Eggs laid by the females were counted and removed frequently for fecundity estimation. Utmost care was also taken to avoid mechanical injury during the transfer of eggs. Feeding data for adults were also followed as described for grub. In case of any mortality of grub or adult, it was replaced by the same age and weight grub or adult from the parallel-treated stock to maintain the constant number in each treatment.

Table 1. Change in total carbon (%), nitrogen (%) and C:N ratio (mean ± SD) of parthenium weed foliage grown in ambient or elevated CO_2 level under ambient or elevated temperature and ANOVA results of main effects of CO_2 and temperature and their interactions effect

Treatment	Carbon (%)		Nitrogen (%)		C:N ratio	
CO_2 effect						
Ambient (395 ppm)	36.42 ± 1.63^{A}		4.87 ± 0.30^{B}		7.74 ± 0.80^{A}	
Elevated (550 ± 50 ppm)	40.39 ± 1.25^{B}		3.85 ± 0.37^{A}		10.68 ± 1.42^{B}	
Temperature effect						
Ambient	38.27 ± 4.25		4.29 ± 0.99		9.43 ± 3.20	
Elevated (ambient ± 2°C)	38.54 ± 1.36		4.34 ± 0.32		8.99 ± 1.01	
Interaction						
eCO_2 + *e*Temp	39.50 ± 1.45^{bc}		4.11 ± 0.40^{ab}		9.67 ± 0.92^{b}	
aCO_2 + *e*Temp	37.58 ± 0.90^{b}		4.57 ± 0.56^{ab}		8.31 ± 0.87^{ab}	
*a*Temp + eCO_2	41.27 ± 1.82^{c}		3.59 ± 0.63^{a}		11.69 ± 1.38^{c}	
*a*Temp + aCO_2	35.26 ± 0.74^{a}		4.99 ± 0.69^{ab}		7.17 ± 0.94^{a}	
Analysis of variance (ANOVA)						
Factor	*F*(1,16)	*P*	*F*(1,16)	*P*	*F*(1,16)	*P*
CO_2	**78.72**	**<0.001**	**4.29**	**0.003**	**90.27**	**<0.001**
Temperature	0.37	0.63	0.05	0.71	2.01	0.37
Temperature × CO_2	**20.85**	**0.002**	**11.55**	**0.001**	**25.84**	**0.004**

Means followed by different letters in the same column are significantly different between different treatments levels by Tukey HSD test at $P = 0.05$ significance level (marked in bold).

Simultaneously, another experiment was conducted to find out the water content in grub and adults. For that purpose, five grubs and adults from each batch of stock culture and treatment were killed and dried to determine the average amount of water in them by taking drought loads. The data of water content were used for various growth indices of grub and adult of *Z. bicolorata*.

Various performance indices relating to grub and adult weight, leaf weight consumed and faecal matter excreted in terms of relative growth rate (RGR), relative consumption rate (RCR), the efficiency of conversion of ingested food (ECI), the efficiency of conversion of digested food (ECD) and approximate digestibility (AD) were calculated following the methods of Waldbauer (1968).

Life table parameter estimation of Z. bicolorata

The computer program, TWOSEX-MS Chart (Chi, 2013), for the age-stage two-sex life table analysis in VISUAL BASIC version 6 for the Windows system, available on http://140.120.197.173/Ecology/ (National Chung Hsing University) was used for life table parameters estimation. Generation time (T), intrinsic rate of increase (*rm*), net reproductive rate (*Ro*), gross reproductive rate (GRR) and finite rate of increase (λ) of *Z. bicolorata* were calculated for treatments effect detection. The standard errors of each population parameter were analyzed via a bootstrap approach with a sample size of 100,000 (Efron and Tibshirani, 1993).

Biochemical analyses of parthenium weed leaves grown under different OTC treatment

Leaf with twig samples from each OTC used in the feeding experiment were analyzed for carbon, nitrogen and their ratio. Samples were dried at 60°C and subsequently ground to powder to determine carbon and nitrogen concentrations. Leaf carbon and nitrogen were measured using a CHN analyzer (Model NA 15000 NA, Carlo Erba Strumentazione, Italy) using standard procedures (Jackson, 1973).

Statistical analyses:

The effect of treatment on biochemical changes in plant, consumption parameters, developmental time and life table parameters of *Z. bicolorata* were analyzed by a General Linear Model (GLM) with CO_2 concentration and temperature levels included as factors (SPSS 21.0, 2018). GLM and analysis of variance (ANOVA) procedures were satisfied the assumptions of normality and homogeneity of variances using suitable transformations of data, if necessary. Data of carbon content in plant and AD in both grub and adult were arcsine transformed before analyses. When a significant interaction occurred between CO_2 and temperature factors in the GLM analysis, Tukey's HSD *posthoc* test was carried out to compare the means at the 5% significance level. The differences among life parameters table treatments were analyzed with a paired bootstrap test at the 5% significance level.

Results

Biochemical analyses of parthenium weed leaves

Leaf nitrogen content was distinctly lower in elevated CO_2-treated parthenium weed foliage (main effect of CO_2 level, $F_{1,16} = 78.72$, $P < 0.001$). While, elevated CO_2 increased carbon content in both ambient and elevated temperature conditions (temperature × CO_2 interactions, $P = 0.002$). Parthenium weed grown under elevated CO_2 were having a significantly higher relative proportion of carbon to nitrogen (C: N ratio) (main effect of CO_2 level, $P < 0.001$). Consequently, the change in the C:N ratio was considerably higher in elevated CO_2 but it decreased under elevated temperature (temperature × CO_2 interactions, $F_{1,16} = 25.84$, $P = 0.004$) (table 1). Increase in temperature of 2°C had no significant effect on biochemical changes in parthenium weed leaves.

Variation in growth and development performance of Z. bicolorata

Elevated CO_2 concentration (as the main factor) grown parthenium weed foliage was significantly affected all the consumption and food utilization parameters of *Z. bicolorata* (tables 2 and 3). Elevated CO_2 and temperature (as the main factor, $P = 0.001$) and its interactions ($P = <0.001$) had significantly changed the consumption of parthenium weed foliage by both grubs and adults of *Z. bicolorata* (tables 2 and 3). Temperature as the main factor was not affected RCR and RGR indices in grub stage while in the adult stage it was significantly affected by both elevated CO_2 and temperature (main factor) and its interaction ($P = <0.001$) (table 3). RGR of both stages was not affected by elevated temperature while in elevated CO_2 it was changed significantly. The main effect of elevated CO_2 and temperature was recorded significant on AD of adult and grubs while the non-significant effect was recorded on interactions of elevated CO_2 and temperature concentrations. The conversion efficiency of ingested food (ECI) in grub and adult stage of *Z. bicolorata* was recorded significantly lower in elevated CO_2 and temperature and its interactions (tables 2 and 3). Parthenium weed grown under elevated CO_2 had a significant negative impact on the conversion efficiency of digested food (ECD) in grub and adult stage ($P < 0.001$) (table 2).

Substantial differences were observed in developmental parameters of *Z. bicolorata* when reared on elevated CO_2 and temperature and their combinations (table 4). Elevated CO_2 (the main effect of CO_2 level, $P < 0.001$) had a significant increase or decrease of the developmental duration of immature stages except for adults of *Z. bicolorata*. Developmental duration of immature stages (egg and grub) were significantly increased under elevated CO_2 condition (main effect of CO_2 level, $P < 0.001$) except third instar grub. In contrast to CO_2, elevated temperature significantly decreased the developmental duration of egg hatching, second, third and fourth instar grubs (main effect of temperature level, $P < 0.001$). At the same time, interactions (temperature × CO_2) recorded a significant impact only on developmental durations of second and third instar grubs (table 4). No significant effect of temperature and CO_2 alteration conditions and its interactions was observed on adult senescence before going to adult diapause (table 4).

Impact of elevated CO_2 and temperature and their interactions on life table parameters of Z. bicolorata

Impact of elevated CO_2 and temperature and their interactions on *Z. bicolorata* life table (net reproductive rate, GRR, intrinsic rate of increase, finite rate of increase, mean generation time) parameters were recorded and summarized in table 5. Elevated CO_2 and temperature showed significant differences (increase or decrease) in all the life table parameters of *Z. bicolorata* ($P < 0.001$) except net reproductive rate (R_0), where elevated temperature impact was non-significant (table 5). The main effect of CO_2 significantly reduced net reproductive rate (R_0) (481.86 ± 86.52 in ambient 201.28 ± 52.33 to temperature × CO_2 interactions, $F_{1,396} = 68.99$, $P < 0.001$). The significant impact of the main factors (CO_2, $F_{1,396} = 2930.01$, $P < 0.001$ and temperature, $F_{1,396} = 2677.10$, $P < 0.001$) and their interactions (temperature × CO_2, $F_{1,396} = 2677.10$, $P < 0.001$) on mean generation time was observed

Table 2. ANOVA results of the main effects of CO_2 and temperature and their interactions effect on consumption and food utilization parameters (mean days ± SD) of *Zygogramma bicolorata*

	Grub indices						Adult indices					
	CO_2		Temperature		Temperature × CO_2		CO_2		Temperature		Temperature × CO_2	
Measured indices	F(1,16)	P	F (1,16)	P	F(1,16)	P	F(1,16)	P	F(1,16)	P	F(1,16)	P
Consumption (mg day^{-1} $ind.^{-1}$)	**80.17**	**<0.001**	**7.84**	**0.013**	**32.52**	**<0.001**	**6447.42**	**<0.001**	**2638.95**	**<0.001**	**1161.80**	**<0.001**
Relative consumption rate (mg day^{-1} $ind.^{-1}$)	**73.18**	**<0.001**	0.001	0.998	**63.45**	**<0.001**	**1325.83**	**<0.001**	**2231.30**	**<0.001**	**550.56**	**<0.001**
Relative growth rate (mg day^{-1} $ind.^{-1}$)	**444.22**	**<0.001**	6.44	0.06	**20.73**	**<0.001**	**484.53**	**<0.001**	3.04	0.100	**7.96**	**0.012**
Approximate digestibility (%)	**20.78**	**<0.001**	**9.29**	**0.008**	0.27	0.606	**59.28**	**<0.001**	**35.12**	**<0.001**	0.009	0.925
Efficiency of conversion of ingested food (%) (ECI)	**544.39**	**<0.001**	**24.90**	**<0.001**	**189.71**	**<0.001**	**747.18**	**<0.001**	**116.71**	**<0.001**	**5.82**	**0.028**
Efficiency of conversion of digested food (%) (ECD)	**224.30**	**<0.001**	2.23	0.154	**49.65**	**<0.001**	**640.38**	**<0.001**	**110.03**	**<0.001**	2.11	0.165

Statistically significant effects at $P = 0.05$ are marked in bold.

Table 3. Consumption and food utilization parameters (mean days ± SD) of *Zygogramma bicolorata* on parthenium weed grown in ambient or elevated CO_2 level under ambient or elevated temperature conditions.

Treatment	Consumption (mg day^{-1} ind. $^{-1}$)	Relative Consumption rate (mg day^{-1} ind. $^{-1}$)	Relative growth rate (mg day^{-1} ind. $^{-1}$)	Approximate digestibility (%)	Efficiency of conversion of ingested food (%) (ECI)	Efficiency of conversion of digested food (%) (ECD)
Grub indices						
CO_2 effect						
Ambient (395 ppm)	8.42 ± 0.87^A	2.28 ± 0.30^A	0.16 ± 0.001^A	84.58 ± 2.87^A	8.77 ± 1.54^B	10.37 ± 1.44^A
Elevated (550 ± 50 ppm)	9.72 ± 0.30^B	2.73 ± 0.29^B	0.20 ± 0.003^B	89.29 ± 1.65^B	6.06 ± 0.72^A	9.80 ± 0.93^B
Temperature effect						
Ambient	8.87 ± 1.51^A	2.50 ± 0.62	0.18 ± 0.03	88.54 ± 2.72^B	7.70 ± 1.05^B	8.76 ± 1.35
Elevated (ambient ± 2°C)	9.27 ± 0.33^B	2.51 ± 0.23	0.17 ± 0.02	85.33 ± 3.94^A	7.12 ± 0.95^A	8.40 ± 1.34
Interactions						
*e*Temp + *e*CO_2	9.51 ± 0.46^{bc}	2.52 ± 0.17^b	0.17 ± 0.004^a	88.12 ± 6.90	6.56 ± 0.45^b	7.45 ± 0.56^a
*a*Temp + *e*CO_2	9.93 ± 0.38^c	2.94 ± 0.15^c	0.16 ± 0.003^a	90.46 ± 5.78	5.54 ± 0.17^a	6.13 ± 0.23^a
*e*Temp + *a*CO_2	9.03 ± 0.24^b	2.49 ± 0.16^b	0.19 ± 0.001^b	82.54 ± 5.27	7.68 ± 0.46^c	9.34 ± 0.87^b
*a*Temp + *a*CO_2	7.80 ± 0.40^a	2.06 ± 0.11^a	0.20 ± 0.003^c	86.61 ± 4.61	9.86 ± 0.49^d	11.38 ± 0.51^c
Adult indices						
CO_2 effect						
Ambient (395 ppm)	3.81 ± 0.55^A	0.61 ± 0.10^A	0.02 ± 0.00^B	81.53 ± 1.87^A	3.87 ± 0.45^B	4.75 ± 0.66^B
Elevated (550 ± 50 ppm)	7.43 ± 2.72^B	0.83 ± 0.31^B	0.01 ± 0.00^A	84.78 ± 1.66^B	1.78 ± 0.71^A	2.11 ± 0.88^A
Temperature effect						
Ambient	6.78 ± 3.65^B	0.87 ± 0.27^B	0.02 ± 0.00	84.41 ± 2.19^B	3.24 ± 0.97^B	2.89 ± 0.94^A
Elevated (ambient ± 2°C)	4.46 ± 1.48^A	0.57 ± 0.15^A	0.02 ± 0.00	81.91 ± 2.41^A	2.41 ± 0.70^A	3.98 ± 1.56^B
Interactions						
*e*Temp + *e*CO_2	5.50 ± 0.13^c	0.61 ± 0.05^b	0.012 ± 0.001^a	83.61 ± 3.40	2.28 ± 0.26^b	2.73 ± 0.32
*a*Temp + *e*CO_2	9.36 ± 0.16^d	1.05 ± 0.06^d	0.013 ± 0.001^a	85.95 ± 1.46	1.28 ± 0.08^a	2.49 ± 0.16
*e*Temp + *a*CO_2	3.41 ± 0.14^a	0.53 ± 0.02^a	0.022 ± 0.003^b	80.20 ± 3.07	4.18 ± 0.19^d	5.22 ± 0.31
*a*Temp + *a*CO_2	4.19 ± 0.13^b	0.68 ± 0.05^c	0.024 ± 0.002^c	82.86 ± 3.16	3.54 ± 0.09^c	4.28 ± 0.41

Means followed by different letters in the same column are significantly different between different treatments levels by Tukey HSD test at $P = 0.05$ significance level.

where the effect of elevated CO_2 increased the mean generation time while elevated temperature shortened it by 3 days.

Discussion

It is well understood that photosynthesis and growth of many plants are stimulated when grown under elevated CO_2 and temperature conditions with the reduction in leaf N content and wider C:N ratio (Stitt and Krapp, 1999; Gao *et al*., 2008; Himanen *et al*., 2008). Similarly, reduction in nitrogen content and protein concentration was observed more than 12% in C3 plant under elevated CO_2 conditions (Ainsworth and Long, 2005). The increased C:N ratio causes a reduction in food quality that might have caused the higher feeding by insects (Rao *et al*., 2012). In the present study, a significant increase (11.69%) in C:N ratio was observed under elevated CO_2 concentration. The increase in plant biomass observed under elevated CO_2 concentration may be due to availability of more carbon and reduced level of protein content, which might have increased the rate of photosynthesis (Singh *et al*., 2018). High carbon with low protein content leads to reduced plant nutritional quality (Rao *et al*., 2012) that might have caused the higher feeding by the grubs and adults in efforts to get more nutrition by eating the foliage of parthenium weed in the present study.

The higher feeding rates were observed by grubs and adults of *Z. bicolorata* when fed on elevated CO_2 grown parthenium weed leaves. It was well-identified that most of leaf-feeding insects showed a compensatory increase in food consumption (Lee *et al*., 2002) due to low nitrogen content, which has also been established in the parthenium weed foliage consumption by *Z. bicolorata* in the present study. The amount of nitrogen found in the leaves affects the development of grubs and adult and their feeding capacity.

Table 4. Developmental time of immature stages and senescence times (mean days ± SE) of adult life stages of *Zygogramma bicolorata* reared on parthenium weed grown in different environmental conditions.

Treatment	Egg	G1[a]	G2	G3	G4	Pupa	Adult
CO_2 effect							
Ambient (395 ppm)	3.69 ± 0.31^{B}	2.08 ± 0.01^{A}	2.62 ± 0.28^{A}	2.73 ± 0.63^{B}	3.91 ± 0.43^{A}	9.70 ± 0.71^{A}	87.41 ± 4.05
Elevated (550 ± 50 ppm)	4.28 ± 0.42^{A}	2.80 ± 0.01^{B}	2.89 ± 0.17^{B}	3.30 ± 0.13^{A}	4.60 ± 0.12^{B}	11.58 ± 0.32^{B}	83.53 ± 1.37
Temperature effect							
Ambient	4.25 ± 0.48^{B}	2.48 ± 0.47	2.88 ± 0.07^{B}	3.30 ± 0.19^{B}	4.45 ± 0.33^{B}	10.78 ± 1.02	87.39 ± 4.08
Elevated (ambient ± 2°C)	3.72 ± 0.36^{A}	2.47 ± 0.57	2.63 ± 0.30^{A}	2.74 ± 0.62^{A}	4.06 ± 0.64^{A}	10.50 ± 1.20	83.55 ± 1.40
Interaction							
*e*Temp + *e*CO_2	4.53 ± 0.09	2.80 ± 0.05	2.96 ± 0.05^{b}	3.26 ± 0.06^{b}	4.85 ± 0.17	12.41 ± 0.18	82.56 ± 5.56
*a*Temp + *e*CO_2	5.28 ± 0.07	2.84 ± 0.05	3.02 ± 0.05^{b}	3.50 ± 0.07^{b}	5.09 ± 0.14	13.23 ± 0.13	84.50 ± 5.75
*e*Temp + *a*CO_2	3.71 ± 0.09	2.08 ± 0.06	2.56 ± 0.06^{a}	2.33 ± 0.08^{a}	3.59 ± 0.09	9.97 ± 0.16	84.54 ± 2.70
*a*Temp + *a*CO_2	4.19 ± 0.08	2.10 ± 0.06	2.82 ± 0.06^{b}	3.23 ± 0.06^{b}	4.54 ± 0.12	10.27 ± 0.12	90.27 ± 4.32

Analysis of variance (ANOVA)

Factor	$F_{(1,396)}$	P	$F_{(1,283)}$	P	$F_{(1,256)}$	P	$F_{(1,230)}$	P	$F_{(1,203)}$	P	$F_{(1,158)}$	P	$F_{(1,124)}$	P
CO_2	**30.40**	**<0.001**	**123.76**	**<0.001**	**14.52**	**<0.001**	**25.23**	**<0.001**	**25.06**	**<0.001**	**19.29**	**<0.001**	0.688	0.409
Temperature	**21.96**	**<0.001**	1.07	0.301	**12.34**	**0.001**	**23.94**	**<0.001**	**8.50**	**0.004**	0.011	0.917	0.672	0.414
Temperature × CO_2	0.845	0.359	1.77	0.184	**4.55**	**0.034**	**6.40**	**0.012**	2.76	0.098	0.129	0.720	0.164	0.687

[a]G1: first instar grub; G2: Second instar grub; G3: third instar grub; G4: fourth instar grub.
Means followed by different letters in the same column are significantly different between different treatments levels by Tukey HSD test at $P = 0.05$ significance level (marked in bold).

Table 5. Life table parameters (mean ± SE) of *Zygogramma bicolorata* reared on parthenium weed in different environmental conditions.

Treatment	R		λ		R_0		T		GRR	
CO_2 effect										
Ambient (395 ppm)	0.15 ± 0.01^{B}		1.16 ± 0.0^{B}		190.37 ± 15.42^{B}		41.73 ± 2.22^{A}		1093.81 ± 52.12^{B}	
Elevated (550 ± 50 ppm)	0.11 ± 0.01^{A}		1.12 ± 0.00^{A}		425.59 ± 32.51^{A}		49.90 ± 1.90^{B}		791.01 ± 46.67^{A}	
Temperature effect										
Ambient	0.12 ± 0.03^{A}		1.13 ± 0.03^{A}		330.66 ± 74.05		47.06 ± 1.53^{B}		977.35 ± 116.27^{B}	
Elevated (ambient ± 2°C)	0.13 ± 0.03^{B}		1.14 ± 0.03^{B}		285.30 ± 53.45		44.57 ± 1.14^{A}		907.47 ± 1.23^{A}	
Interaction										
*e*Temp + *e*CO_2	0.108 ± 0.006		1.114 ± 0.006		201.28 ± 52.33^{a}		48.99 ± 0.49^{c}		758.01 ± 152.99	
*a*Temp + *e*CO_2	0.102 ± 0.007		1.107 ± 0.007		179.47 ± 51.47^{a}		50.82 ± 0.56^{d}		824.02 ± 178.02	
*e*Temp + *a*CO_2	0.147 ± 0.006		1.158 ± 0.007		369.32 ± 75.88^{b}		40.16 ± 0.36^{a}		1056.94 ± 164.28	
*a*Temp + *a*CO_2	0.142 ± 0.004		1.153 ± 0.006		481.86 ± 86.52^{b}		43.30 ± 0.41^{b}		1130.68 ± 158.01	
Analysis of variance (ANOVA)										
Factor	F(1,396)	P	F(1,396)	P	F(1,396)	P	F(1,396)	P	F(1,396)	P
CO_2	**4345.04**	**<0.001**	**4405.03**	**<0.001**	**989.06**	**<0.001**	**2930.01**	**<0.001**	**293.85**	**<0.001**
Temperature	**69.21**	**<0.001**	**69.46**	**<0.001**	7.97	0.06	**2677.10**	**<0.001**	**11.24**	**0.001**
Temperature × CO_2	6.02	0.065	5.25	0.072	**68.99**	**<0.001**	**315.29**	**<0.001**	1.35	0.245

R, intrinsic rate of increase; *λ*, finite rate of increase; R_0, net reproductive rate; *T*, mean generation time; GRR, gross reproductive rate.
Standard errors were analyzed using 100,000 bootstraps replicates.
Means followed by different letters in the same column are significantly different between different treatments levels by the paired bootstrap test (marked in bold).

The lack of nitrogen showed a decrease in the performance of the insects. When insects eat nitrogen-deficient plants, they eat more quantities, which, in turn, increase the inclusion capacity of food (Coviella *et al.*, 2000; Hunter, 2001). Similarly, the consumption pattern of insect herbivores was reported (Robinson *et al.*, 2012) to be influenced due to the dilution of biochemical composition of crop plants grown at elevated CO_2 conditions. Present study results were in line to show the response of *Z. bicolorata* to poor foliage quality, particularly the low N content and wide C:N ratio. Low nitrogen content compelled grubs and adults to chew more foliage of parthenium weed in efforts to get more protein for development and reproduction, which may result in more defoliation of the weed (Coviella *et al.*, 2000).

Growth performance indices (AD, RCR, RGR, ECD and ECI) significantly differed with elevated CO_2 conditions in this study. The RGR of grubs and adults was significantly lower when fed on parthenium weed leaves grown under elevated conditions (temperature and CO_2) as compared to ambient conditions. The AD was found increased in elevated CO_2 and temperature. This is generally supposed that CO_2 induced changes in foliar chemical compounds play the most important role in the activities of plant-feeding insects. In the present study, grubs and adults consumed and digested extra food, but development was slow and took 1–5 days more at various stages of development when reared on different CO_2 treatment combinations than the ambient conditions. High growth performance indices under ambient conditions in our study have also been reported by Omkar and Uzma (2011) in *Z. bicolorata* fed on parthenium weed.

Similarly, Rao *et al.* (2009) reported that herbivores reared on elevated CO_2 conditions exhibited a high consumption rate and low development rate. They also reported that efficiency of conversion of digested food, the efficiency of conversion of ingested food and RGR decreased in case of tested herbivores larvae when insects were reared on foliage grown under increased CO_2 concentrations (550 and 700 ppm). In Coleopteran biocontrol agent, *Gratiana boliviana,* immature survival and developmental time were negatively affected at high $CO_{2,}$ but not at ambient conditions (Diaz *et al.*, 2012). High consumption rate was recorded in *Popillia japonica* when reared on elevated CO_2 and elevated temperature grown leaves (Niziolek *et al.*, 2013). Rao *et al.* (2012) reported similar findings on tobacco caterpillar, *Spodoptera litura* (Fabricius) (Noctuidae: Lepidoptera). Low efficiency of conversion of digested food in these conditions may result from a requisite of tested insects to metabolize digested food in order to turn out into water (Lindroth, *et al.*, 1993).

In the present study, elevated CO_2 and temperature had a significant influence on the entire life table parameters of *Z. bicolorata*. Even though *Z. bicolorata* females were able to lay eggs at all elevated temperatures and CO_2 combinations, but significant changes were observed in life table parameters under elevated CO_2 and temperature conditions. The value of intrinsic rate was introduced as a useful theory for studying insect populations by Huang and Chi (2012). In the present study, a significant decrease in intrinsic rate with increased generation time was noticed with elevated CO_2 conditions. The significant changes of the intrinsic rate of *Z. bicolorata* in the present study could be results of decrease in foliage N because nitrogen is the single most important limiting resource for phytophagous insects (Gao *et al.*, 2008). The GRRs were gradually decreased in elevated CO_2 and temperature compared to ambient conditions. Significant changes in life table parameters in repose to increased CO_2 (Johns *et al.*, 2003; Rao *et al.*, 2012) and temperature (Chen *et al.*, 2017; Dyer *et al.*, 2013) were recorded in leaf chewing insects in the line of the present study.

Conclusion

The present study revealed the significant impacts of elevated CO_2 and interaction with elevated temperature on leaf nitrogen and carbon content in parthenium weed foliage. Growth performance indices (AD, RCR, RGR, ECD and ECI) and developmental time of various stages of *Z. bicolorata* were changed significantly in response to elevated CO_2 and/or elevated temperature. The values of life table parameters *viz.,* intrinsic rate of increase, finite rate of increase, net reproductive rate and GRR were reduced significantly under elevated CO_2 and/or interaction with elevated temperature. The mean generation time was significantly reduced in elevated temperature while it was increased in elevated CO_2 and its combination with temperature. Present findings indicated that the interactive effects of CO_2 and temperature would have changed the biological parameters of parthenium weed and its biocontrol agent, *Z. bicolorata.* It also points with an advantage of high feeding rate and negatively low reproduction efficiency of this potential weed controlling biocontrol agent. Further studies are needed to examine the mechanisms involved in the results of the present study.

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