Host plant (*Ricinus communis* Linn.) mediated effects of elevated CO_2 on growth performance of two insect folivores

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Elevated atmospheric CO_2 expected in the near future as a consequence of increasing emissions will alter the quantity and quality of plant foliage, which in turn can influence the growth and development of insect herbivores. Feeding trials with two foliage feeding insect species, *Achaea janata* and *Spodoptera litura* were conducted using foliage of castor plants grown under four concentrations of CO_2, viz. 700 ppm CO_2 inside open top chamber (OTC), 550 ppm CO_2 inside OTC, ambient CO_2 (350 ppm) inside OTC and ambient CO_2 in the open. Biochemical analysis of foliage revealed that plants grown under elevated CO_2 had lower N, and higher C, C/N ratio and polyphenols. Compared to the larvae fed on ambient CO_2 foliage, the larvae fed on 700 and 550 ppm CO_2 foliage exhibited greater consumption. Larval duration also increased by two days. The 700 and 550 ppm CO_2 foliage was more digestible with higher values of approximate digestibility. The relative consumption rate of larvae increased whereas the efficiency parameters, viz. efficiency of conversion of ingested food (ECI), efficiency of conversion of digested food (ECD), and relative growth rate (RGR) decreased in case of larvae grown on 700 and 550 ppm CO_2 foliage. The consumption and weight gain of the larvae were negatively and significantly influenced by leaf nitrogen, which was found to be the most important factor affecting consumption and growth of larvae.

Keywords. *Achaea janata*, biochemical analysis, castor, consumption, elevated CO_2, insect performance indices, *Spodoptera litura*.

CARBON cycle models project atmospheric carbon dioxide concentration of 540–970 ppm by the end of next century as a result of fossil fuel use and global deforestation[1]. Many plant species respond to enriched atmospheric CO_2 by enhanced photosynthetic rates and increase in biomass[2] as well as alterations in leaf quality factors. This might affect growth of leaf eating insects through altered consumption and digestibility[3]. In plants grown in enriched CO_2 condition, reduction in leaf nitrogen can result in a nutritionally depleted food source for leaf eating insects[4]. Because leaf nitrogen is considered essential for growth and reproduction of insects[5], a reduction in nitrogen content of leaves grown under elevated CO_2 may elicit strong responses by them. As a consequence of these tight ecological linkages, the interplay between plants and herbivorous insects in the tropics can be affected by the perturbations of climate change.

The effect of elevated atmospheric CO_2 on leaf quality of castor (*Ricinus communis*) and its impact on growth characteristics of two leaf feeding caterpillars are reported here. The castor semilooper, *Achaea janata* and the tobacco caterpillar, *Spodoptera litura* occur during early and late stages of growth of castor respectively. Both larvae feed on the foliage and complete their life cycle. Castor is an important non-edible oilseed crop grown in many parts of the arid and the semi-arid regions of India. The crop is grown for its beans from which oil is extracted. Castor oil and its derivatives have several industrial applications.

The incidence of semilooper is noticed up to early reproductive phase of castor plant[6]. During outbreaks, it causes extensive defoliation, affecting gross photosynthesis. Caterpillars also consume tender capsules. It is estimated that yields can decrease by 30–50% due to the semilooper alone. The tobacco caterpillar occurs during the late stage of castor plants and causes extensive defoliation. Larvae attack tender capsules and can cause yield losses of 25–40%. To investigate how CO_2 mediated changes in leaf phytochemistry affect growth characteristics of *A. janata* and *S. litura* larvae, feeding trials were conducted in the laboratory.

Materials and methods

Production of leaf material

Three square type open top chambers (OTCs) of $4 \times 4 \times 4$ m dimensions, were constructed at Central Research Institute for Dryland Agriculture (CRIDA), Hyderabad, two for maintaining elevated CO_2 concentrations of 700 ± 25 and 550 ± 25 ppm CO_2 and one for ambient CO_2. An

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automatic CO_2 enrichment technology was developed by adapting the software SCADA to accurately maintain the desired levels of CO_2 inside the OTCs. The concentration of CO_2 in the chambers was monitored by a non-dispersive infrared (NDIR) gas analyzer. Castor (variety DCS9) plants were grown during the monsoon season of 2004–05 in the three OTCs and also in the open, outside the OTCs. The concentration of CO_2 in the atmosphere (ambient) was taken as 350 ± 25 ppm[7]. Thus, castor plants were grown under four CO_2 conditions: 700 ± 25 ppm CO_2 inside OTC (700 CO_2), 550 ± 25 ppm CO_2 inside OTC (550 CO_2), ambient CO_2 inside OTC (350 CO_2 OTC) and ambient CO_2 in the open (350 CO_2 open).

Biochemical analysis of foliage

Leaf tissue from each plant used in the feeding experiment was analysed for carbon, nitrogen and polyphenols. To determine carbon and nitrogen concentrations, samples were dried at 80°C and subsequently ground to powder. Leaf carbon and nitrogen were measured using a CHN analyzer (Model NA 1500 N, Carlo Erba Strumentazione, Italy) using standard procedures[8]. Total soluble polyphenols (hydrolysable tannins, condensed tannins and non-tannin polyphenols) were determined by the Folin–Denis method[9]. For this, leaf samples were dried at 40°C for 48 h. Dried leaf samples were ground to powder and phenolics were extracted with CH_3OH. The concentration of polyphenols in the extract was determined spectrophotometrically using tannic acid as the standard, and the results were expressed as percentage tannic acid equivalents (TAE).

Feeding trials

A laboratory colony was established using eggs obtained from insect culture maintained at CRIDA. Stock cultures of castor semilooper, and tobacco caterpillar were maintained on leaves of castor plants grown in the open condition, i.e. 350 CO_2. At 10 am on the day of initiating the feeding trial, freshly hatched neonates were placed in petri dishes of 110 mm diameter and 10 mm height. Ten neonates were kept in each petri dish, forming one replication. Five such replications were kept for each of the four CO_2 conditions (treatments). Before placing the neonates, a moistened filter paper was kept at the bottom of the petri dish to maintain leaf turgidity. A castor leaf disc of 4 cm was punched out from a fully grown leaf obtained from a corresponding treatment, weighed, and placed on the moist filter paper, and the 10 neonates were placed on the leaf disc. The petri dishes were closed after placing a moistened paper towel of 5×1.5 cm on the inner surface of the lid to maintain air humidity. The petri dishes were then placed in a controlled chamber maintained at 20°C with a 14-h day/10-h night cycle. Light intensity inside the chamber during the 14 h day period was maintained at 550 μmol m^{-2} s^{-1}. At 10 am, the next day, the petri dishes were opened, the weight of the ten larvae together was recorded and the larvae were returned to a petri dish prepared in the same manner as described earlier, with a new leaf disc of known weight. The leaf remaining after feeding and faecal matter excreted by the 10 larvae was dried to a constant weight at 40°C in an oven and dry weights were recorded. The same process was repeated each day for 4 days. The weight of the 10 larvae was divided by 10 to arrive at mean single larva weight. In the same way, mean leaf weight consumed per larva and faecal matter per larva were calculated. Statistical analysis was performed using these means. At 10 am on the fifth day after initiating the trial, each of the 4-day-old larvae was transferred to a transparent plastic jar of 10 cm diameter and 10 cm height to prevent congestion and competition among larvae. A moistened filter paper was placed at the bottom of the jar and a one inch strip of moistened filter paper was run around the wall of the jar to maintain leaf turgidity and air humidity. An entire fully grown leaf of known weight was placed in the jar and the 4-day-old larva was placed on the leaf. The jars were covered with muslin cloth and kept in the control chamber. At 10 am the next day, each of the jars was opened, the weight of the larva was recorded and the larva was returned to the jar with new moistened filter papers and a new leaf. The leaf remaining after feeding and faecal matter excreted by the larva was dried and weighed. The same process was repeated until the larvae pupated. Although individual larvae were weighed, the weights of the 10 larvae derived from each petri dish (one replication) were aggregated and the mean was calculated. Mean leaf weight consumed and faecal matter per larva were also calculated similarly. Statistical analysis was performed using these means.

On each day up to the fourth, the leaf from which the leaf disc was punched was dried and the water content was determined. From the fifth day onwards, a leaf very similar to the one offered to the larvae was dried and its water content was determined. Throughout the feeding trial, a parallel set of stock larvae was maintained on 350 CO_2 open castor leaves which were abundant and on each sampling day, larvae of the same age as those in the feeding trial were killed by piercing and dried to determine water content. These water contents were used to convert fresh weights of leaves and larvae actually used in the feeding trials into dry weights.

Using the data relating to larval weight, leaf weight consumed, and faecal matter excreted, various insect performance indices[10], viz. relative growth rate (RGR, larval weight gain per day as a fraction of body weight), relative consumption rate (RCR, weight of leaf ingested per day as a fraction of larval body weight), efficiency of conversion of ingested food (ECI, larval weight gain per unit weight of leaf ingested expressed as percentage), efficiency of

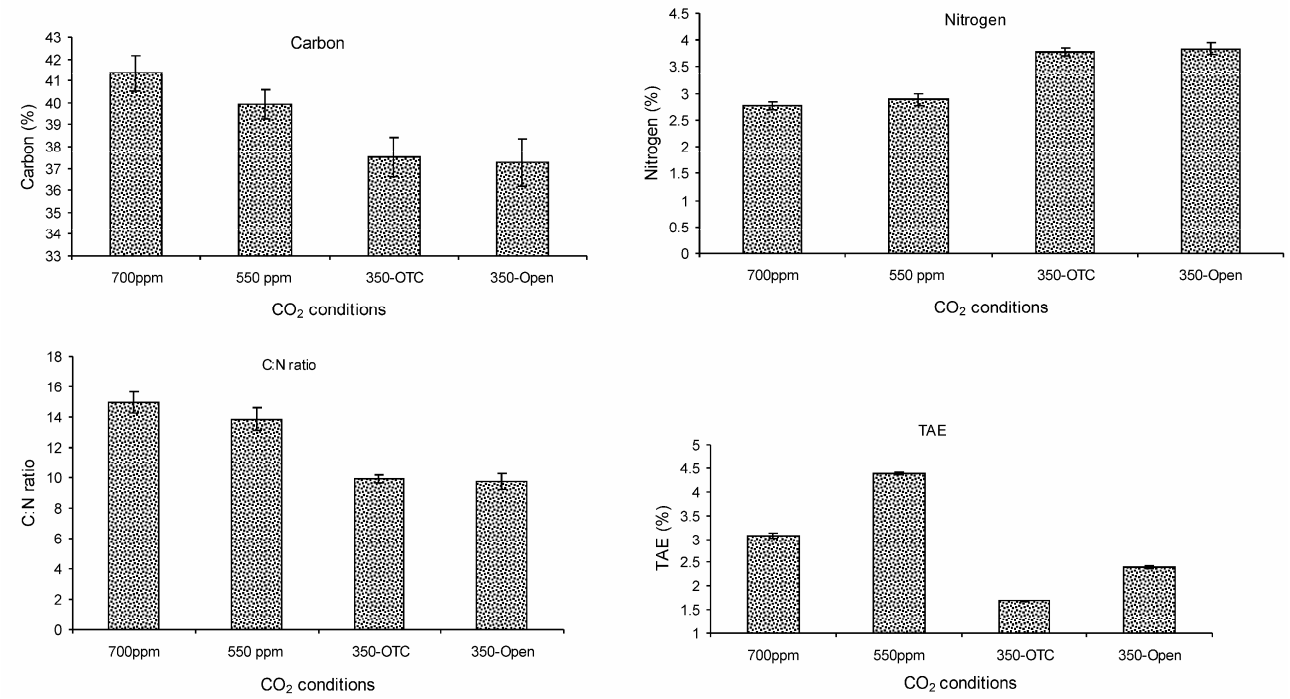

Figure 1. Variation of biochemical constituents of castor foliage under elevated CO_2.

conversion of digested food (ECD, larval weight gain per unit weight of leaf digested expressed as percentage) and approximate digestibility (AD, ratio of weight of leaf digested and weight of leaf ingested expressed as percentage) were computed. Weight of leaf digested was obtained by subtracting weight of faecal from weight of leaf ingested.

The effects of CO_2 treatments on larval parameters were analysed using one-way ANOVA. Treatment means were compared and separated by least significant difference at $p < 0.05$. In order to examine the effects of leaf biochemical constitution on feeding and growth, weight of leaf consumed and larval weight were regressed on leaf N, C and polyphenols. For each of these three variables, extra sum of squares[11] called sequential sum of squares was estimated to find out the relative contribution of the three variables to the explained variation in the larval consumption and growth (dependent variable). Further, exponential trend equations were estimated for each treatment in order to examine the growth rate of larvae under different CO_2 conditions. All statistical analyses were done using SPSS[12] version 16.0

Results and discussion

Biochemical analysis of leaf samples

Leaf nitrogen content was distinctly lower in elevated CO_2 foliage (Figure 1). In contrast, carbon content was higher in elevated CO_2 foliage. Consequently, the change in the relative proportion of carbon to nitrogen (C : N ratio) was considerably higher in elevated CO_2 foliage. Elevated CO_2 foliage had higher polyphenol content too, compared to ambient CO_2.

Larval growth performance

Larval duration, or time from hatching to pupation in larvae of both the species was significantly influenced by the CO_2 condition under which leaves offered to them were produced. Larval duration for both larvae was extended by about two days when fed with elevated CO_2 foliage (Table 1). Larval dry weights measured during the feeding period differed significantly among CO_2 conditions (Figure 2). Larvae ingested significantly higher quantity of elevated CO_2 foliage compared to ambient CO_2 foliage. For instance, *A. janata* consumed 62.6% more of 700 CO_2 foliage than 350 CO_2 foliage. The rate of consumption (RCR) was also higher in case of elevated CO_2 foliage. Thus, larvae fed with elevated CO_2 foliage consumed more each day and over a longer period, resulting in considerably increased ingestion. Larval weights prior to pupation were also significantly affected by the foliage offered, being higher with elevated CO_2 foliage, but differences in larval weight were not as marked as differences in the amount of leaf ingested. Larval growth rates (RGR) were significantly lower with elevated CO_2 foliage in case of *A. janata*, whereas in case of *S. litura*, the differences were not significant (Table 1).

The efficiency with which ingested food was converted into body weight was lower with elevated CO_2 foliage in

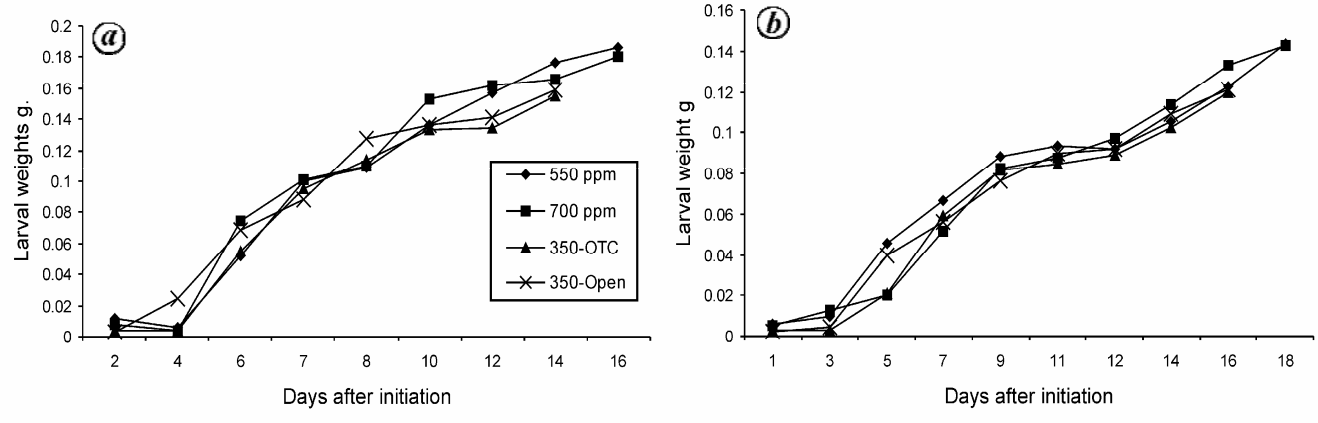

Figure 2. Effect of elevated CO_2 on larval weights: ***a***, *A. janata*; ***b***, *S. litura*.

Table 1. Effect of elevated CO_2 on *A. janata* and *S. litura* on castor

CO_2 condition	Weight of leaf ingested (g)	Larval weight (g)	Larval duration (days)	AD (%)	ECI (%)	ECD (%)	RCR (mg mg^{-1} d^{-1})	RGR (mg mg^{-1} d^{-1})
A. janata								
550 CO_2	3.071 ± 0.470	0.171 ± 0.008	16.11 ± 0.054	87.34 ± 1.88 (69.27)*	5.57 ± 0.012 (13.73)	6.38 ± 1.28 (14.69)	219.29 ± 33.58	12.228 ± 0.582
700 CO_2	3.284 ± 0.631	0.169 ± 0.004	16.29 ± 0.089	86.66 ± 2.33 (68.60)	5.18 ± 0.970 (13.27)	5.96 ± 1.21 (14.33)	234.35 ± 45.09	12.137 ± 0.265
350 CO_2 OTC	2.021 ± 0.178	0.154 ± 0.003	14.33 ± 0.222	82.06 ± 1.56 (64.96)	7.63 ± 0.715 (16.07)	9.30 ± 0.96 (17.81)	168.45 ± 14.91	12.861 ± 0.289
350 CO_2 Open	2.138 ± 0.218	0.157 ± 0.003	14.33 ± 0.422	78.21 ± 1.67 (62.80)	7.37 ± 0.718 (15.81)	9.41 ± 0.80 (17.81)	178.22 ± 18.17	13.138 ± 0.301
SEm ±	0.152	0.004	0.058	1.121 (1.01)	0.412 (0.25)	0.004 (0.292)	10.812	0.212
LSD (p = 0.05)	0.524	0.013	0.180	3.921 (3.51)	1.396 (0.87)	0.016 (1.02)	37.37	0.734
CV (%)	9.97	4.34	4.86	2.31 (2.65)	10.15 (2.95)	9.97 (3.15)	9.24	3.27
S. litura								
550 CO_2	0.820 ± 0.131	0.137 ± 0.002	18.27 ± 0.113	70.19 ± 3.99 (56.9)	17.05 ± 2.88 (24.29)	24.49 ± 5.53 (29.57)	45.57 ± 7.32	7.631 ± 0.159
700 CO_2	0.869 ± 0.054	0.137 ± 0.001	18.22 ± 0.195	74.51 ± 2.96 (59.70)	15.93 ± 2.32 (23.49)	21.49 ± 4.07 (27.56)	48.27 ± 3.01	7.645 ± 0.611
350 CO_2 OTC	0.594 ± 0.044	0.117 ± 0.006	16.11 ± 0.253	58.61 ± 4.01 (50.00)	19.83 ± 1.83 (26.43)	34.09 ± 5.62 (35.68)	37.12 ± 2.79	7.333 ± 0.344
350 CO_2 Open	0.588 ± 0.192	0.118 ± 0.002	16.13 ± 0.083	57.02 ± 7.23 (49.10)	20.23 ± 0.95 (27.42)	35.76 ± 3.79 (36.69)	36.74 ± 0.19	7.425 ± 0.152
SEm ±	0.048	0.003	0.085	0.031 (1.03)	1.210 (1.08)	3.01 (2.24)	2.81	0.312
LSD (p = 0.05)	0.166	0.011	0.261	0.106 (3.57)	NS	10.51 (7.78)	9.621	NS
CV (%)	11.59	4.70	3.10	8.13 (7.60)	11.65 (7.41)	10.23 (12.01)	11.24	0.519

*Figures in parentheses are angular transformed values.

case of *A. janata*, but in *S. litura* there were no significant differences. The efficiency of conversion of digested food into body mass (ECD) was lower with elevated CO_2 foliage for both species of larvae. The digestibility (AD) of elevated CO_2 foliage was significantly higher than ambient CO_2 foliage for both the species, more so in case of *S. litura* (Table 1).

The data of larval weight were fitted to a compound growth function of the form $y = ax^b$, where y is larval weight in mg, x time in days, a a constant and b, a coefficient that indicates the growth rate. Differences in growth rates of *S. litura*, which were not visible from relative growth rate calculations, became clear with the growth functions. The daily growth rates of *S. litura* were

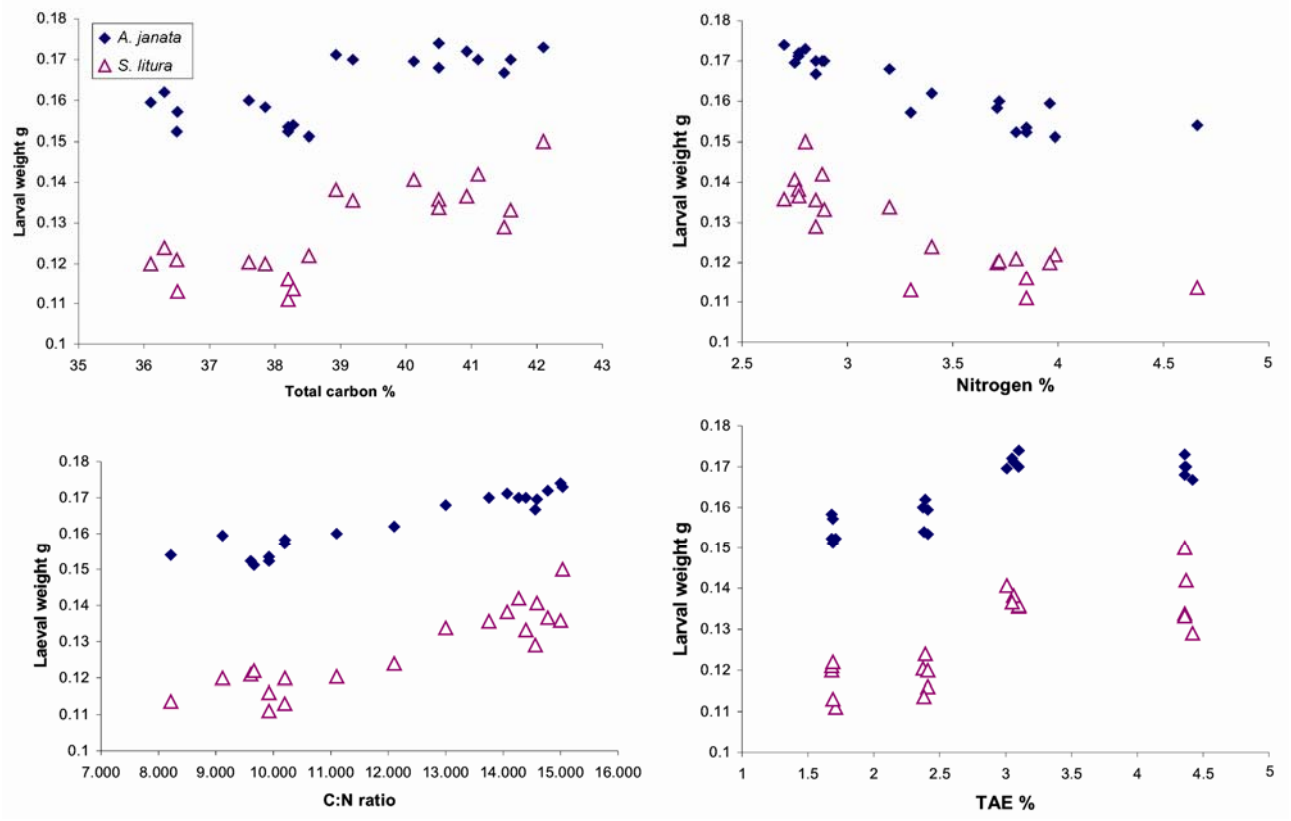

Figure 3. Relation between larval weights and biochemical constituents.

Table 2. Estimated exponential trend equations of growth rates of insect species (larvae) on castor

CO_2 condition	Constant	Coefficient	R^2	P value	Growth (%)
A. janata					
550 CO_2	0.009	0.229	0.70	0.005	25.73
700 CO_2	0.008	0.243	0.65	0.009	27.50
350 CO_2 OTC	0.003	0.335	0.71	0.008	39.79
350 CO_2 Open	0.006	0.291	0.69	0.011	33.64
S. litura					
550 CO_2	10.68	0.171	0.77	0.001	18.53
700 CO_2	8.262	0.188	0.87	0.000	20.92
350 CO_2 OTC	3.31	0.27	0.80	0.001	30.99
350 CO_2 Open	4.13	0.26	0.77	0.002	29.69

considerably lower with elevated CO_2 foliage (Table 2). While the daily growth rate was 30.99% with 350 CO_2 OTC foliage, it was just 18.53% with 550 CO_2 foliage. In *A. janata* also, the daily growth rates were markedly lower with elevated CO_2.

Relationship of larval performance with leaf biochemical parameters

To find out which biochemical constituent(s) of the leaf-influenced larval consumption and growth, and to what extent, the data of larval weight and weight of foliage consumed were plotted against each of the biochemical constituents (carbon, nitrogen, C : N ratio and polyphenols) (Figures 3 and 4). Leaf consumption and larval weights were positively and significantly correlated with leaf carbon, polyphenols and C : N ratio, and negatively (–0.804 to –0.834) with leaf nitrogen content (Table 3).

Multiple regression equations were estimated with larval weight and weight of foliage consumed as dependent variable and leaf biochemical parameters as independent variables (Table 4). The weights of larvae and weight of foliage consumed by both the pests were negatively and significantly influenced by nitrogen content of foliage. The effects of carbon and polyphenols were not consistent. Partitioning of the variation explained by the three biochemical parameters together, using sequential sum of squares procedure showed that leaf nitrogen content accounted for more than three-fourths of the explained variation, whereas carbon and polyphenols contents together accounted for less than one-fourth of the explained variation (Table 5).

Discussion

Increase in the concentration of CO_2 in the atmosphere as a result of global climate change results in increased photosynthesis and growth of plants[13] which can lead to dilu-

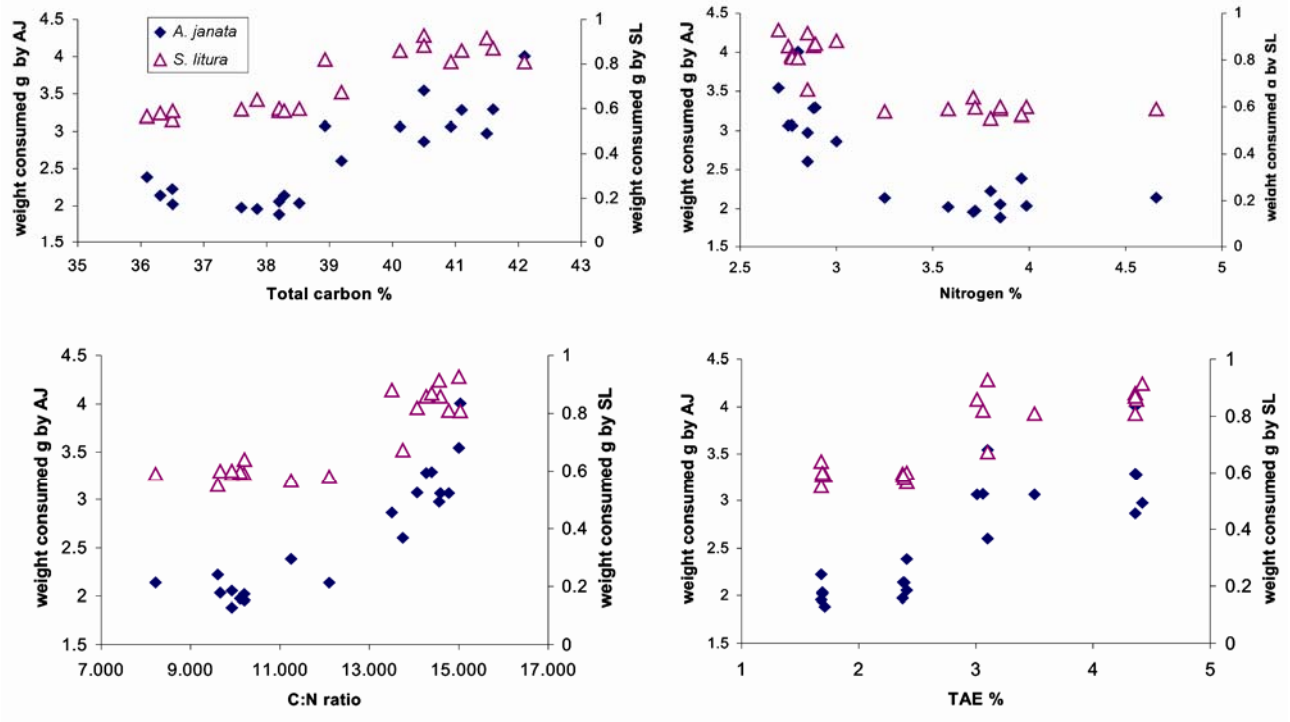

Figure 4. Relation between weights of foliage consumed by larvae and biochemical constituents.

Table 3. Correlation coefficients between larval parameters and biochemical constituents of castor foliage

	Weight of foliage consumed		Larval weight	
CO_2 condition	*A. janata*	*S. litura*	*A. janata*	*S. litura*
Carbon	0.835	0.885	0.736	0.766
Nitrogen	–0.804	–0.834	–0.901	–0.832
C : N ratio	0.898	0.886	0.846	0.897
Polyphenols	0.837	0.848	0.785	0.768

Table 4. Estimated multiple linear regression equations between larval characteristics and biochemical constituents

	Unstandardized coefficients		Standardized coefficients	
Model	*B*	Std. error	Beta	R^2
Achaea janata				
Y (weight of foliage consumed)				
Constant	–0.764	2.677		0.818
Nitrogen	–0.407*	0.165	–0.369	
Carbon	0.108	0.069	0.329	
Polyphenols	0.188	0.129	0.303	
Y (larval weight)				
Constant	0.950*	0.142		0.872
Nitrogen	–0.048*	0.009	–0.684	
Carbon	0.000	0.004	–0.015	
Polyphenols	0.013*	0.007	0.340	
Spodoptera litura				
Y (weight of foliage consumed)				
Constant	–0.419	0.484		0.878
Nitrogen	–0.088*	0.030	–0.561	
Carbon	0.035*	0.012	0.477	
Polyphenols	0.027	0.023	0.194	
Y (larval weight)				
Constant	0.548*	0.257		0.784
Nitrogen	–0.052*	0.016	–0.536	
Carbon	0.006	0.007	0.202	
Polyphenols	0.013	0.012	0.238	

tion of nitrogen in the tissues by 15–25% (ref. 3) and increased C : N ratios, mainly due to the accumulation of non-structural carbohydrates[14]. In this study, nitrogen concentration in castor leaves decreased by about 25% when castor plants were grown under elevated CO_2 conditions. With increased carbon intake, the carbon content of the leaf tissues also increased. Both of these together resulted in an increase of C : N ratio as reported by Hughes and Bazzaz[15]. Because nitrogen is the chief constituent of proteins, this may suggest that plants grown under elevated CO_2 conditions have lower protein in their tissues. In the present study, C : N ratio of castor leaves increased by about 12% under elevated CO_2. Polyphenols, non-structural carbon compounds that constitute one of the defence mechanisms of plants and offer antifedancy to herbivores, are also known to increase in leaves under elevated CO_2 conditions up to 31% (ref. 16). In this study also, the content of polyphenols in leaves differed among the plants grown under different CO_2 conditions, being higher in elevated CO_2 foliage.

Leaf consumption and growth of larvae are influenced by the nitrogen content of the foliage[5]. As nitrogen is an important limiting factor for phytophagous insects, a re-

Table 5. Sequential sum of squares (SSQ) and percentage contribution of biochemical parameters to explained variation in larval parameters

	Achaea janata				*Spodoptera litura*			
	Weight of foliage consumed		Larval weight		Weight of foliage consumed		Larval weight	
Variable	SSQ	% variation explained	SSQ	% variation explained	SSQ	% variation explained	SSQ	% variation explained
Nitrogen	4.744 (55.24)	77.0	0.025 (100)	96.2	0.244 (86.76)	75.1	0.041 (50.46)	89.1
Carbon	1.236 (14.39)	20.1	0.001 (4.0)	3.8	0.077 (27.38)	23.7	0.004 (4.927)	8.7
Polyphenols	0.181 (2.10)	2.9	0.0 (0.0)	0.0	0.004 (1.42)	1.2	0.001 (1.23)	2.2
Reg SS	6.161	100	0.026	100	0.325	100	0.046	100

Figures in parentheses are *F* values.

duction in percentage of nitrogen may have potent effects on insect performance. Insects increase their consumption and assimilation rates when fed with nitrogen-poor foliage. However, the efficiency of conversion of food into larval biomass is reduced, resulting in lower growth rates[17]. In this study, larvae fed on elevated CO_2 foliage consumed and assimilated more (higher values of RCR and AD) but grew slower (lower RGR) and took longer time (two days more than ambient) to pupation. Lincoln[18] and Osbrink[19] reported that insect herbivores exhibited compensatory increases in foliar consumption rate or a delay in development when reared on plants grown in elevated CO_2 environments. Further, they also reported decreased food conversion efficiency. In this study also, both larval species were less efficient in converting digested elevated CO_2 castor foliage into body mass as evidenced by lower ECD and ECI values. Higher respiratory activity and the requirement of larvae to metabolize digested food to produce water as observed in case of many insects[20] could be the reasons for lower food conversion efficiencies and lower growth rates associated with elevated CO_2 castor foliage. In this study, the growth rates of *A. janata* exhibited a marked reduction under elevated CO_2 conditions but the growth rates of *S. litura* were not significantly affected. Relative growth rates (RGR) of gypsy moth (*Lymantria dispar*) were reported to be reduced by 30% in larvae fed on *Quercus petraea* exposed to high CO_2 (ref. 20). Larval consumption and weight gain are influenced by the biochemical composition of the leaf tissue. This relationship between larval parameters and biochemical composition was further confirmed by the regression analysis which showed a significant negative relationship of larval weight and larval consumption with leaf nitrogen content and positive relationship with carbon content. The content of polyphenols (TAE) was not found to have a significant effect on larval parameters. Further, among the three biochemical constituents, nitrogen content was more important in influencing the consumption and growth of the larvae, as reflected by the relative contribution of these three variables to the total explained variation. In the present study, there were small differences between the foliage obtained from 700 and 550 ppm CO_2 levels. The larvae fed with 700 CO_2 foliage exhibited higher consumption and growth rates and lower values for ECI and ECD, compared to the larvae fed with 550 CO_2 foliage. After performing *t*-test and ANOVA it was found that these differences were not statistically significant.

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