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Response to elevated CO_2 of multiple generations of semilooper, *Achaea janata* L. (Noctuidae: Lepidoptera) feeding on castor

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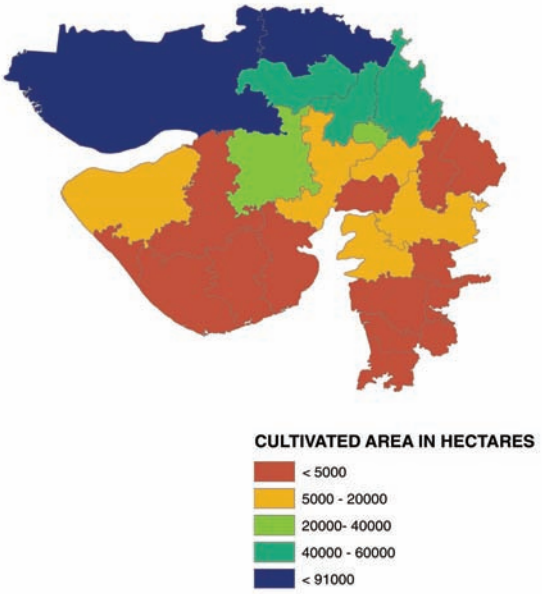
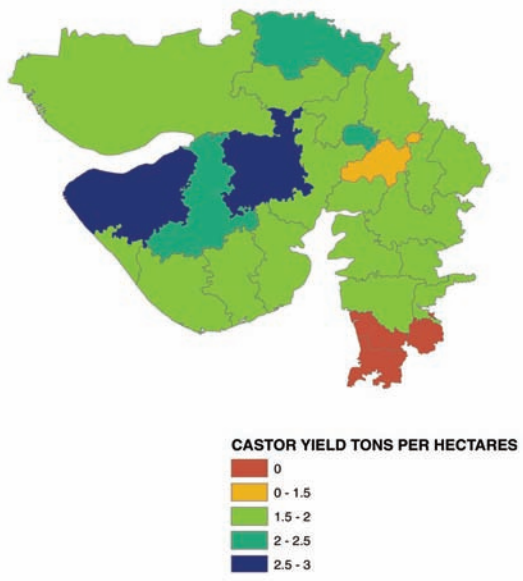
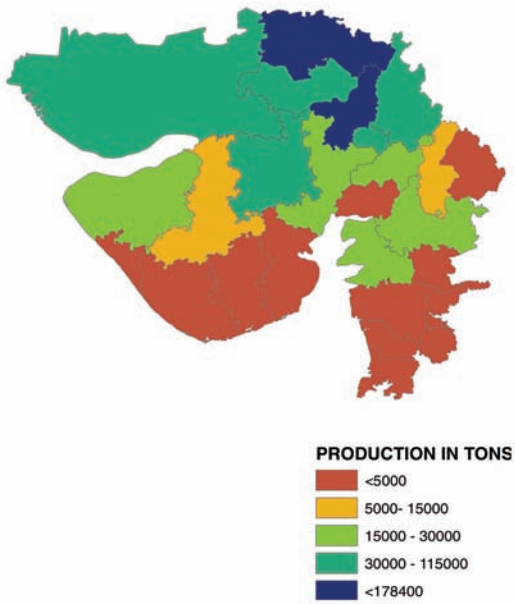
GUJARAT DISTRICTS
CASTOR AREA IN HECTARES



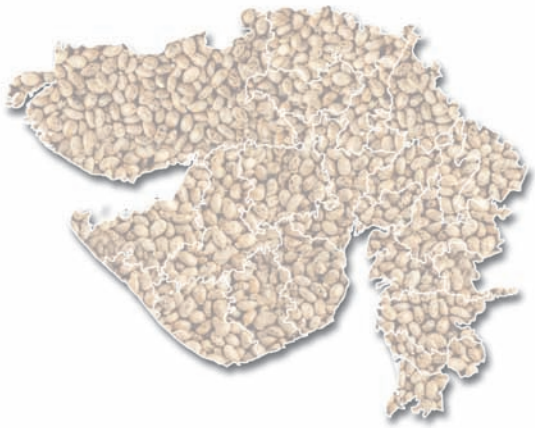
GUJARAT DISTRICTS
CASTOR YIELD IN TONS PER HECTARES



GUJARAT DISTRICTS
CASTOR PRODUCTION IN TONS



Castor cultivation in Gujarat State



AREA ('000 HA)	329.3
PRODUCTION ('000 TN)	635.3
YIELD (KGS./ HA.)	1924.3

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CONTENTS

Executive Summary

The growth, development and consumption of four successive generations of castor semilooper, *Achaea janata* reared on castor (*Ricinus communis* L.) foliage grown under elevated carbon dioxide (550 and 700 parts per million) concentrations in open top chambers were estimated at CRIDA, Hyderabad, India. Significantly lower leaf nitrogen , higher carbon , higher relative proportion of carbon to nitrogen (C: N) and higher polyphenols expressed in terms of tannic acid equivalents were observed in castor foliage grown under elevated carbon dioxide levels. Significant influence of elevated carbon dioxide on life history parameters of *A. janata* over four generations was noticed. Longer larval duration, differential pupal weights and increased larval survival rates of *A. janata* in successive four generations were observed under elevated carbon dioxide than ambient. Reduced fecundity was observed over generations under each elevated carbon dioxide level. The consumption per larva of *A. janata* fed on castor foliage grown under elevated carbon dioxide increased from first to fourth generation. Potential population increase index for successive generations was found lower in both elevated carbon dioxide concentrations than in case of ambient. The present findings indicate that elevated carbon dioxide levels significantly altered the quality of the castor foliage resulting in higher consumption by larvae, better assimilation (higher values of relative consumption rate and approximate digestibility, slow growth (lower relative growth rate) and took longer time (two days more than ambient) to pupation to produce in less fecund adults over generations.

Key words: *Achaea janata*, castor, elevated CO_2, generations, insect performance indices, potential population increase index

Response to elevated CO_2 of Multiple Generations of Semilooper, *Achaea janata* L. (Noctuidae: Lepidoptera) feeding on castor

Introduction

Climate change, especially the rise in temperature and atmospheric carbon dioxide (CO_2) concentrations, is the major concern of today. The Third IPCC report predicts that global average surface temperature will increase by 1.4 to 5.8° C by 2100 with atmospheric CO_2 concentrations expected to rise between 540 to 970 ppm during the same period (Houghton *et al*., 2001). Effects of elevated atmospheric CO_2 on plants are well documented. Elevated CO_2 conditions generally result in increased photosynthesis (Drake *et al*., 1997), increased plant growth (Saxe *et al*., 1998) and greater biomass (Leadly *et al*., 1999). Increased carbon levels, decreased nitrogen content and increased C: N ratios were observed in the plants grown under elevated CO_2 conditions (Lincoln *et al*., 1993; Lindroth *et al*., 1995). The nutritional quality of plants changes under elevated CO_2 conditions (Hunter *et al*., 2001). These changes elicit responses from herbivore insects. Feeding on plants grown in elevated CO_2 conditions affects the survival, growth, development and reproduction of insect herbivores.

Castor (*Ricinus communis L.*) is cultivated around the world because of the commercial importance of its oil. India is the world's largest producer of castor seed and meets most of the global demand for castor oil. India produces 8 to 8.5 lakh tonnes of castor seed annually, and accounting for more than 60% of the entire global production. Because of its unlimited industrial applications, castor oil enjoys tremendous demand world-wide. The current consumption of Castor Oil and its derivatives in the domestic market is estimated at about 300,000 tonnes. India is also the biggest exporter of castor oil and its derivatives at 87% share of the international trade in this commodity. Castor is an important non-edible oilseed crop and is grown especially in arid and semi arid region. It is originated in the tropical belt of both India and Africa.

It is cultivated in different countries on commercial scale, of which India, China and Brazil is major castor growing countries accounting for 90 per cent of the world's production.

India is the world's largest producer of castor beans. Brazil and China are the other major producers of castor beans and castor oil in the world. The global demand for castor oil is estimated to be about 1 billion pounds worth US$ 500 million. During the year 2007-08, the crop was grown in about 7.87 lakh ha in the country giving a total output of nearly 10.53 lakh tones with an average yield of 1.33 t/ha. Gujarat, Andhra Pradesh and Rajasthan are the major castor producing states in India. During the triennium ending 2007-08, these three states accounted for about 89 per cent of area and 94 per cent of production in the country. The yields are however much higher in Gujarat compared to the situation in Andhra Pradesh where it is largely grown as a rainfed crop. There is considerable variation across districts within the state in the yield levels (Fig. 1). For example, most of the castor is grown in the northern parts where the yields are relatively low at 1-1.5 t/ha. In Andhra Pradesh, it is concentrated in the South Telngana Zone where the yields are about 1 t/ha. The cultivation of castor assumes greater importance because of its relatively low water requirement and the potential demand in the domestic and international market.

The area sown to castor largely depends on the area sown to its competing crops such as cotton, sunflower, sorghum, pigeonpea, etc, which are also grown under rainfed conditions. The crop faced competition from cotton in particular in the Telangana regions of Andhra Pradesh (Rama Rao, 2000). Because of the high profitability of cotton, farmers replaced castor with cotton in their cropping mix. Cotton is an investment-intensive crop as it is highly prone to a number of pests and diseases and other problems. The price situation of cotton is also volatile and depends on the government's policy with regard to exports and imports. The high risk associated with cotton caused farmers again switched back to castor. Other important factors that determine the area under castor include the relative prices of castor and the competing crops, onset of monsoon and rainfall conditions. The area under castor tends to increase especially when the onset of monsoon is delayed because the yield of castor is not as much sensitive to the sowing time as that of other crops such as sorghum.

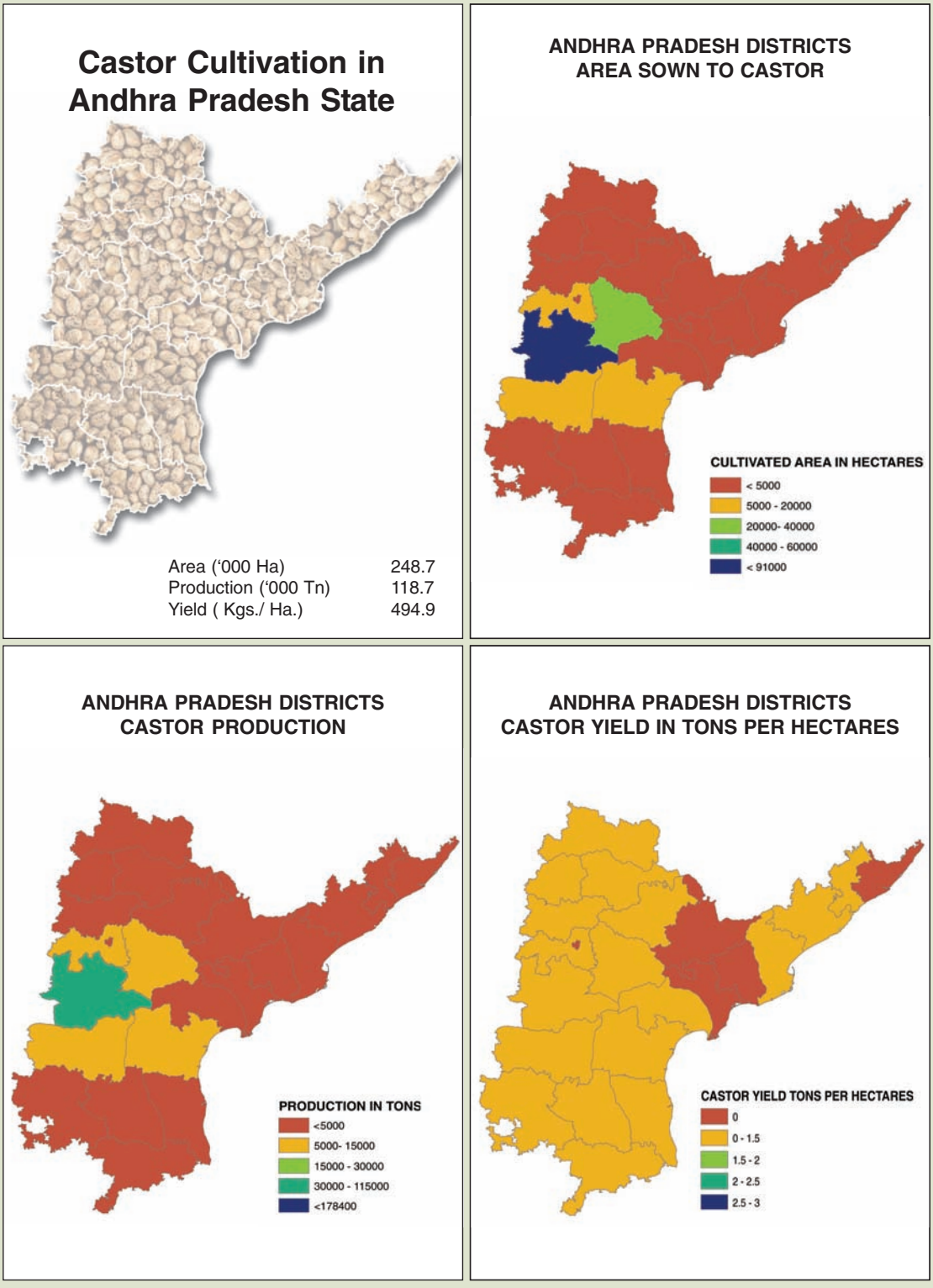


Fig. 1 : Districtwise Castor area, production and productivity in AP

The castor semilooper, *Achaea janata* (Noctuidae: Lepidoptera) occurs during early stage of castor. The semilooper feeds on the foliage and completes its life cycle on the plant. The incidence of semilooper is noticed up to early reproductive phase of castor plant (Basappa & Lingappa, 2001). 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.

Substantial information is available on the responses of insect herbivores to the direct effects of elevated CO_2 through multiple generations (Bezemer & Jones, 1998; Brooks *et al* 1998 & 1999; Chen, 2004; Wu *et al*, 2006; Chen *et al* 2007; Yin *et al*., 2010). Majority of the published work deals with short term or single generation studies pertaining to the insect performances under elevated CO_2 (Bezemer *et al*., 1998). Multiple generation studies are required as they can effectively highlight the differential responses of the herbivores through successive generations, (Lindroth *et al*., 1995). The cumulative effects of elevated CO_2 on insect individuals and population levels can be known by conducting multi-generation studies. This information is useful to accurately estimate and develop insect models which are central to population dynamics (Williams *et al*., 1997).

This study aimed to understand the effects of elevated atmospheric CO_2 on leaf quality of castor *(Ricinus communis)* and to study its impact on growth characteristics of leaf feeding caterpillar (*A. janata*) over consecutive generations. In addition to the impacts, we also estimated the potential population increase index and potential population consumption of *A. janata* under elevated CO_2 conditions.

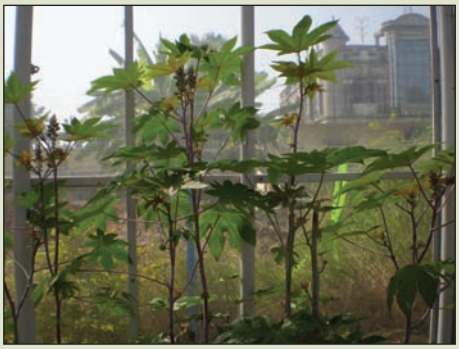
Materials and Methods

Open Top chambers

Three square type open top chambers (OTC) of 4x4x4 m dimensions, were constructed at the Central Research Institute for Dryland Agriculture (CRIDA), Hyderabad (17.38^{0}N ;78.47^{o}E), two for maintaining elevated CO_2 concentrations of 550 ± 25 ppm CO_2 and 700 ± 25 ppm CO_2 , and one for ambient CO_2. Carbon dioxide gas was supplied to the chambers and maintained at set levels using manifold gas regulators, pressure pipelines, solenoid valves, rotameters, sampler, pump, CO_2 analyzer, PC linked Program Logic Control (PLC) and Supervisory Control and Data Acquisition (SCADA).

Crop growing conditions

Castor (variety DCS 9) seeds were sown during second fortnight of June in all three OTCs during the monsoon season of 2008-2009. The soils in OTCs are typical representative alfisols with red soil type. Thus, castor plants were grown under three CO_2 conditions inside OTCs; 550 ± 25 ppm (550 CO_2 -Elevated I), 700 ± 25 ppm (700 CO_2 - Elevated II) and ambient CO_2 (380 ± 25 CO_2 OTC). Pure CO_2 mixed with ambient air was supplied to the chamber from seedling emergence to harvest of the crop.



Biochemical analysis of foliage

Plant defense against herbivory or host-plant resistance (HPR) describes a range of adaptations evolved by plants which improve their survival and reproduction by reducing the impact of herbivores. Plants use several strategies to defend against damage caused by herbivores. The elevated concentration of atmospheric CO_2 may result in a decline of leaf nutritional quality (especially N) and an increase in some kinds of defensive secondary components (such as phenolics). The changes in the phytochemistry of trees, combined with the effect of elevated CO_2 per se, have a potential negative influence on insect herbivores.

Both host plant quality and non-biological environmental factors influence the insect's food choice and recognition behaviors before ingestion and the food consumption during ingestion, and also influence the food utilization rate and insect performance after ingestion (Scriber and Slansky, 1981). Therefore, in theory, both high CO_2 per se and CO_2-induced changes in the host-plant physiology will influence the consumption, growth and development of leaf-chewing insects (Williams *et al.,* 2003). It is generally believed that CO_2-induced changes in foliar chemistry play the most important role on the performance of leaf feeding insects. The changes in the insect growth and consumption were largely attributed to the 'host mediated effect', hence the biochemical constituents of castor foliage was carried out as follows:

Estimation of biochemical constituents will be taken up as per the standard procedure.

- Organic carbon - WALKLEY-BLACK method (1934)
- Nitrogen – Kjeldahl using Block digestion and Steam distillation
- C: N ratio can be derived based on CHNS Analyzer (Elementar Analysensysteme GmbH, Germany)
- Tannins- Folin- Denis method (1993)

Determination of carbon

Plants commonly respond to elevated CO_2 by increasing their rates of photosynthesis. Higher rates of photosynthesis usually result in higher accumulation of carbon- rich carbohydrates.

Carbon in the residues was determined by using the wet oxidation procedure of Walkley and Black (1934) for soil organic carbon, but small samples (0.05 g) of finely ground plant residues were taken, and after addition of H_2SO_4, external heat was applied by heating for half an hour at 150^{o}C on a hot plate to achieve complete oxidation.

Determination of nitrogen

Leaf nitrogen concentration is the key factor that affects the consumption, digestion, growth and development and the reproduction of herbivorous insects (Williams et al., 1994; Saxon et al., 2004).

Nitrogen in plant material was determined by kjeldahl digestion and distillation (Jackson, 1973). Samples (0.1g) of finely ground plant material were weighed into 250 ml digestion tubes. Sulfuric acid (7 ml) and catalyst (selenium) tablets were added and the tubes

were shaken and left to stand for two hours. The tube rack was then inserted into a preheated digester block (1015 digester, Tecator AB, Sweden) and the contents were digested at 420°C for 40 minutes. After completion of digestion, the tube rack was removed and the digests were cooled and diluted. Nitrogen in the digests was quantitatively determined using an automated distillation-titration unit (Kjeltec Auto 1030 Analyzer, Tecator AB, Sweden) by distillation with 40 per cent NaOH and titration with 0.1N H_2SO_4.

Determination of C and N

C: N ratio has major implications for the concentrations of defensive compounds in the leaves, the so called secondary chemicals. Carbon based secondary chemicals often increase and deter insect feeding. The overall effect of increased CO_2 on insect herbivores is to decrease plant palatability because of decrease in nitrogen levels and increase in secondary chemicals.

Nitrogen is essential for all living organisms. The synthesis of cellular proteins, amino acids, nucleic acids, purine and pyrimidine nucleotide are dependent upon N. It is most abundant mineral element in plant tissues which is derived from the soil. However, excess N may cause significant biochemical changes in plants and may lead to nutritional imbalances (Mills and Jones, 1979).

Carbon and nitrogen in the samples were determined by solid sample dry combustion method using Elementar Vario El Cube CHNS Analyzer (Elementar Analysensysteme GmbH, Germany. About 5 mg of finely ground samples were weighed into tin boats and the boats were loaded into a sample carousel which transfers the samples into the combustion tube one at a time using a ball valve. The sample is combusted at 950 °C and the gases formed are passed through a reduction tube heated to 600 °C, resulting in conversion of C to CO_2 and N to N_2. The gases, carried by helium carrier gas, are separated chromatographically and detected by a thermal conductivity detector (TCD).

Determination of polyphenols

Phenolics, sometimes called phenols, consist of an aromatic 6- carbon ring bonded to a hydroxyl group. Phenolics used for defense in plants are: lignin, silymarin and cannabinoids. Condensed tannins, polymers composed of 2-50 (or more) flavonoid molecules, inhibit herbivore digestion by binding to consumed plant proteins and making them more difficult for animals to digest, and by interfering with protein absorption and digestive enzymes.

Total soluble polyphenols (hydrolysable tannins, condensed tannins and non-tannin polyphenolics) were determined by the Folin-Denis method as described by Anderson and Ingram (1993). About 0.75 g of plant material was weighed (W) into a 50 ml beaker. 20 ml of 50 per cent methanol was added and the beaker was covered with parafilm and placed in a water bath at 77- 80°C for 1 hr. The extract was quantitatively filtered through Whatman No. 1 filter paper into a 50 ml volumetric flask using 50 per cent aqueous methanol to rinse, and was made up with water, and mixed well. 1 ml of the aliquot was pipetted into a 50 ml volumetric flask, and 20 ml water, 2.5 ml Folin-Denis reagent and 10 ml 17 per cent sodium carbonate were added. The volume was made up with water and the contents were mixed well and allowed to stand for 20 minutes. The absorbance of the solution was read at 760 nm. The concentration of polyphenols (C) was obtained from a standard graph. Total soluble polyphenols were determined as follows:

$$\% \text{ Polyphenols} = \frac{(C \times 5)}{W}$$

Folin-Denis reagent: 50 g sodium tungstate, 10 g phosphomolybdic acid and 25 ml orthophosphoric acid were added to 375 ml of water and refluxed for 2 hours with glass beads to prevent overheating and bumping. The contents were then cooled and diluted to 500 ml with water.

Leaf tissue from each plant used in the feeding experiment was analyzed for carbon, nitrogen and polyphenols. To determine carbon and nitrogen concentrations, samples were dried at 80^0 C and subsequently ground to powder. Leaf carbon and nitrogen were estimated using a CHN analyzer (Jackson, 1973). Total soluble polyphenols (hydrolysable tannins, condensed tannins and non tannin polyphenols) were determined by the Folin-Denis method, (Anderson *et al*., 1993). For this, leaf samples were dried at 40^0 C for 48 hrs. Dried leaf samples were ground to powder and phenolics were extracted with methyl alcohol. 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).

Insect stocks

An insect colony was established using eggs obtained from insect culture maintained in the laboratory. Stock cultures of castor semilooper were maintained on leaves of castor plants. The cultures were maintained in a controlled chamber maintained at 20^0 C with a 14-h day/10-h night cycle. Light intensity inside the chamber during the 14-h day

period was maintained at 550m mol m^{-2} s^{-1}. Relative humidity was maintained at 60% (day) and 70% (night).

Feeding trials

First generation experiments were initiated in the second fortnight of July 2008. At 10 am on the day of initiating the feeding trial, freshly hatched neonates obtained from insect culture maintained in the lab were placed in petridishes of 110 mm diameter and 10 mm height. Ten neonates were kept in each petridish, forming one replication. Five such replications were kept for each of the three CO_2 conditions. The feeding trials were continued up to four generations. Feeding trials with first to four generation larvae were conducted maintaining the treatment associations, i.e., all four generations received foliage from the same respective CO_2 growing conditions. All feeding trails were conducted as per procedure given by Srinivasa Rao *et al*. (2009). Larval life span was calculated as the period from hatching to pupation. Pupal weight was measured about 24 hrs after pupation was observed. The rate of pupation and pupal duration was also recorded. The emergence of the adults was noticed after a pupal period and recorded treatment wise. Adults were sexed and the ratio of females to males was recorded. Newly emerged adults were released in a wooden cage of size (30cm X 30cm X 30cm) for two days and then paired 1:1 (Male: Female) and released in plastic

jar (15x15x15 cm) and closed with a muslin cloth. Adults started laying the eggs within 48hrs after the release and eggs were counted daily. The muslin cloth cover was replaced daily. The hatching percentage of eggs per female was recorded daily. The first instar larvae of *A. janata* obtained from first generation were reared individually and separately with five replications as per CO_2 treatment wise. The life history parameters of successive (consecutive) second, third and fourth generations of *A. janata* were measured as in the first generation described earlier.

Insect performance indices

Various insect performance indices were determined using the data relating to larval weight, leaf weight consumed, and fecal matter excreted (Waldbauer, 1968; Srinivasa Rao *et al*., 2009). viz., relative growth rate (RGR $g.g^{-1}.d^{-1}$), relative consumption rate (RCR $g.g^{-1}.d^{-1}$), efficiency of conversion of ingested food (ECI %), efficiency of conversion of digested food (ECD %) and approximate digestibility (AD %) were computed. The potential population increase index and potential population consumption were estimated as per procedure followed by Wu *et al*.(2006).

Formulae adopted

Using the data relating to larval weight, leaf weight consumed, and fecal 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 %), efficiency of conversion of digested food (ECD, larval weight gain per unit weight of leaf digested expressed as %) and approximate digestibility (AD, ratio of weight of leaf digested and weight of leaf ingested expressed as %) were computed. Weight of leaf digested was obtained by subtracting weight of frass from weight of leaf ingested.

RGR= increase in mg larval body weight per average g insect body weight per day

RCR= mg bolls ingested/ average g larval body weight per day

ECI = mg larval body weight gained/ mg bolls ingested X 100

ECD= mg larval body weight gained/ (mg bolls ingested – mg frass produced) X 100

AD = (mg bolls ingested – mg frass produced)/ mg bolls ingested X 100

Data analysis

The effects of CO_2 treatments on larval parameters were analyzed using one-way ANOVA. Treatment means were compared and separated using least significant difference (LSD) at $p<0.05$ and 0.01.The data on weight of foliage ingested, larval weight, weight of faecal matter, larval life span and pupal weight were analyzed using ANOVA with CO_2 and generations as sources of variability where CO_2 level was main factor and semilooper generation as sub factor deployed in a split plot design.

Analysis of covariance (ANCOVA) was suggested to analyze the ratio based nutritional indices, (Raubenheimer *et al*., 1992). ANCOVA tests whether certain factors have an effect on the outcome variable after removing the variance for which quantitative predictors (covariates) account. The inclusion of covariates can increase statistical power (significance) because it accounts for some of the variability. ANCOVA adjusts scores on dependent variable for initial differences on other variables. Hence the data on insect performance indices (ratio based) were analyzed using ANCOVA with initial weight as a covariate for RCR and RGR. The food consumption was taken as a covariate for ECI to correct for the effect of variation in the growth and food assimilated on intake and growth (Raubenheimer *et al*., 1992). The food assimilated was used as a covariate to analyse the ECD parameter (Hagele *et al*., 1999). Mean values were separated using the LSD test. All statistical analyses were done using SPSS version 16.0.

Results

1. *Growth and development of A. janata in four successive generations*

Larval duration

Significantly longer larval life span for third and fourth generations ($F_{3, 36}$ = 4.156, P=<0.05) was observed under elevated CO_2 conditions ($F_{2, 8}$= 120.27, P =<0.01) compared to ambient. The interaction between CO_2 and generations with respect to larval duration was not significant ($F_{6, 36}$ = 1.02, P =>0.05) (Table1) Fig. 2.

Pupal weights

The variation in pupal weights was not significant across CO_2 conditions ($F_{2, 8}$= 0.57, P =>0.01) and generations ($F_{3, 36}$ = 1.15, P =>0.05). The pupal weights were in the range of 0.308-0.322 g (Table1) Fig. 3.

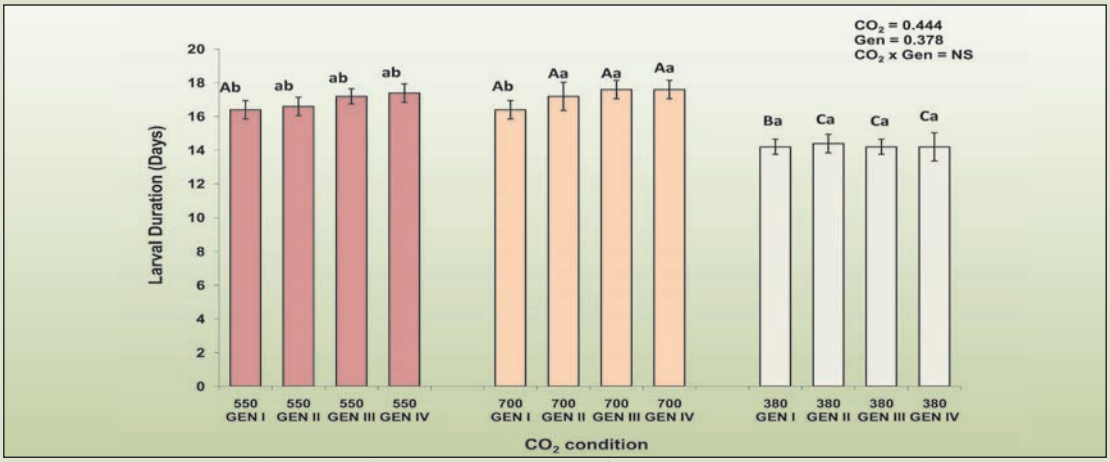


Fig. 2 : Larval duration of *A. janata* on castor in four successive generations unde ECO_2

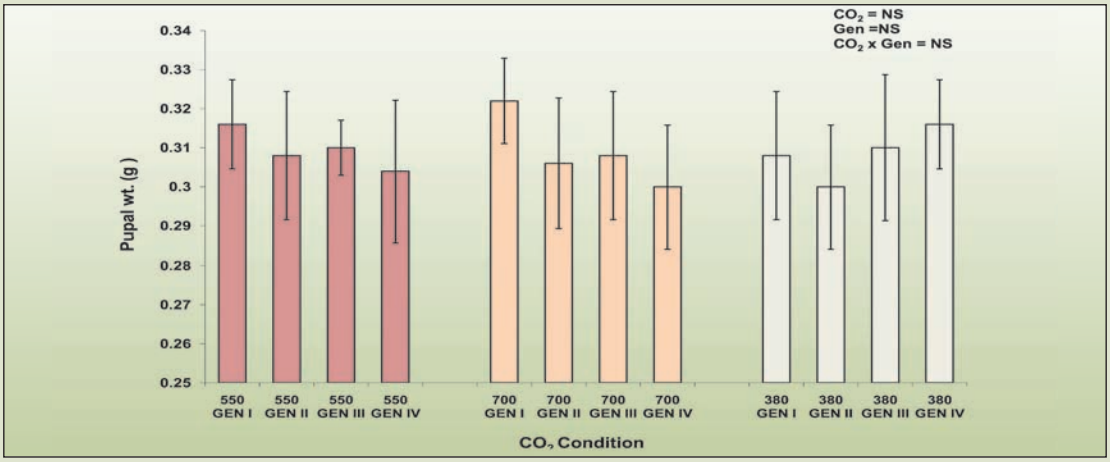


Fig. 3 : Pupal weights of *A. janata* on castor foliage in four successive generations under ECO_2

Survival rate

The survival rates of larvae did not vary significantly among CO_2 concentrations ($F_{2,8}$=1.47, p=>0.01) or over generation ($F_{3,36}$ = 0.01, P =>0.05) though these rates appeared somewhat lower in case of larvae grown under elevated CO_2 conditions. Lower survival rate was observed in the larvae in the elevated CO_2 conditions and from one generation to another generation and the effects were not significantly different for either CO_2 concentration ($F_{2,8}$ = 1.47, P =>0.01) or semilooper generation. ($F_{3,36}$ = 0.01, P =>0.05) (Table1).

Fecundity

The egg laying capacity (fecundity) of females was reduced significantly under elevated CO_2 concentrations ($F_{2, 8}$ = 9.31, P =<0.01) and was not affected significantly across all four generations ($F_{3, 36}$ = 0.42, P =>0.05).The interaction between CO_2 concentrations and generations was also found not significant. (Table1).

Table 1 Life history parameters of four successive generations of *A. janata* fed on castor grown under ambient and elevated CO_2 concentrations.

Generation	Life History Parameters	CO_2 concentrations (ppm)		
		550	700	Ambient
F1	Larval Lifespan (days)	16.4 ± 0.548 A b	16.4±0.548 A b	14.2±0.447 B a
	Pupal weight (g)	0.30±0.0158	0.322±0.01	0.308±0.016
	Survival rate (%)	89.6±3.578	88.8±5.21	87.2±6.57
	No. eggs laid / female.d^{-1}	339.2±23.09 AB a	333.4±25.20 B ab	347.4±23.90 A bc
F2	Larval Lifespan (days)	16.6±0.548 B ab	17.2±0.837 A a	14.4±0.548 C a
	Pupal weight (g)	0.308±0.016	0.306±0.017	0.30±0.016
	Survival rate (%)	88.8±1.79	88.0±4.89	89.6±2.19
	No. eggs laid / female. d^{-1}	332.0±31.21A ab	333.4±25.21AC ab	344.4±17.94 AB c
F3	Larval Lifespan (days)	16.8±0.447B ab	17.4±0.548 A a	14.4±0.548 C a
	Pupal weight (g)	0.31±0.007	0.308±0.0164	0.31±0.019
	Survival rate (%)	88.0±7.48	88.0±4.89	89.6±7.26
	No. eggs laid / female. d^{-1}	324.4±23.54 B b	325.4±22.88 BC b	354.0±18.84 A ab
F4	Larval Lifespan (days)	16.8±0.837 B ab	17.4±0.548 A a	14.4±0.548 C a
	Pupal weight (g)	0.314±0.0152	0.30±0.0158	0.30±0.016
	Survival rate (%)	87.2±6.57	87.2±5.93	91.2±5.215
	No. eggs laid / female. d^{-1}	326.0±10.25 B b	338.0±21.09 B a	363.0±21.68 A a
	LSD p=<0.05	**CO_2**	**Generation**	**CO_2 x Gen**
	Larval Lifespan (days)	0.444 *	0.378	NS
	Pupal weight (g)	NS	NS	NS
	Survival rate (%)	NS	NS	NS
	No. eggs laid / female. d^{-1}	12.84*	9.24	NS

* significant at p= <0.01

Consumption of foliage by larvae

The impact of CO_2 concentrations and generations was significant on insect species. The weight of foliage (dry) consumed by *A. janata* on castor was significantly varied by CO_2 levels ($F_{2, 8}$ = 282.56, P =<0.01) and generations ($F_{3, 36}$ =16.08, P =<0.01). The interaction between CO_2 conditions and generations was found significant ($F_{6, 36}$=3.34, P=<0.05) (Fig.4).

Larval weights

Larval weights of *A. janata* fed on leaves of castor grown under elevated CO_2 were not significantly different among four successive generations ($F_{3, 36}$= 2.41, P =>0.05). Significantly higher larval weights were recorded in elevated CO_2 treatment ($F_{2, 8}$ = 352.58, P =<0.01). The interaction between CO_2 conditions and generations with respect to larval weights was found to be not significant ($F_{6, 36}$ =1.04, P= >0.05) (Fig. 5).

Faecal matter release

Frass released by *A. janata* larvae was significantly more when larvae fed on castor leaves grown under elevated CO_2 concentrations ($F_{2, 8}$= 20.57, P =<0.01) and frass produced per larva was not varied over generations ($F_{3, 36}$ = 2.54, P =>0.05). The interaction between CO_2 and generations was not significant ($F_{6, 36}$ = 1.27, P=>0.05) (Fig. 6).

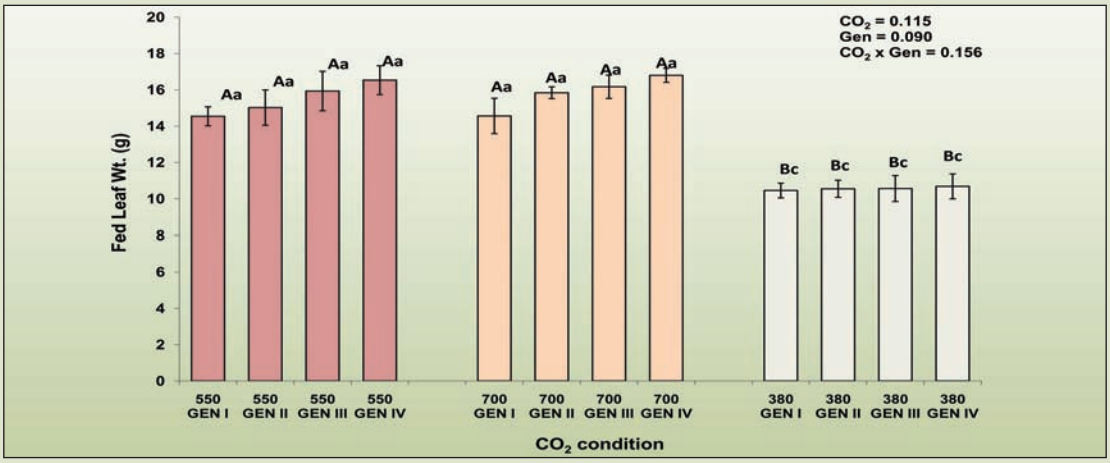


Fig. 4 : Weight of foliage consumed in four successive generations of *A. janata* on castor under ECO_2

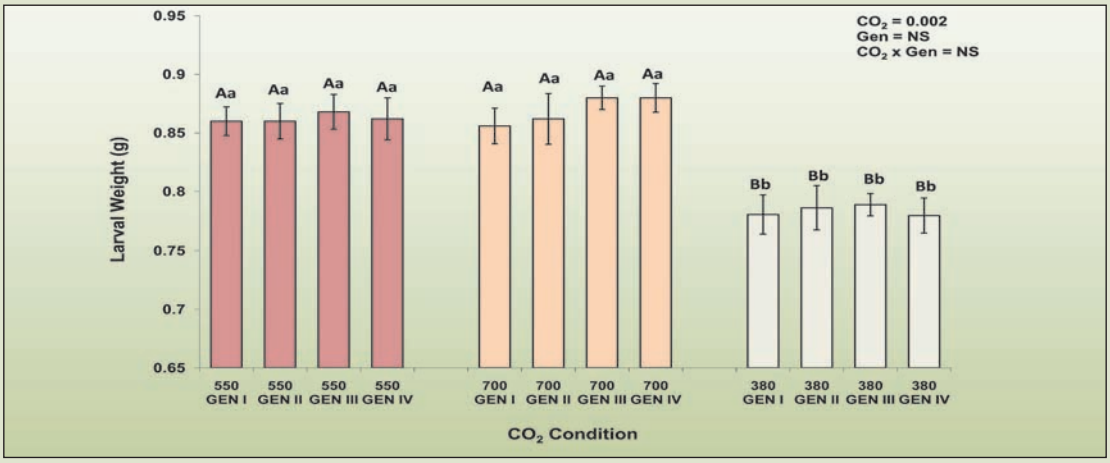


Fig. 5 : Weight of the larva in four successive generations of *A.janata* on castor under ECO_2

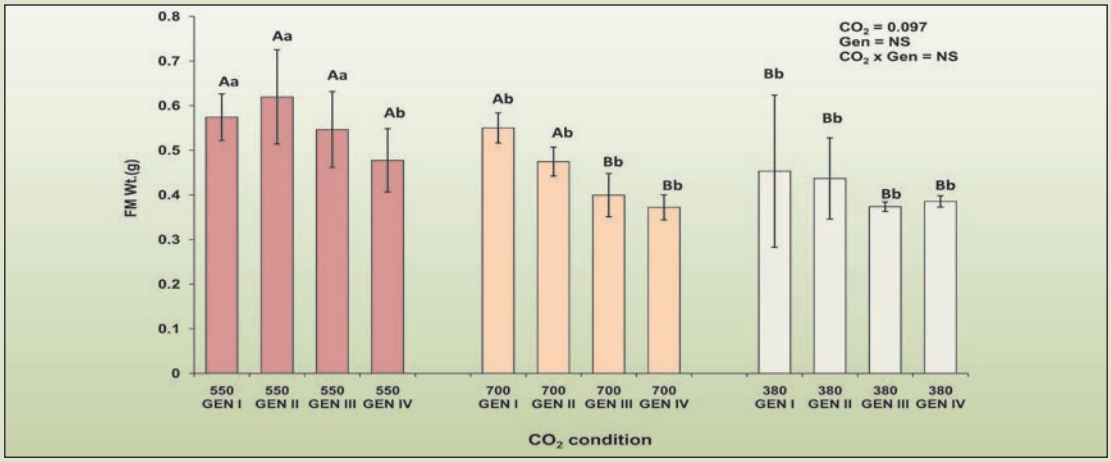


Fig. 6 : Faecal matter of *A. janata* on castor in four successive generations under elevated CO_2 conditions

2. Insect performance indices

The impact of elevated CO_2 ($F_{2, 8}$ = 17.44, P = <0.01) on approximate digestibility (AD) of castor foliage by *A. janata* was significant over four generations ($F_{3, 36}$ = 4.61, P = <0.01). The results indicated that CO_2 levels adversely affected the quality of castor foliage and increased the RCR ($g.g^{-1}.d^{-1}$) of *A. janata* larvae.

The impact of elevated CO_2 on RCR ($F_{2, 8}$ = 37.136, P =<0.01) was significant over four generations ($F_{3, 36}$=10.163, P = <0.01).The interaction between CO_2 and generations was found significant ($F_{6, 36}$ = 2.044, P=<0.05) (Table 2). ECI (%) for *A. janata* larvae fed on castor foliage under elevated CO_2 concentrations was significantly reduced over generations ($F_{3, 36}$ =6.85, P = <0.05) and also due to elevated CO_2 concentrations ($F_{2, 8}$ = 123.0, P = <0.01). The impact of elevated CO_2 ($F_{2, 8}$ = 67.77, P =<0.01) on ECD of larvae was significant over four generations ($F_{3, 36}$=8.94, P = <0.01).

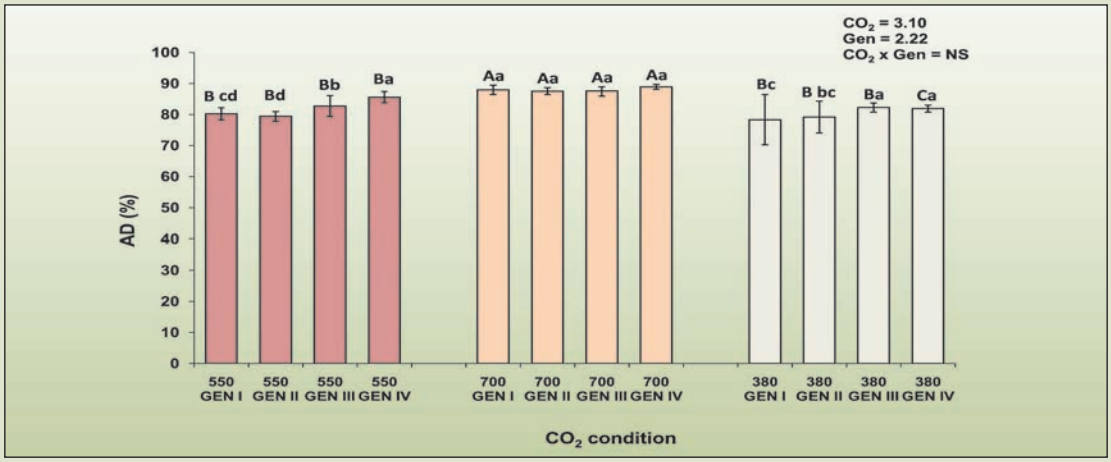


Fig. 7 : Approximate digestibility of castor foliage by *A. janata* in four successive generations under ECO_2

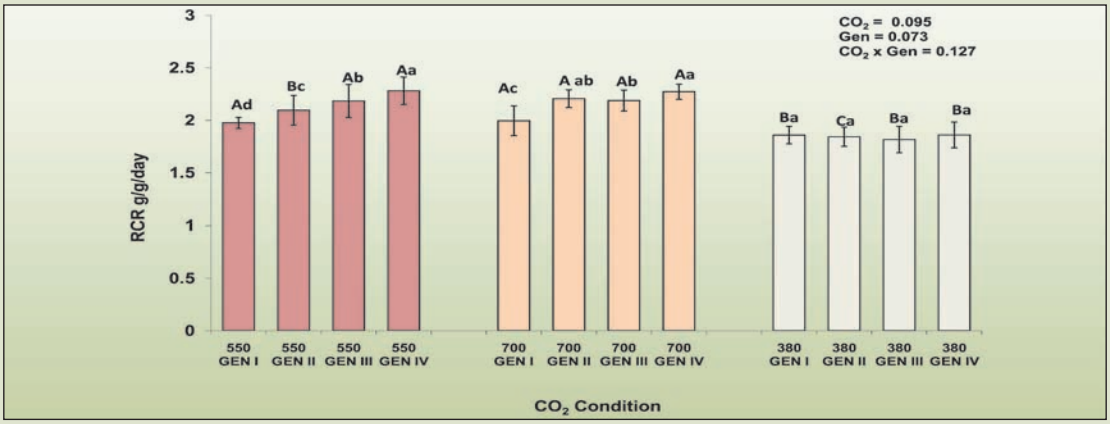


Fig. 8 : Relative consumption rate of *A. janata* on castor foliage in four successive generations unde ECO_2

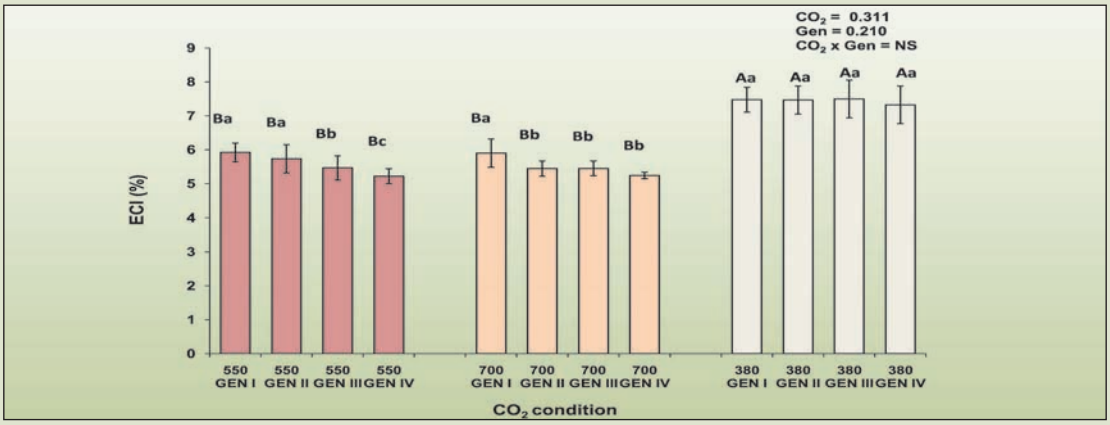


Fig. 9 : Efficiency of conversion of ingested food by *A. janata* on castor in four successive generations under ECO_2

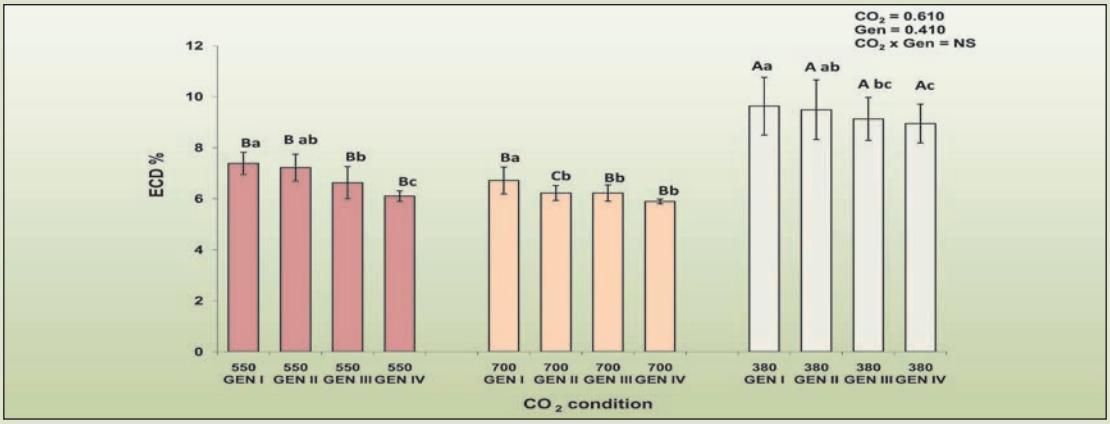


Fig. 10 : Efficiency of conversion of digested food fy *A. janata* on castor in four successive generations under ECO_2

The interaction between CO_2 and generations was not significant ($F_{6, 36}$ = .069, P= >0.05). RGR of larvae decreased significantly when fed on castor foliage under elevated CO_2 ($F_{2, 8}$ = 1711.5, P =<0.05) and did not vary significantly over generations ($F_{3, 36}$ =0.624, P = >0.05). The interaction between CO_2 and generations was found not significant ($F_{6, 36}$ = 1.473, P=>0.05) (Table 2).

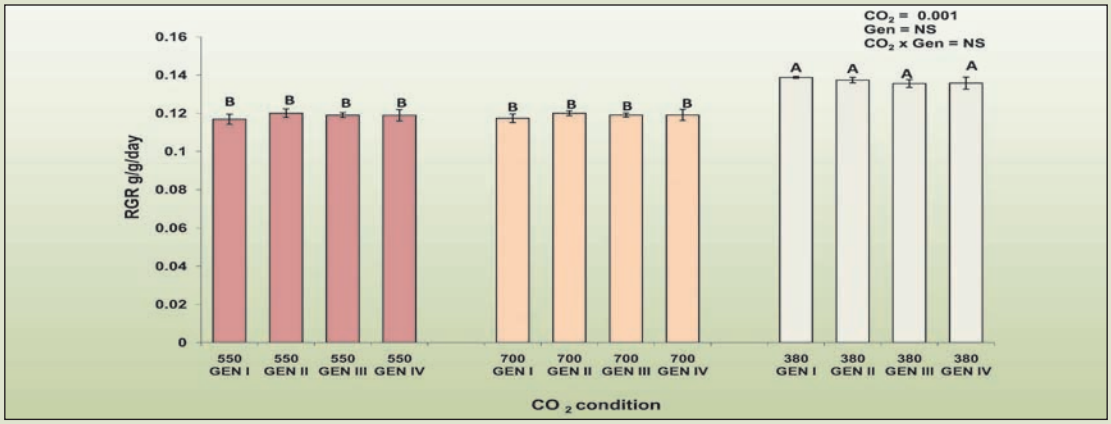


Fig. 11 : Relative growth rate of *A. janata* on castor foliage in four successive generations under ECO_2

Table 2 Insect performance indices of four successive generations of *A.janata* fed on castor grown under ambient and elevated CO_2 concentration

Generation	Insect performance indices	CO_2 concentrations (ppm)		
		550	700	380
F1	AD %	80.23 ± 1.973 B cd	87.92 ± 1.51A a	78.32 ± 8.086 B c
	ECI %	5.92 ± 0.275 B a	5.90 ± 0.416 B a	7.47 ± 0.364 A a
	ECD%	7.38 ± 0.435 B a	6.71 ± 0.529 B a	9.62 ± 1.12 A a
	RGR $g.g^{-1}.d^{-1}$	0.116 ± 0.002 B	0.117 ± 0.002 B	0.138 ± 0.0005 A
	RCR $g.g^{-1}.d^{-1}$	1.975 ± 0.052 A d	1.996 ± 0.141 A c	1.859 ± 0.083 B a
F2	AD %	79.42 ± 1.519 B d	87.53 ± 1.129 A a	79.16 ± 5.128 B bc
	ECI %	5.73 ± 0.416 B a	5.445 ± 0.223 B b	7.46 ± 0.411 A a
	ECD%	7.21 ± 0.529 B ab	6.222 ± 0.293 C b	9.489 ± 1.166 A ab
	RGR $g.g^{-1}.d^{-1}$	0.119 ± 0.002 B	0.120 ± 0.001 B	0.137 ± 0.001 A
	RCR $g.g^{-1}.d^{-1}$	2.096 ± 0.141 B c	2.206 ± 0.084 A ab	1.844 ± 0.091 C a
F3	AD %	82.71 ± 3.38 B b	87.62 ± 1.71 Aa	82.24 ± 1.50 B a
	ECI %	5.47 ± 0.356 B b	5.45 ± 0.218 B b	7.49 ± 0.554 A a
	ECD%	6.62 ± 0.633 B b	6.223 ± 0.321 B b	9.12 ± 0.841 A bc
	RGR $g.g^{-1}.d^{-1}$	0.119 ± 0.001 B	0.119 ± 0.109 B	0.136 ± 0.002 A
	RCR $g.g^{-1}.d^{-1}$	2.18 ± 0.157 A b	2.188 ± 0.100 A b	1.816 ± 0.125 B a
F4	AD %	85.58 ± 1.83 B a	88.92 ± 0.764 A a	81.92 ± 1.11 C a
	ECI %	5.22 ± 0.221 B c	5.24 ± 0.096 B b	7.32 ± 0.551 A a
	ECD%	6.10 ± 0.21 B c	5.89 ± 0.094 B b	8.95 ± 0.763 A c
	RGR $g.g^{-1}.d^{-1}$	0.119 ± 0.003 B	0.119 ± 0.003 B	0.136 ± 0.003 A
	RCR $g.g^{-1}.d^{-1}$	2.282 ± 0.130 A a	2.273 ± 0.072 A a	1.861 ± 0.124 B a
	LSD p=<0.05	**CO_2**	**Generation**	**CO_2 x Gen**
	AD %	3.10	2.22*	NS
	ECI %	0.311*	0.210	NS
	ECD%	0.610*	0.410*	NS
	RGR $g.g^{-1}.d^{-1}$	0.001	NS	NS
	RCR $g.g^{-1}.d^{-1}$	0.095*	0.073*	0.127

* significant at p= <0.01

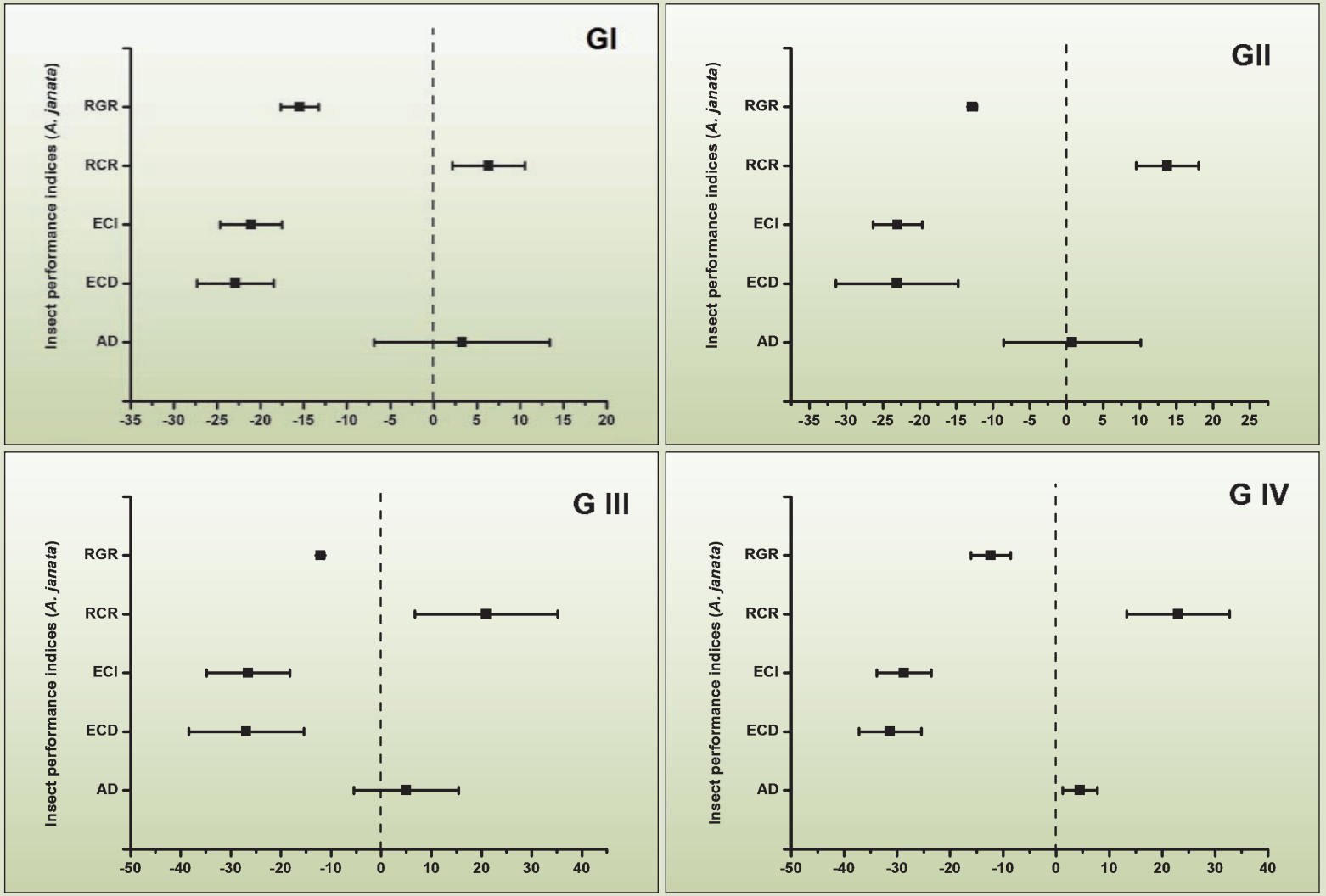


Fig. 12 : Percent change in the indices under ECO_2 (550 ppm) over ambient

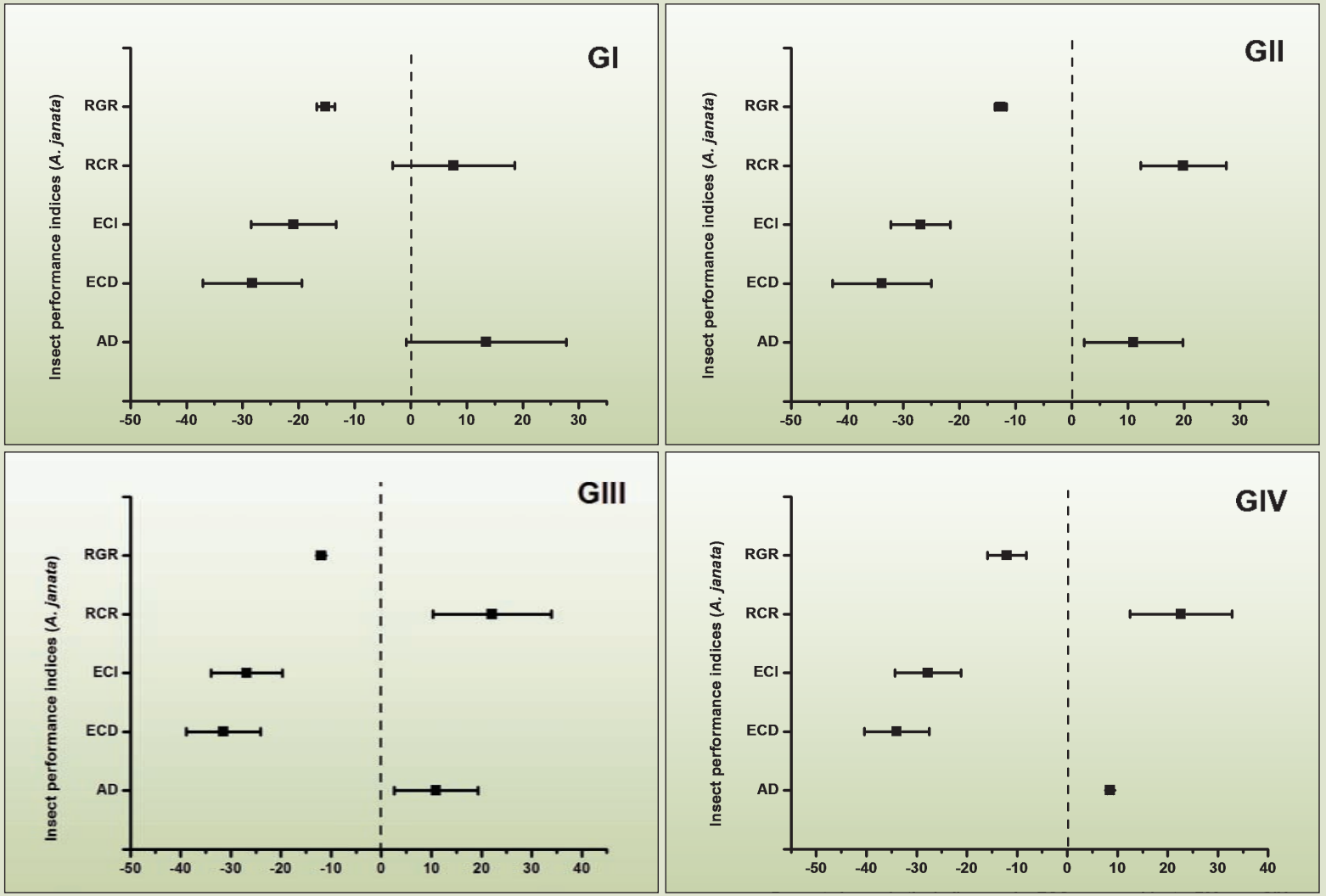


Fig. 13 : Percent change in the indices under ECO_2 (700 ppm) over ambient

3. Biochemical analysis of foliage

Significantly lower leaf nitrogen content (P =<0.01), higher carbon (P =<0.01), higher relative proportion of carbon to nitrogen (C: N) (P =<0.01) and higher polyphenols expressed in terms of tannic acid equivalents (P =<0.01) were observed in castor foliage grown under elevated CO_2 levels (Table 3). The percent variation of bio chemical constituents under two elevated CO_2 levels over ambient was depicted in Fig. 14. The percent reduction of nitrogen content (21-25) and increased percent of carbon (6-10), C: N ratio (43-45) and TAE (Tannic acid equivalents) (80 to > 100) under elevated CO_2 over ambient was observed.

Table 3 Effect of elevated CO_2 on bio chemical constituents of castor foliage grown under elevated and ambient CO_2

Biochemical constituent	CO_2 concentrations (ppm)			F(P)	LSD p=<0.01
	550	700	380		
Nitrogen (%)	2.767±0.076 B	2.95±0.217 B	3.786±0.07 A	43.16 p=<0.01	0.373
Carbon (%)	39.936±0.673 A	41.366±0.808 A	37.516±0.89 B	41.09 p=<0.01	1.439
C:N ratio	14.446±0.637 A	14.199±1.06 A	9.909±0.298 B	112.68 p=<0.01	1.143
TAE (%)	3.069±0.051 B	4.379±0.035 A	1.69±0.017 C	376.93 p=<0.01	0.070

4. Potential population increase index

The population consumption and number of larval individuals were observed to be significantly lower from second to fourth generations of A. *janata* when fed on castor foliage grown under elevated CO_2 conditions when compared to the ambient. The impact of CO_2 concentrations and generation was significant on potential number of larvae of insect species. Significantly lower individuals were observed over generations ($F_{3, 36}$=190.04, P=<0.05) and across CO_2 conditions ($F_{2, 8}$ = 7.83, P =<0.05). The interaction between CO_2 conditions and generations was found significant ($F_{6, 36}$ =4.74, P=<0.05) (Table 4). The potential larval individuals were reduced by 0.84, 12.15 %; 10.32, 29.34% and 19.82, 43.13% in second, third and fourth generations under two elevated CO_2 conditions, respectively. The total number of eggs laid by all females was significantly affected by CO_2 levels ($F_{2, 8}$= 13.30, P =<0.05) and generation ($F_{3, 36}$ = 150.25, P =<0.05). The interaction between CO_2 conditions and generations was also found significant ($F_{6, 36}$ =7.13, P=<0.05).

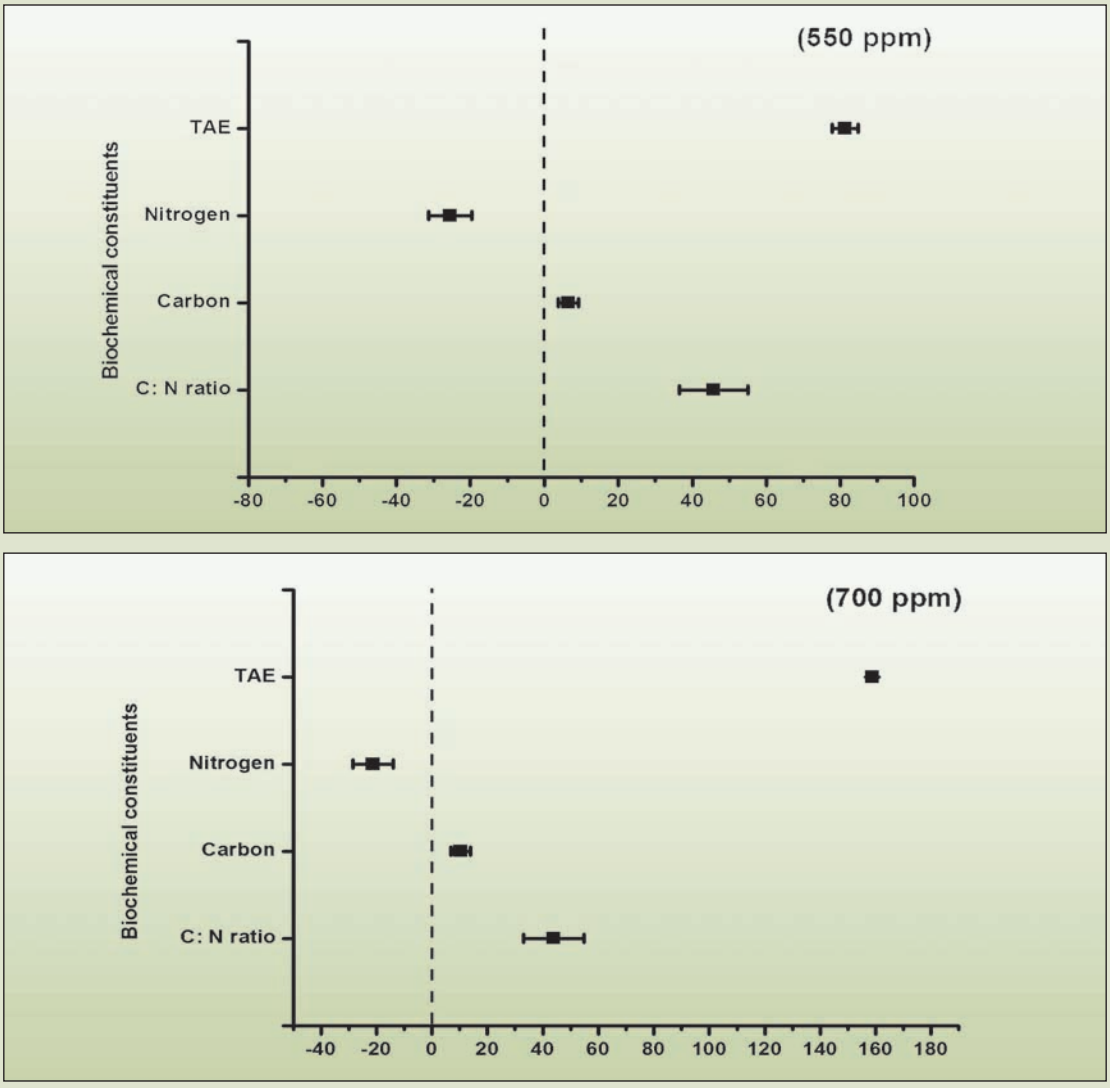


Fig. 14 : Percent change in the biochemical constituents of castor foliage under ECO_2 over ambient

Similarly the 'potential population increase index' for successive generations was found lower in elevated CO_2 concentrations than those in the ambient. The Index values were 130.95 ± 10.42 in second generations, 135.58 ±15.85 in third generation and 136.51±16.51 in fourth generation of *A. janata* fed on castor grown under 550 ppm CO_2 concentration. These index values were still lower under 700 ppm concentration and in the range of 116.36 ± 9.17 to 125.39± 11.51than ambient (146.08±12.93 to 158.35±10.41). The percent reduction of index under elevated CO_2 was in the range of 10.35 - 20.54 than ambient and decrease of index was more evident in second to fourth generations (Table 4).

Table 4 Estimation of potential population increase index and potential population consumption of *A.janata* in successive four generations fed on castor grown under elevated CO_2 concentrations.

Gen.	Parameter	550 ppm	700 ppm	380 ppm
F1	Initial no. of larval individuals	20 ± 0	20 ± 0	20 ± 0
	Total eggs laid by all females[1]	$0.32*10^4 \pm 0.035*10^4$	$0.28*10^4 \pm 0.042*10^4$	$0.32*10^4 \pm 0.03*10^4$
	Total larval consumption	2.91 ± 0.10	2.906 ± 0.20	2.0908 ± 0.08
F2	Potential initial no. of larval individuals[2]	2767.60 ± 292.41 A b	2451.88 ± 386.47 A b	2791.14 ± 339.43 A b
	Potential total eggs laid by all females	$42.35*10^4 \pm 7.37*10^4$ A c	$33.20*10^4 \pm 6.88*10^4$ B c	$47.41*10^4 \pm 9.08*10^4$ A c
	Potential Population increase index[3]	130.95 ± 10.42 B a	116.36 ± 9.17 C b	146.07 ± 12.92 A b
	Potential total larval consumption[4]	7224.23 ± 929.51 b	6392.35± 1561.62 b	5096.52 ± 785.18 b
F3	Potential initial no. of larval individuals	$38.09 *10^4 \pm 7.12*10^4$ A c	$30.01*10^4 \pm 6.17*10^4$ A c	$42.48*10^4 \pm 8.15*10^4$ A c
	Potential total eggs laid by all females	$5804.65*10^4 \pm 1460.0*10^4$ B b	$4123.46*10^4 \pm 1290.29*10^4$ C b	$7288.91*10^4 \pm 1996.33*10^4$ A b
	Potential Population increase index	135.57 ± 15.84 B a	125.39 ± 13.46 C ab	151.39 ± 19.84 A ab
	Potential total larval consumption	$101.18*10^4 \pm 22.34*10^4$ c	$84.49*10^4 \pm 23.40*10^4$ c	$81.12*10^4 \pm 19.77*10^4$ c
F4	Potential initial no. of larval individuals	$5266.28*10^4 \pm 1361.11*10^4$ B a	$3735.07*10^4 \pm 1160.09*10^4$ C a	$6567.85*10^4 \pm 1780.16*10^4$ A a
	Potential total eggs laid by all females	$807856.3*10^4 \pm 284376.7*10^4$ B a	$524201.27*10^4 \pm 191796.87*10^4$ C a	$1146628.30*10^4 \pm 294374.07*10^4$ A a
	Potential Population increase index	136.50 ± 16.51 B a	129.75 ± 11.50 B a	158.34 ± 10.41 A a
	Potential total larval consumption	$15311.8 *10^4 \pm 14.2*10^4$ a	$10985.17*10^4 \pm 3766.85*10^4$ a	$12785.79*10^4 \pm 3533.10*10^4$ a

LSD p=<0.05	CO_2	Generation	CO_2 x Generation
Potential initial no of larval individuals	$415.15 *10^4$	$538.39*10^4$	$932.52*10^4$
Potential total eggs laid by all females	$7.01*10^4$	$9.64*10^4$	$16.69*10^4$
Potential Population increase index	8.755	9.992	NS
Potential total larval consumption	NS	$1750.88*10^4$	NS

Total eggs laid by all females[1] = Initial numbers of larval individuals X larval survival rate X pupation rate X rate of adults emergence X ratio of female X eggs laid per female

Potential initial numbers of larval individuals for the second or third generation[2] = (potential) total eggs laid by all females in previous generation X hatch rate

Potential population increase index for the second or third generation[3] = total eggs laid by all females in this generation/total eggs laid by all females in previous generation

Potential total larval consumption (g) for the second or third generation[4] = Potential initial numbers of larval individuals for the second or third generation X larval survival rate X consumption per larvae.

Means within a row indicated by different letters are significantly different (LSD test, $P < 0.05$)

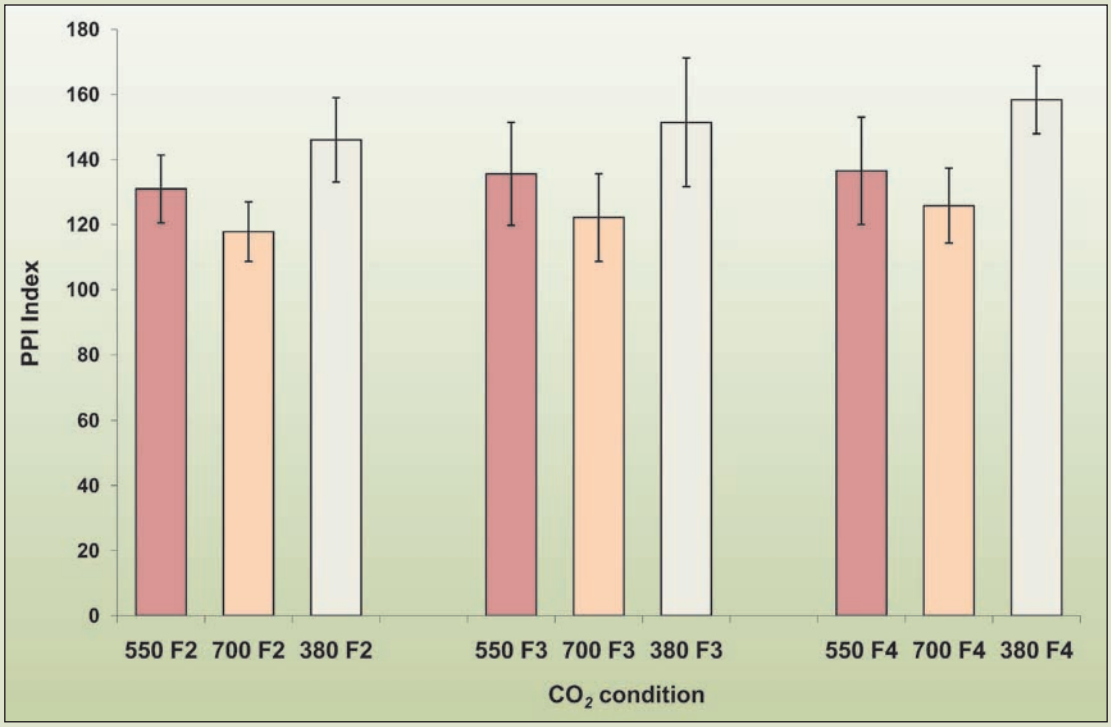


Fig. 15 : PPII in successive generations of *A. janata* on castor across CO_2 concentrations

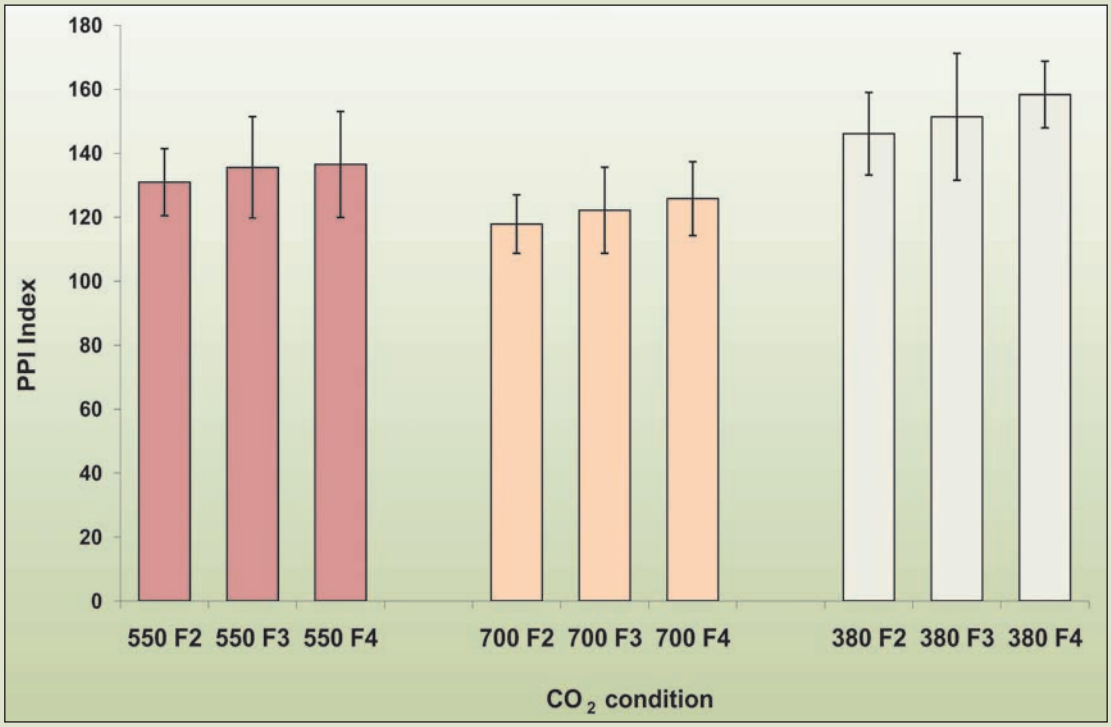


Fig. 16 : PPII if *A.janata* on castor across generations

Discussion

Climate change is likely to affect agriculture by 2100 though the effects are expected to vary with crop and region. The principal components of climate change are increase in temperature and carbon dioxide concentrations in the atmosphere. These predicted changes, particularly changes in atmospheric CO_2 will have significant effect on growth of crops. As CO_2 is a principal source of carbon, it is very clear that changes in concentrations of carbon dioxide have marked effects on growth of crops .There is little evidence of any direct effects of CO_2 on herbivorous or phytophagous insects and mostly the impact of elevated CO_2 is mediated through host crop. 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.

The impact of elevated CO_2 on the phytochemistry of the plants was well studied (Hunter, 2001). In this study also, nitrogen concentration in castor leaves decreased by about 21-25 per cent when plants were grown under elevated CO_2 conditions. With increased carbon intake, the carbon content of the leaf tissues also increased (6-10%). Both of these together resulted in an increase (43-45%) of C: N ratio and these findings are similar to those reported by earlier authors (Hugher *et al*., 1997). Since nitrogen is the chief constituent of proteins, this suggests that plants grown under elevated CO_2 conditions have lower protein in their tissues. Polyphenols, non-structural carbon compounds that constitute one of the defense mechanisms of plants and offer antecedence to herbivores are also known to increase up to 80% in leaves under elevated CO_2 conditions (Bezemer *et al*., 1998). In this study also, the higher concentration of polyphenols was observed in leaves of plants grown under elevated CO_2 conditions. Consumption and growth of larvae are influenced by nitrogen content of the foliage.

Nitrogen is known to be a most important limiting factor in the growth and development of herbivorous insects and thus a slight reduction in foliar nitrogen content would have profound effects on their performance (Mattson *et al*., 1980). Insects increase their consumption and assimilation rates when fed with nitrogen-poor foliage. However, the efficiency of conversion of food into biomass is reduced, resulting in lower growth rates (Lindroth *et al*., 1995).

Our results indicated significant influence of elevated CO_2 on life history parameters of *A. janata* over four generations. Larval duration of *A. janata* increased by 15-20% in successive four generations under elevated CO_2 compared with ambient CO_2. This

increased larval life span (upto 6%) was also noticed in fourth generation over first generation. Differential effect of CO_2 on pupal weights and larval survival rates (4%) over four successive generations of A. *janata* was observed in elevated CO_2 compared with ambient. Similar generation effects were observed within the each CO_2 level. Our studies further indicated that fecundity (egg laying capacity) of *A. janata* was reduced by 2-4% in first generation, 3 % in second generation, 8% in third generation and 10% in fourth generation under elevated CO_2 than ambient. Similarly reduction in fecundity was observed over generations i.e. from first to fourth generations (2-4%) under each elevated CO_2 level.

The present results showed that insect performance indices of *A. janata* larvae when fed on castor foliage grown under elevated CO_2 varied in four generations than ambient. An increase of 0.32 - 12.26% of AD was observed in all four generations under elevated CO_2 than ambient. ECI decreased in first and second generations under elevated CO_2 compared to ambient. ECD (23-34%) and RGR (12-15%) decreased in four generations under elevated CO_2 than ambient. Increased consumption (RCR) by 6-22% was recorded under elevated CO_2 than ambient. Within each elevated CO_2 level also increased AD (about 1-6%) and RCR (13-15%) were observed in fourth generation over first generation. Larvae consumed more castor foliage grown under elevated CO_2 and assimilated better (higher values of RCR and AD) but grew slower (lower RGR) and took longer time (two days more than ambient) to pupation. A reduction in nitrogen content may be accompanied by decreased efficiency of conversion to body mass and reduced growth rate (Masters *et al*., 1998).

Herbivores respond to increased levels of CO_2 by increasing their food consumption, prolonging development time, and reducing their growth rates and food conversion efficiency (Watt *et al*., 1995). Changes in the performance of herbivorous insects, usually in the larval stages are correlated with changes in the quality of the food plants in terms of nitrogen level, C:N ratio and concentration of phenolics. In general, host plant quality declines in elevated CO_2 with decreased leaf nitrogen and increased phenolics. Changes in nitrogen content are correlated with changes in food consumption and changes in phenolics with changes in food digestibility. These correlations were well proven earlier by the authors, Srinivasa Rao *et al*.(2008) with *A. janata* on castor grown under elevated CO_2. Present results showed higher consumption levels of larvae under elevated CO_2 conditions over four generations. The consumption per larva of *A. janata* fed on castor foliage grown under elevated CO_2 increased by 39-57 % from first to fourth generation.

Similarly potential population increase index (PPII) for successive generations was found lower in elevated CO_2 concentrations than in case of ambient. The percent PPII decreased by 10.35 - 20.34 under elevated CO_2 than ambient and the decrease was more evident in second and third generations of *A.janata* fed on castor grown under 700 ppm CO_2 concentration. The potential total no. of eggs laid by all females was significantly lower in two elevated CO_2 concentrations than ambient over second to fourth generations. The potential total no. of eggs laid by all females decreased by 10.66, 30.0 %; 20.36, 43.42% and 29.54, 54.28 % in second, third and fourth generations under two elevated CO_2 conditions respectively. Wu *et al*., 2006, observed a similar reduction in PPII in cotton boll worm on wheat and attributed it to integrative effect of longer larval life span and lower fecundity and similar trend was observed in the present experimentation too. The potential larval consumption of castor foliage was found lower (-14.08%) under 700 ppm CO_2 concentration than ambient and 550 ppm CO_2 concentrations in fourth generation.

The present study showed that growth and development of *A. janata* when fed on castor foliage grown under elevated CO_2 conditions varied across four generations than ambient. The cumulative effect of elevated CO_2 on insect performance indices of *A. janata* was significant over successive generations. This data on insect parameters for more than one generation will give a better picture of effects of elevated CO_2 and can help in understanding the population dynamics of pests in the future climate change scenarios.

Acknowledgements

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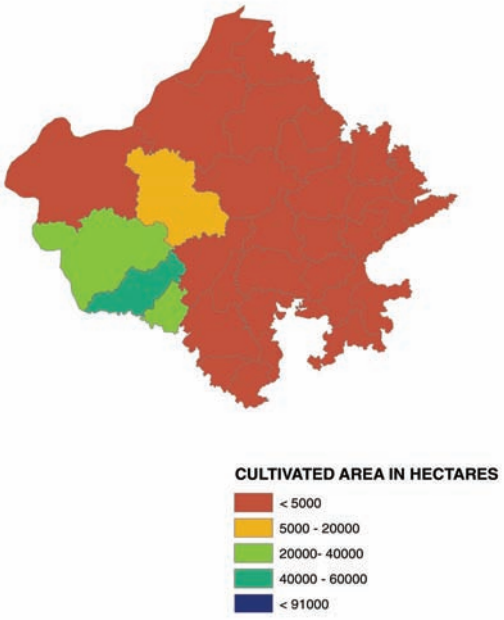
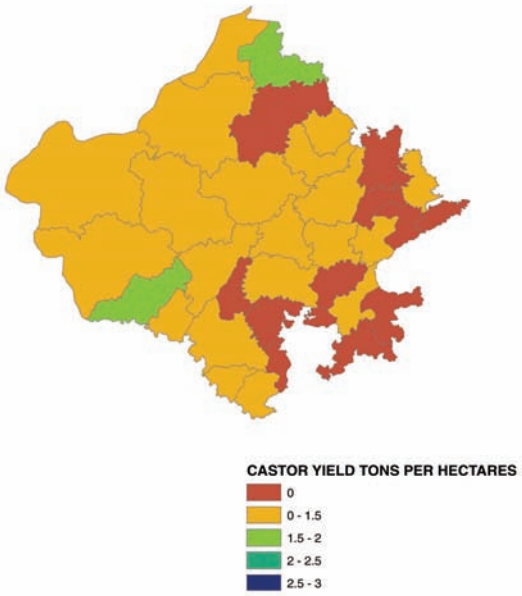
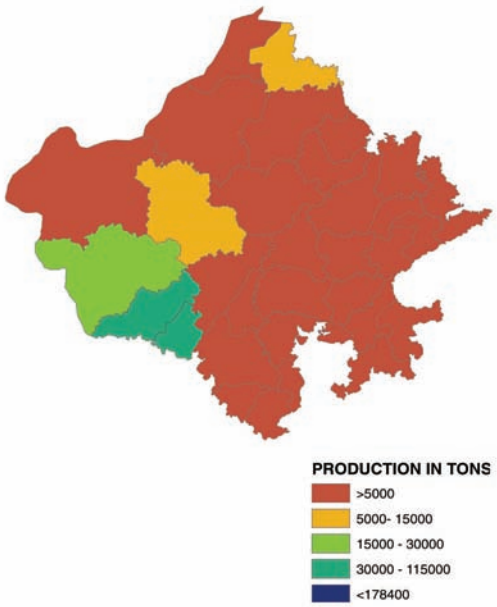
RAJASTAN DISTRICTS
CASTOR AREA IN HECTARES



RAJASTHAN DISTRICTS
CASTOR YIELD IN TONS PER HECTARES



RAJASTHAN DISTRICTS
CASTOR PRODUCTION IN TONS



Castor cultivation in Rajasthan State

AREA ('000 HA)	98.2
PRODUCTION ('000 TN)	133.0
YIELD (KGS./ HA.)	1351.2

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