

Meta analysis of Impact of elevated CO₂ on host - insect herbivore interactions



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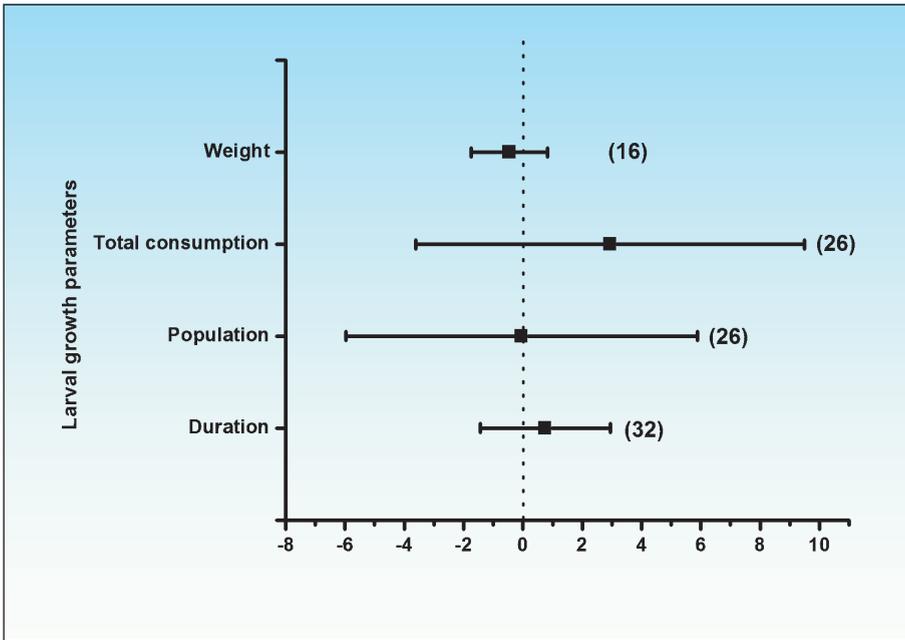


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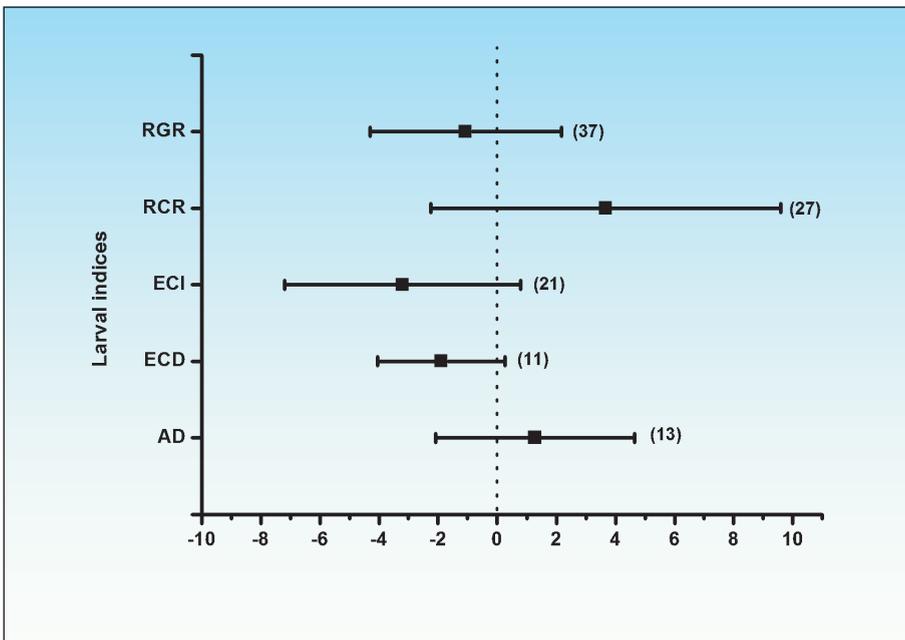
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National Initiative on Climate Resilient Agriculture (NICRA)
Central Research Institute for Dryland Agriculture
Santoshnagar, Saidabad, Hyderabad – 500 059.



Mean effect size of larval growth parameters under eCO₂



Mean effect size of larval performance Indices under eCO₂

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Executive Summary

An alternative procedure to deal with the limitations of the qualitative synthesis of studies was put forward and came to be known as 'meta analysis'. The quantification of impact of elevated carbon dioxide (eCO₂) on the incidence of insect pests through statistical synthesis of published results or meta-analysis is attempted here. Integration of findings of independent studies by calculating the magnitude of treatment effects i.e., "effect size" is estimated. Data for the meta analysis were gathered from the published studies (88 articles) in selected journals (28) for comparing the growth and development of insect herbivores under eCO₂ conditions and compared with ambient CO₂ condition. The basic requirements of the each study were identified as follows The following criteria were identified for each study: 1) Studies pertaining to elevated CO₂ levels. 2) Studies reporting information on the mean of the parameters along with a measures of variance (standard error, standard deviation , coefficient of variance and confidence intervals). 3) Studies that reported the design of experimentation and sample size for all the treatments. The mean effect sizes for various insect parameters varied significantly. Among the insect primary parameters consumption (2.94) and duration of insect species (0.751) were found to be significantly positive under eCO₂ and other parameters like weight (-0.46) and population abundance (-0.05) of species were negative. Insect performance indices showed positive effect size for approximate digestibility, AD (1.281) and relative consumption rate, RCR (3.61) and negative with respect to efficiency of conversion of ingested food, ECI (-3.20), efficiency of conversion of digested food, ECD (-1.891) and relative growth rate, RGR (-1.072). Meta analysis of biochemical constituents of host plants indicated that the effect sizes were found to be negative (Nitrogen) and positive (Carbon and C: N ratio) indicating a significant variation of constituents under eCO₂ condition than ambient CO₂ condition. The implications and limitations of meta analysis were discussed.

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1. Introduction

The possible impacts of elevated CO₂ (eCO₂) on growth and development behavior of insect pests attracted the attention of researchers. Several reviews of such studies were attempted to draw conclusions on the impact of elevated CO₂ on insect pest incidence. These reviews were mainly qualitative summaries of the studies and the conclusions drawn are not based on any statistical or quantitative analysis. These reviews were subjective and often based on vote-counting method. They did not consider the magnitude of the impact and sample size observed in the individual studies and in the process the valuable information available in the original studies is lost. When studies reporting differential impact are included in the review, it becomes that much more difficult to draw conclusion on the overall impact of the treatment under question. Hence, the validity of these conclusions remains questionable. It is only possible to draw some generalizations, which have little statistical validity, and it is also not possible to quantify the magnitude of the effect of treatment.

Most of the reviews (Coviella and Trumble, 1999; Hunter, 2001; and Srinivasa Rao *et al* 2006) attempted to examine the impact of elevated CO₂ on insect pest incidence also suffer from the above mentioned limitations. The summary of qualitative literature survey on the impact of elevated CO₂ on insect pests was documented by earlier reviewers. From such exercises, only subjective generalizations can be drawn rather than any quantified effect of interest, which has some statistical validity.

An alternative procedure to deal with the limitations of the qualitative synthesis of studies was put forward initially by Glass (1976) and came to be known as meta analysis. Quantification of effect of eCO₂ on the incidence of insect pests through statistical synthesis of published results or meta analysis is attempted here. The purpose of this bulletin is to synthesize the information on the elevated CO₂ – insect pest population relationships and to draw statistically valid conclusions using meta analysis as a tool.

2. Meta analysis

2.1 About Meta analysis

Meta analysis is secondary analysis of published results. As a concept it was used by the statisticians to combine results from several independent studies. The method, however, gained ground in research after Glass (1976) proposed that a large body of literature, often yielding

conflicting results, could be subjected to a secondary analysis that would integrate the findings. This analysis, also called ‘analysis of analyses’ was extensively used in social and medical sciences. However, it is applied rarely in entomological studies. There were a few such attempts to synthesize the impact of climate change on the incidence of insect pests. On the other hand, the method was described as ‘wave of the future’ and as being potentially useful tool for policy makers in dealing with conflicting evidences regarding the problem at hand.

One of the extensively used measures in meta analysis is the ‘effect size’ which integrates the results from different experiments on a given subject into an index. In other words, the effect size gives the relative magnitude of the experimental treatment (Thalheimer and Cook, 2002). When computed across different experiments, the effect sizes allow us compare the magnitude of effect observed in different experiments. Although percent improvements can be used to compare the elevated CO₂ condition over ambient conditions, such calculations are difficult to interpret and often difficult to use in fair comparisons across different studies. Among other uses, effect size measures play an important role in meta analysis studies that summarize findings from a specific area of research, and in statistical power analyses.

A meta analysis combines the results of several studies that address a set of related research hypotheses and here impact of elevated CO₂ on insect pests was considered.. In its simplest form, this is normally by identification of a common measure of effect size, for which a weighted average might be the output of a meta-analyses. Here the weighting might be related to sample sizes within the individual studies. More generally there are other differences between the studies that need to be allowed for, but the general aim of a meta analysis is to more powerfully estimate the true “effect size” as opposed to a smaller “effect size” derived in a single study under a given single set of assumptions and conditions.

Meta analyses are often, but not always, important components of a systematic review procedure. Here it is convenient to follow the terminology used by the Cochrane Collaboration, and use “meta analysis” to refer to statistical methods of combining evidence, leaving other aspects of ‘research synthesis’ or ‘evidence synthesis’, such as combining information from qualitative studies, for the more general context of systematic reviews.

2.2 Materials and Methods

Meta analysis is a sequential and methodical process and starts with careful selection of studies keeping the objective of the analysis in view. Once the studies were selected, the key features of the studies are organized into a database that enables a better interpretation of the results of the analysis.

Selection of studies. A review of the literature covering the period from 1984 to 2010 was conducted on twenty eight journals. The details of these journals are given in separate table 1.

Table 1 : The Journals used to source the articles included in the Meta analysis

S.No	Name of the journal	No. of Articles
1	Acta Ecologica Sinica	1
2	Agricultural and Forest Entomology	2
3	Agriculture Ecosystems and Environment	1
4	<i>Ann. Entomol. Soc. Am</i>	1
5	Behavioural Ecology and Sociology	1
6	Current Science	2
7	<i>Ecological Applications</i>	2
8	Ecological Entomology	1
9	<i>Ecology</i>	4
10	<i>Entomologia Experimentalis et Applicata</i>	4
11	<i>Environmental entomology</i>	10
12	Environmental and Experimental Botany	2
13	<i>Functional Ecology</i>	2
14	<i>Global Change Biology</i>	21
15	Insect science	1
16	JEN	1
17	Journal of Agriculture and Food Chemistry	1
18	Journal of Applied Entomology	2
19	<i>Journal of Chemical Biology</i>	1
20	<i>Journal of Experimental Botany</i>	2
21	Journal of Plant Research	1
22	Nature	1
23	New Physiologist	2
24	<i>New Phytology</i>	1
25	<i>Oecologia</i>	18
26	<i>OIKOS</i>	1
27	<i>Science</i>	1
28	The 1998 BRIGHTON CONFERENCE – Pests & Diseases	1

The following criteria were identified for each study: 1) Studies pertaining to elevated CO₂ levels. 2) Studies reporting information on the mean of the parameters along with a measure of variance (standard error, standard deviation, coefficient of variance and confidence intervals). 3) Studies that reported the design of experimentation and sample size for all the treatment. Several research papers were not included as these papers did not report the complete data required for analysis. Studies with levels of CO₂ lower than present-day ambient (i.e., preindustrial concentrations) were also not included for analysis.

Data for the meta analysis were gathered from the published studies in these journals for comparing the growth and behavior of insect pests under elevated carbon dioxide (CO₂) versus ambient level of CO₂; differences in different parameters of insect behavior were computed with respect to those observed under ambient CO₂ conditions. The selection of the published articles for the analysis was restricted by the following conditions; (1) only studies on agro and forest ecosystems were considered; (2) experiments that were conducted under both laboratory and field conditions; (3) where results were expressed as number of insects/ damage/consumption per treatment. Additionally the meta analysis contained studies that provided means, standard deviations (or standard errors) and sample size of elevated CO₂ and ambient groups, variables necessary for calculation of effect sizes. In addition to this, various articles reporting standard error of mean and least significant difference and 't' tests were also included.

When two or more two elevated CO₂ concentrations were reported in the same experimentation, only the highest concentration of elevated CO₂ was included for analysis. (e.g., 550,650 or 450,700 ppm). Ambient CO₂ concentrations ranged between 270 and 420 ppm, whereas elevated CO₂ concentrations ranged between 550 and 1032 ppm. Response mean values (\bar{X}_{ambient} and $\bar{X}_{\text{elevated}}$), standard deviations (S_{control} and S_{elevated}) and sample size (N_{control} and N_{elevated}) were gathered from tables and/or figures from each study included in the review. When data were available on graphs, the values of means and standard deviations were measured by were measured by using graph paper and interpolated the actual scale values.

A total of eighty eight studies were collected after thorough screening and scanning of the reported information which could satisfy our above mentioned criteria for conducting the meta analysis.

Separate meta analyses were conducted on all insect herbivore reported on several parameters like consumption (includes total consumption, leaf consumption, food eaten, food consumed, larval consumption etc.), duration (longevity, development time, duration of instar, development index, life span etc.), weight (weights of different stages of insects like larval instars, pupa, final mass and adult) population abundance (fecundity, number of nymphs, no of individuals absolute no, population size).

Further meta analysis was conducted on data reported on food efficiency parameters or nutritional indices or insect performance indices like approximate digestibility (AD), efficiency of conversion of ingested food (ECI), efficiency of conversion of digested food (ECD), relative consumption rate (RCR) and relative growth rate (RGR).

Although there was wide variation in the calculation of insect parameters in the papers reviewed, we only included in our analysis studies that have used nutritional indices based on standard formulas as summarized. In some studies, the authors reported effects of elevated CO₂ on several host plants and/or herbivore species, or results were reported separately by herbivore gender, generation and/or host plant genotype. Although different manipulations reported in the same study are not necessarily independent, the loss of information caused by omission of such non independent comparisons might bias the results even more than the inclusion of these comparisons (Koricheva et al., 1998).

Selection of data. Some experiments in the selected studies were performed in a confounded manner (factorial analysis or split-plot designs). In those cases, only results within the same variable were considered. For example, if the experiment was conducted as a 2x2 factorial, where levels a₀ and a₁ of factor A (CO₂) were compared with levels b₀ and b₁ of factor B (ozone or any other gas), only the results for a₀b₀ and a₁b₁ were used in the meta analysis. To reduce the effects of non-dependence, the results for only one species or life stage and one treatment per study were considered.

The choice of the species was based, first, on the focus of the paper; if all species were given the same level of importance, the most abundant and important one was chosen. When results were presented for several sampling dates, we selected the date of highest difference between elevated CO₂ and ambient plots. When more than one CO₂ concentration was compared with the ambient levels, the concentration of greatest difference from the control or ambient was selected.

One of the indices, the effect size (Cohen, 1977), has been used widely in meta analysis (Glass, 1977, Glass et al, 1981; Strube and Hartmann, 1989; Wolf 1986). The effect size(*g*) expresses the standardized difference between means (*i*) of treatments(*t*) and control groups(*c*) so that

$$g = (\mu_t - \mu_c) / \sigma$$

Where σ is the standard deviation.

The combined effect size of a series of experiments indicates the magnitude of the effect observed. Replacing the sample estimates for the population parameters we get

$$g_i = (m_t - m_c) / s_c$$

where g_i is the effect size for experiment *i*, m_t and m_c are means for treatments (elevated CO₂ condition) and control (ambient CO₂ condition) groups, respectively, and s_c is the standard deviation of the control group.

However, Hedges (1981, 1982) demonstrated that g_i and s_c are biased estimators, and proposed the following alternative methods for unbiased estimates of pooled variance and effect size.

$$s_i^2 = [(n_t - 1)(s_t)^2 + (n_c - 1)(s_c)^2] / (n_t + n_c - 2)$$

where

s_i = pooled variance

n_t = sample size of treatments

n_c = sample size of control

s_c = standard deviation of control

s_t = standard deviation of treatment

$$d_i = g * [1 - \{3/(4n-2)-1\}]$$

d_i = unbiased estimate of effect size g

In most of the literature this distinction between g and d_i is not observed and hence g is taken as effect size. In this bulletin, we computed the effect size d , corrected for small sample bias as mentioned above.

Thus data on means and standard deviation are the minimum data set required to compute effect size for a given study. However, many of the studies do not report such information in which case appropriate alternative formulae were used to compute the effect size. For the studies that did not report the standard deviations, the effect size was calculated based on the standard error mean (SEm), least significant difference (LSD or CD) and t - values. The following formulae (Thalheimer and Cook, 2002) were used for the purpose.

When an experiment that uses a t -test does not list standard deviations, g is calculated as follows

$$g = t * \{[(n_t + n_c) / (n_t n_c)] \{ (n_t + n_c) / (n_t + n_c - 2) \}\}^{0.5}$$

where

t = t value

n_t = sample size of treatments

n_c = sample size of control

When an experiment that uses a t -test does not list standard deviations but does list standard errors (SE), the following relationship was used

$$S = SE \sqrt{n}$$

S = Standard deviation

SE = Standard error

n = sample size

The pooled effect size from several studies is usually calculated under the condition of large n_t and n_c (e.g. Smith & Glass, 1977; Harris & Rosenthal, 1985; Gurevitch et al., 1992). However, data for our analysis consisted mostly of small sample sizes, which generally corresponded to plot means. In this situation, the effect sizes and their variances are considerably biased if the methods developed for large sample sizes are used (Hedges & Olkin, 1985). Where n_t and n_c are small ($n < 10$) and the number of studies, k , is large, the common effect size can be calculated by a weighted linear combination of d (Hedges & Olkin, 1985). The weighted mean of effect sizes, d_+ , can be estimated by:

$$d_+ = d_1 w_1 + \dots + d_k w_k$$

The weights of individual studies w_i , are estimated from the variances of effect sizes, v_i :

$$w_i = (1/v_i) / \sum (1/v_i)$$

$$v_i = a + b d_M^2$$

Where d_M is the mean of d_i for $i = 1, \dots, k$ studies, and the constants a and b are estimated by:

$$a = (N-2)[c(N-2)]^2 / [(n_t - n_c)/N] (N-4)$$

$$b = \{(N-2)[c(N-2)]^2 - (N-4)\} / (N-4)$$

The variance of d_+ with k large enough is calculated by

$$v = [\sum (1/v_i)]^{-1}$$

$$N = \sum n_i$$

The methods presented above are based on the assumption that effect sizes from different studies are homogenous, i.e. differences are due only to sampling error (Hedges & Olkin, 1985). The homogeneity of effect sizes can be tested by the Q test (Hedges 1982).

$$Q = \sum (d_i - d_+)^2 / v_i$$

If the Q statistic is higher than the chi-square value for $k-1$ degrees of freedom, the hypothesis of homogeneity of effect sizes is rejected (Hedges 1982; Hedges & Olkin, 1985).

One of the criticisms of meta analysis is that it does not consider the unpublished results which might contain non-significant results which may result in overestimates of population effect size. A measure called 'failsafe N' (N_{fs}), defined as the number of non-significant studies required to bring the effect size to a specific level, is suggested to address this issue.

The fail safe N is given by

$$N_{fs} = N_{total} (\text{mean effect size } d_+ - D_{crit}) / D_{crit}$$

Where N_{total} is the total number of studies and D_{crit} is the specified d value.

A failsafe N for a d value of 0.5 is computed here which is considered as moderate effect size.

We conducted an initial meta analysis by including all the studies for various parameters viz., consumption of foliage by insects, duration and weight of insect as basic parameters. We performed a further meta analysis of data including various insect performance indices like approximate digestibility (AD), relative consumption rate(RCR), efficiency of conversion of ingested food (ECI), efficiency of conversion of digested food (ECD) and relative growth rate (RGR) also.

All the analysis was done using the software developed by Schwarzer (http://web.fu.berlin.de/gesund/gisu*engle/meta-e.htm).

3. Results

3.1 Status of studies

All the papers included were characterized in terms of the taxonomical classification of the species studied, feeding behavior, facility used to elevate CO₂ concentration, host plant and were compiled into a database. All database were depicted in graphs and figures in parentheses over columns indicate no.of studies considered. A look at such a database indicated that about 58% of the studies focused on the lepidopteran insects and 18% on homopterans (Fig 1). Within the lepidopteran insects, the economically important family Noctuidae received considerable attention with 20 studies addressing the insects belonging to this family. Lymantridae,

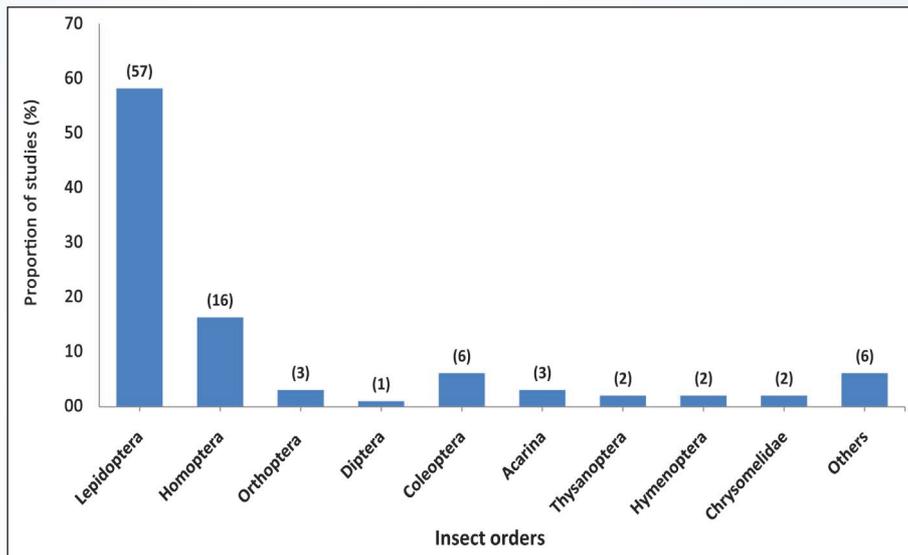


Fig. 1 : Percentage of studies reviewed in the meta analysis according to Herbivore orders (N=98)

Lasiocampidae and Gelechiidae are the other families that the studies included in the analysis considered (Fig 2).

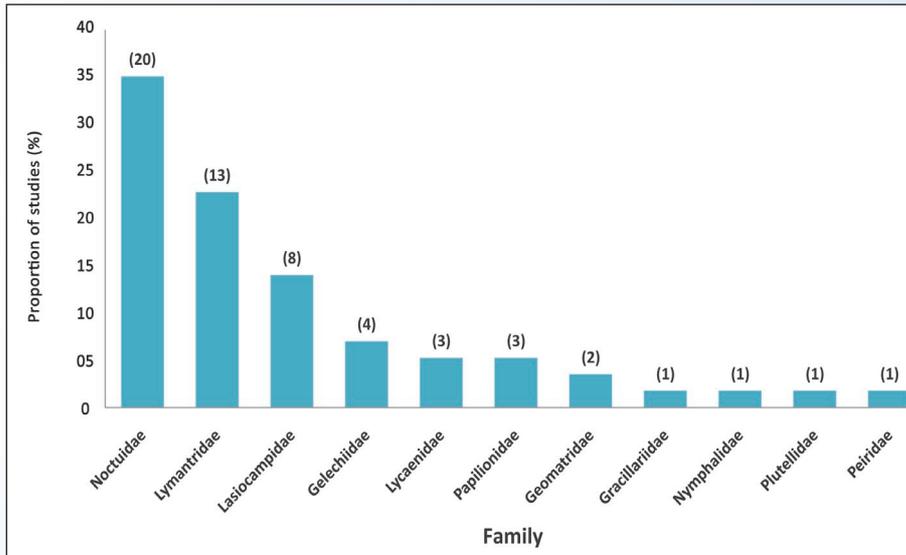


Fig. 2 : Percentage of independent comparisons from the meta analysis according to family of the Herbivore from Lepidoptera (N=57)

When feeding habit was considered, as many as 67% of papers studied chewing insects, 15% studied suckers and 7% focused on scrapers. Further, a majority of the papers (59%) studied consumption behavior (Fig 3). Other aspects of insect behaviour such as relative growth rate

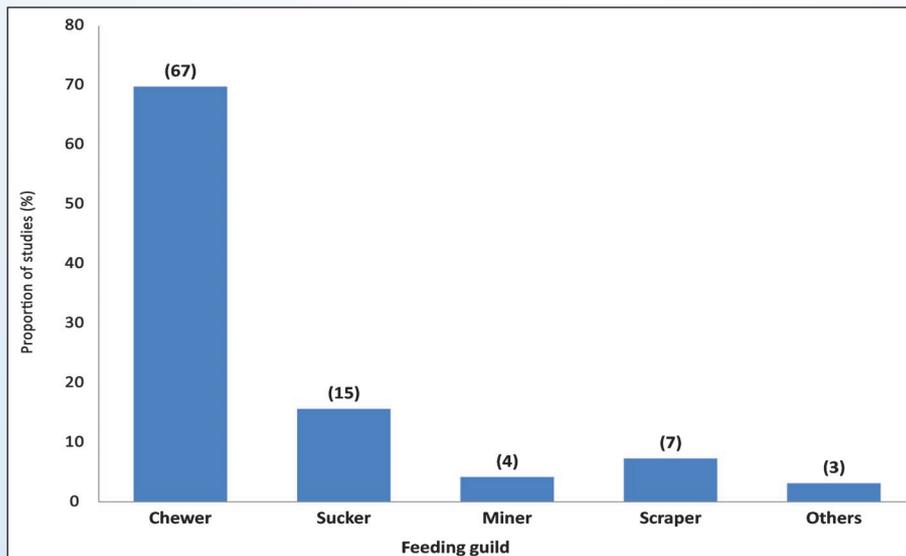


Fig. 3 : Percentage of studies reviewed in the meta analysis according to feeding guild (N=96)

(41%), longevity (36%) and population behavior (27%) were also the subject of interest in the studies chosen to be included in the analysis (Fig 4).

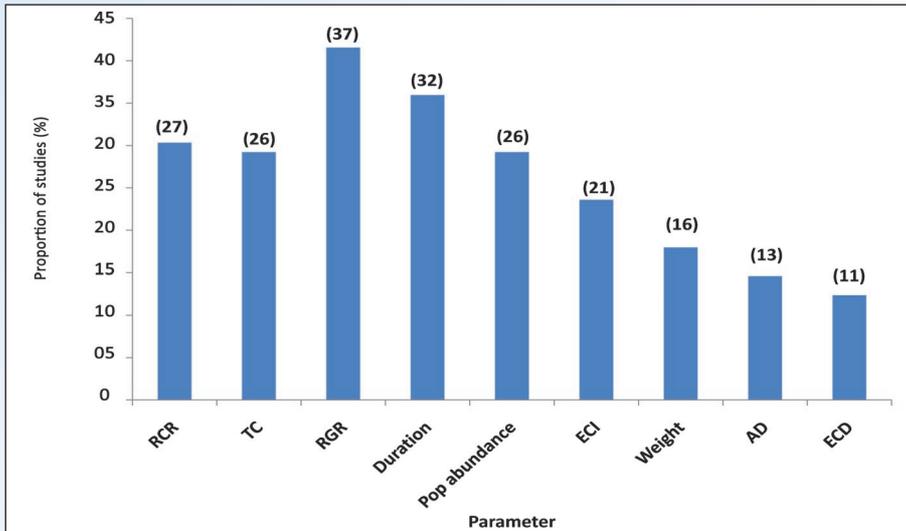


Fig. 4 : Percentage of independent parameters in the meta analysis (N=209)

In order to increase the concentration of CO₂, most of the studies (41%) used controlled environment chambers, 24% used open top chambers and 17% each used CO₂ growth chambers and FACE (Fig 5). In most of these studies, leaves were detached from the plants under ambient and elevated CO₂ conditions to examine the changes in insect behavior. Only a few studies allowed the plants as well as insects to experience the elevated and ambient CO₂ levels. However,

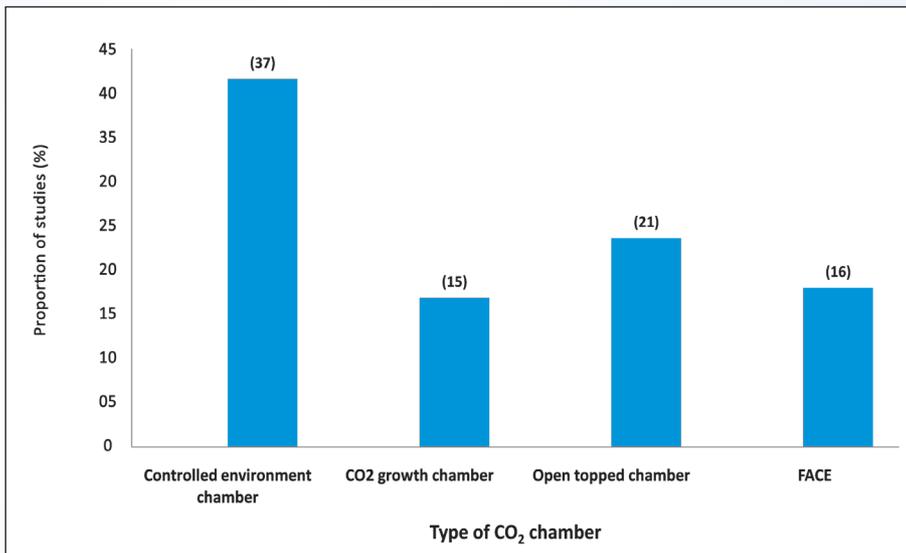


Fig. 5 : Percentage of independent comparisons from the meta analysis according to type of CO₂ chamber (N=89)

even the latter group of studies observed little in terms of direct effects of elevated CO₂ levels on the insect behavior. Before going further into analysis, the hypothesis that the type of facility used to elevate the CO₂ levels would make a difference to the observations being made was rejected by an F-test.

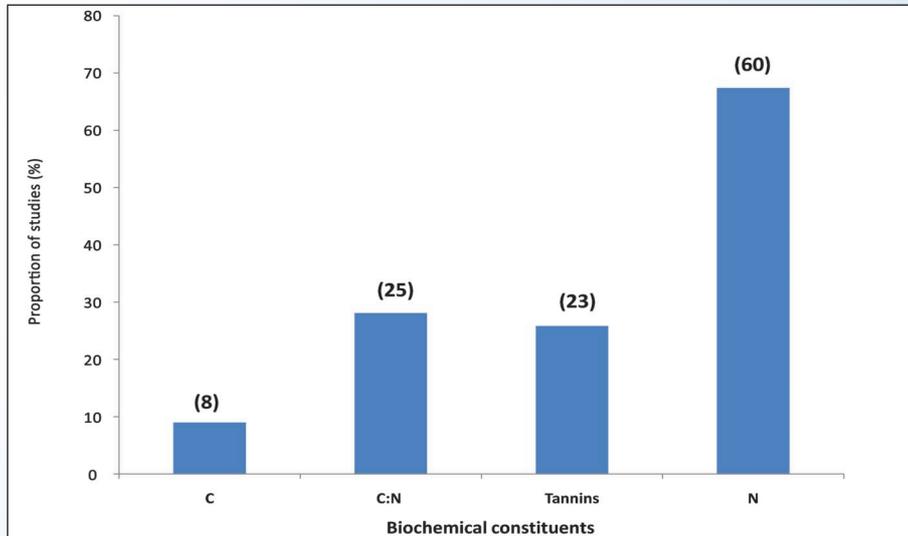


Fig. 6 : Percentage of biochemical studies reviewed for meta analysis (N=116)

Effect of type of CO₂ chamber on consumption of insect pests

Source	Sum of squares	df	MSS	F value	sig
Intercept	174.085	1	174.085	4.229	0.045
chamber	106.316	3	35.439	0.861	0.468

3.2 Insect Primary Parameters

a. Consumption

Following the criteria described above, twenty six studies were identified which evaluated the consumption behavior in terms of quantity of foliate consumed by the larvae and the related parameters such as relative consumption, consumption, leaf consumption, food consumption and larval consumption by different insect species. In addition, there were another thirteen studies which were not included in the analysis as they did not report the information necessary to compute the effect size. Measures of variability were not presented to test the differences across different treatments. The selected papers covered a wide range of situations, pests, trees, crops, grasses, weeds and forms of chambers employed and present a heterogeneous situation which is reflected in the d values (Table 2). The level of CO₂ concentrations ranged between

Table 2 : Summary of the data included in the meta analysis and corresponding effect sizes (d) consumption of foliage by insect

S.No.	Insect sp.	Order	Host plant	g	d	Study
1	<i>L. dispar</i>	L	<i>P. tremuloides</i>	11.88	11.86	Lindroth <i>et al.</i> , 1993
2	<i>M. disstria</i>	L	<i>P. tremuloides</i>	30.95	30.88	Lindroth <i>et al.</i> , 1993
3	<i>L. dispar</i>	L	<i>B. papyrifera</i>	0.53	0.53	Roth & Lindroth, 1994
4	<i>L. dispar</i>	L	<i>P. strobus</i>	2.47	2.47	Roth & Lindroth, 1994
5	<i>G. viridula</i>	Col	<i>R. obtusifolius</i>	-2.89	-2.72	Pearson & Brooks, 1996
6	<i>C. flaveola</i>	Col	<i>E. tereticornis</i>	1.77	1.77	Lawler <i>et al.</i> , 1997
7	<i>L. dispar</i>	L	<i>P. tremuloides</i>	2.73	2.69	Lindroth <i>et al.</i> , 1997
8	<i>L. dispar</i>	L	<i>P. tremuloides</i>	8.18	8.05	Kinney <i>et al.</i> , 1997
9	<i>L. dispar</i>	L	<i>P. tremuloides</i>	-0.82	-0.81	Lindroth & Kinney, 1998
10	<i>O. brumata</i>	L	<i>Q. robur</i>	-2.82	-2.70	Buse <i>et al.</i> , 1998
11	<i>L. monacha</i>	L	<i>P. abies</i>	-0.16	-0.15	Hattenschwiler & Schafellner, 1999
12	<i>P. icarus</i>	L	<i>L. corniculatus</i>	1.07	1.07	Goverde <i>et al.</i> , 1999
13	Leaf miners	L	<i>Q. myrtifolia</i>	3.77	3.69	Stilling <i>et al.</i> , 1999
14	<i>O. leucostigma</i>	L	<i>B. papyrifera</i>	-0.63	-0.62	Agrell <i>et al.</i> , 2000
15	<i>L. dispar</i>	L	<i>A. rubrum</i>	-0.77	-0.71	Williams <i>et al.</i> , 2000
16	<i>L. dispar</i>	L	<i>A. saccharum</i>	2.40	2.22	Williams <i>et al.</i> , 2000
17	<i>P. vitellinae</i>	Col	<i>S. myrsinifolia</i>	1.05	1.04	Veteli <i>et al.</i> , 2002
18	<i>S. litura</i>	L	<i>V. radiata</i>	9.02	8.15	Srivastava <i>et al.</i> , 2002
19	<i>M. disstria</i>	L	<i>P. tremuloides</i>	0.89	0.85	Kopper & Lindroth, 2003
20	<i>F. occidentalis</i>	Thy	<i>T. repens</i>	2.81	2.74	Heagle, 2003
21	<i>H. armigera</i>	L	<i>T. aestivum</i>	-1.41	-1.40	Chen <i>et al.</i> , 2005
22	<i>M. disstria</i>	L	<i>B. papyrifera</i>	2.47	2.45	Agrell <i>et al.</i> , 2005
23	<i>M. alpina</i>	Orth	<i>V. uliginosum</i>	-0.35	-0.33	Roman Asshoff & Hattenschwiler, 2005
24	<i>H. armigera</i>	L	<i>T. aestivum</i>	1.17	0.78	Wu <i>et al.</i> , 2006
25	<i>C. philodice</i>	L	<i>T. pratense</i>	-0.10	-0.09	Karowe, 2007
26	<i>P. sericeus</i>	Col	<i>P. tremuloides</i>	2.54	2.04	Hillstorm <i>et al.</i> , 2010

L : Lepidoptera (Chewer), Col : Coleoptera (Chewer), Thy : Thysanoptera (Scraper)

350-1032 ppm in these studies. The values of consumption of foliage by larvae under elevated CO₂ were compared with ambient CO₂ condition. The effect sizes in the studies included ranged from 30.88 to -2.72 with a mean effect size of 2.94. The effect size was found to be significant as the confidence interval (95% to 99%) did not include zero. It indicates that the average consumption of insect species was 2.94 standard deviations more or higher under elevated CO₂ conditions than under ambient CO₂. The effect size was positive in a majority of studies (eighteen cases) indicating a higher consumption under elevated CO₂ conditions than ambient CO₂. Only in eight cases the effect size was found negative, which means reduced consumption by insect pest species under elevated CO₂. The number of replications ranged from three to three hundred and twenty with a median of four.

b. Duration

Significant variation in duration of insect stages (egg/larva/instars/pupa/adult) under elevated CO₂ conditions was reported by several studies. This parameter was considered for separate meta analysis. In total thirty two studies were selected for analysis (Table 3).

The values of duration by different stage of insects under elevated CO₂ were compared with ambient CO₂ condition. The effect sizes in the studies included ranged from 4.46 to -5.68 with a mean effect size of 0.75. The effect size was found to be significant as the confidence interval (95% or 99%) did not include zero. It indicates that the mean duration of insect species was 0.751 standard deviations more or higher under elevated CO₂ conditions than under ambient CO₂. The effect size was positive in a majority of studies (twenty one cases) indicating an extension of duration under elevated CO₂ conditions compared to that under ambient CO₂. Only in eleven cases was the effect size found negative, which means reduction of duration by insect pest species under elevated CO₂. The number of replications ranged from three to thirty with a median of four.

c. Weight of stage

Significant variation in weight of different insect stages was noticed under elevated CO₂ conditions by several researchers. Seventeen studies that examined the weights of different stages under elevated CO₂ were compared with ambient CO₂ condition insects were subjected to m.

The effect sizes in the studies included ranged from 1.26 to -2.84 with a mean effect size of -0.46 and were found to be significant also. It indicates that the mean weights insect species was -0.46 standard deviations less under elevated CO₂ conditions than under ambient CO₂. The effect size was positive in an eight studies out of seventeen studies indicating a higher weight gain under elevated CO₂ conditions than ambient CO₂. In nine cases effect size was found negative, which means reduction of weights by insect pest species under elevated CO₂. (Table 4).

Table 3 : Summary of the data included in the meta analysis and corresponding effect sizes (d) duration of insect stages

S.No	Insect sp.	Order	Host plant	Parameter	g	d	Study
1	<i>J. ceonia</i>	L	<i>P. lanceolata</i>	DT Early instar	0.74	0.73	Fajer <i>et al.</i> , 1989
2	<i>J. ceonia</i>	L	<i>P. lanceolata</i>	Time to pupation	0.23	0.22	Fajer <i>et al.</i> , 1989
3	<i>L. dispar</i>	L	<i>P. tremuloides</i>	DT(larval)	4.46	4.45	Lindroth <i>et al.</i> , 1993
4	<i>M. disstria</i>	L	<i>P. tremuloides</i>	DT(larval)	2.22	2.21	Lindroth <i>et al.</i> , 1993
5	<i>L. dispar</i>	L	<i>B. papyrifera</i>	Duration	2.34	2.34	Roth & Lindroth, 1994
6	<i>L. dispar</i>	L	<i>P. strobus</i>	Duration (IV instar)	3.23	3.22	Roth & Lindroth, 1994
7	<i>L. dispar</i>	L	<i>B. populifolia</i>	DT (larval)	3.71	3.70	Traw <i>et al.</i> , 1996
8	<i>L. dispar</i>	L	<i>P. tremuloides</i>	Dur (IV Stadium)	-0.85	-0.83	Lindroth <i>et al.</i> , 1997
9	<i>L. dispar</i>	L	<i>P. tremuloides</i>	Dur (IV Stadium)	2.52	2.48	Kinney <i>et al.</i> , 1997
10	<i>A. solani</i>	H	<i>V. faba</i>	DT	1.88	1.86	Awmack <i>et al.</i> , 1997
11	<i>O. brumata</i>	L	<i>C. vulgaris</i>	DI	-1.25	-1.24	Kerslake <i>et al.</i> , 1998
12	<i>M. disstria</i>	L	<i>P. tremuloides</i>	Dur (IV Stadium)	3.44	3.43	Roth <i>et al.</i> , 1998
13	<i>L. dispar</i>	L	<i>P. tremuloides</i>	Dur (IV Stadium)	1.37	1.35	Lindroth & Kinney, 1998
14	<i>C. syngenesiae</i>	D	<i>S. oleraceus</i>	DT	0.41	0.41	Smith & Jones, 1998
15	<i>B. brassicae</i>	H	<i>B. oleracea</i>	DT	1.00	0.57	Bezemer <i>et al.</i> , 1999
16	<i>P. icarus</i>	L	<i>L. corniculatus</i>	Larval DT	-0.17	-0.17	Goverde <i>et al.</i> , 1999
17	<i>O. leucostigma</i>	L	<i>B. papyrifera</i>	DT(Female)	1.30	1.28	Agrell <i>et al.</i> , 2000
18	<i>O. leucostigma</i>	L	<i>B. papyrifera</i>	DT (larval)	-1.05	-1.04	Kopper <i>et al.</i> , 2001
19	<i>P. icarus</i>	L	<i>L. corniculatus</i>	DT	-5.88	-5.68	Bazin <i>et al.</i> , 2002
20	<i>D. scariella</i>	L	<i>E. plantagineum</i>	DT (larval)	1.23	1.21	Johns and Hughes, 2002
21	<i>C. pamphilus</i>	L	Grass sp.	DT(M)	-0.18	-0.17	Goverde <i>et al.</i> , 2002
22	<i>M. disstria</i>	L	<i>P. tremuloides</i>	DT (Female)	2.38	2.15	Kopper & Lindroth, 2003
23	<i>C. pamphilus</i>	L	<i>A. stolonifer</i>	DT	1.03	1.03	Goverde & Erhardt, 2003
24	<i>M. disstria</i>	L	<i>P. tremuloides</i>	DT (larval)	-1.16	-1.15	Holton <i>et al.</i> , 2003
25	<i>C. betulaefoliae</i>	H	<i>B. papyrifera</i>	DT	2.80	2.24	Awmack <i>et al.</i> , 2004
26	<i>H. armigera</i>	L	<i>G. hirsutum</i>	Dur (Larval)	0.92	0.92	Chen <i>et al.</i> , 2005
27	<i>H. armigera</i>	L	<i>T. aestivum</i>	Dur (Larval)	0.00	0.00	Chen <i>et al.</i> , 2005
28	<i>A. gossypi</i>	H	<i>G. hirsutum</i>	DT	-0.38	-0.34	Chen & Parajulee, 2005
29	<i>A. gossypi</i>	H	<i>G. hirsutum</i>	Dur (Nymphal)	-0.63	-0.58	Chen & Parajulee, 2005

30	<i>H. armigera</i>	L	<i>T. aestivum</i>	Larval DT	4.43	4.40	Wu <i>et al.</i> , 2006
31	<i>C. philodice</i>	L	<i>T. pratense</i>	Dur (5 th Instar)	-0.95	-0.93	Karowe, 2007
32	<i>P. sericeus</i>	Col	<i>P. tremuloides</i> & <i>B. papyrifera</i>	Longevity (Female)	-4.08	-4.04	Hillstorm <i>et al.</i> , 2010

L : Lepidoptera (Chewer), Col : Coleoptera (Chewer), H : Homoptera (Sucker), D : Diptera (Miner),
DT : Development Time, DI : Development Index, Dur : Duration

Table 4 : Summary of the data included in the meta analysis and corresponding effect sizes (d) – Weight of insect stage

S.No	Insect sp.	Order	Host plant	Parameter	g	d	Study
1	<i>T. ni</i>	L	<i>P.lunatus</i>	P.W	0.22	0.22	Osbrink <i>et al.</i> , 1987
2	<i>L. dispar</i>	L	<i>A.populifolia</i>	Pupal mass(mg)	-0.85	-0.85	Traw <i>et al.</i> , 1996
3	<i>L. dispar</i>	L	<i>A.populifolia</i>	Larval mass(mg)	1.26	1.26	Traw <i>et al.</i> , 1996
4	<i>P.fagi</i>	H	<i>F. sylvatica</i>	Nymph Wt.	-2.50	-2.31	Docherty <i>et al.</i> , 1997
5	<i>L. dispar</i>	L	<i>P. tremuloides</i>	Final mass	0.86	0.84	Kinney <i>et al.</i> , 1997
6	<i>O.brumata</i>	L	<i>Q. robur</i>	Pupal mass	0.27	0.26	Buse <i>et al.</i> , 1998
7	<i>O.brumata</i>	L	<i>Q. robur</i>	Larval mass	-0.77	-0.74	Buse <i>et al.</i> , 1998
8	<i>C.syngenesiae</i>	D	<i>S. oleraceus</i>	Pupal Wt.	-2.41	-2.40	Smith & Jones, 1998
9	<i>O. leucostigma</i>	L	<i>B. papyrifera</i>	P.mass	1.17	1.16	Kopper <i>et al.</i> , 2001
10	<i>M. disstria</i>	L	<i>P.tremuloides</i>	Pupal wt	-0.35	-0.34	Percy <i>et al.</i> , 2002
11	<i>M. persicae</i>	H	<i>B.oleracea</i>	Wt	-2.96	-2.84	David & Mark, 2002
12	<i>B. brassicae</i>	H	<i>B.oleracea</i>	Wt	8.43	8.07	David & Mark, 2002
13	<i>M. disstria</i>	L	<i>P. tremuloides</i>	P.mass	0.38	0.38	Holton <i>et al.</i> , 2003
14	<i>C. betulaefoliae</i>	H	<i>B. papyrifera</i>	Adult wt	-0.80	-0.64	Awmack <i>et al.</i> , 2004
15	<i>H. armigera</i>	L	<i>T.aestivum</i>	Pupal wt	-0.03	-0.03	Chen <i>et al.</i> , 2005
16	<i>L. dispar</i>	L	<i>P. pseudosimonii</i>	L. wt	-1.88	-1.85	Xiaowei <i>et al.</i> , 2006
17	<i>C. philodice</i>	L	<i>T. pratense</i>	Pupal wt.	0.50	0.49	Karowe, 2007

L: Lepidoptera (Chewer), H : Homoptera (Sucker), D : Diptera (Miner), Wt : Weight

d. Population abundance

The published information indicated that the population of insect species varied significantly under elevated CO₂ conditions. A separate meta analysis was conducted on twenty six studies indicating the parameter of population abundance of insects (table 5). The effect sizes in the studies included ranged from 11.29 to -0.3517 with a mean effect size of 1.01 and were found to be significant also. It indicated that the mean abundance increased by one standard deviation

Table 5 : Summary of the data included in the meta analysis and corresponding effect sizes (d) – Population abundance of insect

S.No	Insect sp.	Order	Host plant	Parameter	g	d	Study
1	<i>F. occidentalis</i>	Thy	<i>A. syriaca</i>	Pop abun	0.78	0.76	Hughes & Bazzaz, 1997
2	<i>P.fagi</i>	H	<i>F. sylvatica</i>	Fecundity	-0.44	-0.40	Docherty <i>et al.</i> , 1997
3	<i>M.persicae</i>	H	Ecotron comnty.	Pop abun	3.56	3.37	Jones <i>et al.</i> , 1998
4	<i>G. viridula</i>	Col	<i>R. obtusifolius</i>	Fecundity	-6.55	-6.44	Brooks & Whittaker, 1998
5	<i>B. brassicae</i>	H	<i>B. oleracea</i>	Pop size	-1.17	-0.67	Bezemer <i>et al.</i> , 1999
6	<i>N. lineatus</i>	H	<i>J. squarrosus</i>	No.of nymphs/spittle	1.03	0.90	Brooks & Whittaker, 1999
7	<i>R. padi</i>	H	F. arundinacea	Aphids/plant	-4.31	-4.22	Newman <i>et al.</i> , 1999
8	<i>T. urticae</i>	A	<i>G. hirsutum</i>	No.of mites	23.77	23.67	Karban & Thaler, 1999
9	<i>T. urticae</i>	A	<i>P. vulgaris</i>	No.of Nymphs	-11.33	-11.29	Joutei <i>et al.</i> , 2000
10	<i>A. pisum</i>	H	<i>V.faba</i>	No.of aphids/plant	-4.77	-4.64	Hughes & Bazzaz, 2001
11	<i>C. stevensis</i>	H	<i>P. tremuloides</i>	Pop abun	3.75	3.51	Percy <i>et al.</i> , 2002
12	<i>D. scariella</i>	L	<i>E.plantagineum</i>	Pop abun	-5.95	-5.89	John & Hughes, 2002
13	<i>T. urticae</i>	A	<i>T. repens</i>	No. of eggs	2.32	2.19	Heagle <i>et al.</i> , 2002
14	<i>T. urticae</i>	A	<i>T. repens</i>	Pop abun	2.91	2.75	Heagle <i>et al.</i> , 2002
15	Undetermined		<i>Q. myrtifolia</i>	Pop abun (Chewers)	-3.12	-3.11	Stiling <i>et al.</i> , 2002
16	Undetermined		<i>Q. myrtifolia</i>	Pop abun (Miners)	-4.10	-4.09	Stiling <i>et al.</i> , 2002
17	<i>M. persicae</i>	H	<i>B. oleracea</i>	Fecundity	1.14	1.09	David & Mark, 2002
18	<i>B. brassicae</i>	H	<i>B. oleracea</i>	Fecundity	1.57	1.51	David & Mark, 2002
19	<i>F. occidentalis</i>	Thy	<i>T. repens</i>	Pop abun	-0.15	-0.15	Heagle, 2003
20	<i>S. avenae</i>	H	<i>T. aestivum</i>	No.of nymphs/pot	2.42	2.42	Chen <i>et al.</i> , 2004
21	<i>C. betulaefoliae</i>	H	<i>B. papyrifera</i>	Pop abun	-1.98	-1.79	Awmack <i>et al.</i> , 2004
22	Arthropod comnty.			Herbivore abundance	-0.56	-0.53	Sanders <i>et al.</i> , 2004
23	<i>A.pisum</i>	H	<i>V. faba</i>	Pop abun	0.38	0.35	Mondor <i>et al.</i> , 2005
24	<i>H. armigera</i>	L	<i>G. hirsutum</i>	Fecundity	-0.73	-0.72	Chen <i>et al.</i> , 2005
25	<i>H. armigera</i>	L	<i>G. hirsutum</i>	Fecundity	-0.47	-0.47	Chen <i>et al.</i> , 2005
26	<i>M. euphorbiae</i>	H	<i>S. dulcamara</i>	Pop abun	0.55	0.53	Flynn <i>et al.</i> , 2006

Thy : Thysanoptera (Scraper), A : Acarina (Scraper), L : Lepidoptera (Chewer), H : Homoptera (Sucker),
 Pop abun : Population abundance, Comnty : Community.

under elevated CO₂ conditions than under ambient CO₂. The effect size was positive in twelve studies out of twenty six studies indicating a higher population under elevated CO₂ conditions than ambient CO₂. In fourteen cases effect size was found negative, which means reduction of population of insect pest species under elevated CO₂.

3.3 Insect Performance Indices

Insects, like all living organisms, require energy and nutrients to survive, grow and reproduce. The nutritional components (e.g. protein, carbohydrates, fats, vitamins, minerals) of ingested food may or may not be digested and absorbed. The proportion of ingested food that is actually digested is denoted by AD, the assimilation efficiency (also called “approximate digestibility”). Of the nutrients absorbed, portions are expended in the processes of respiration and work. The proportion of digested food that is actually transformed into net insect biomass is denoted by ECD, the efficiency of conversion of digested food. A parallel parameter, ECI, indicates the efficiency of conversion of ingested food ($ECI = AD \times ECD$). In short, AD indicates how digestible a food is, whereas ECD and ECI indicate how efficient a herbivore is in converting that food into biomass. These efficiency values may be calculated for specific dietary nutrients as well as for the bulk diet. For instance, nitrogen use efficiencies are informative because levels of plant nitrogen (an index of protein) are often times limiting to insect performance. (Lindroth,1993). Separate analyses were conducted on published information of these indices and presented hereunder.

Approximate digestibility (AD)

Thirteen studies were identified on AD parameter and included in the meta analysis. The AD values of foliage by insect species larvae under elevated CO₂ were compared with ambient CO₂ condition. The effect sizes in the studies included ranged from 7.46 to -3.98 with a mean effect size of 1.28. The effect size was found to be significant as the confidence interval (95% or 99%) did not include zero. It indicates that approximate digestibility of foliage was 1.28 standard deviations higher under elevated CO₂ conditions compared to that observed under ambient CO₂. The effect size was positive in about half of the studies included in the analysis indicating a higher digestibility of foliage under elevated CO₂ conditions than ambient CO₂. (Table 6)

Efficiency of conversion of digested food (ECD)

There eleven studies that compared the ECD of insects raised on the plants grown under elevated and ambient CO₂ levels. The effect sizes in the studies included ranged from 2.01 to -5.25 with a mean effect size of -1.89. The effect size was found to be significant and negative. It indicates that ECD of insect larvae was 1.89 standard deviations less under elevated CO₂ conditions than under ambient CO₂. The effect size was negative in nine cases out of eleven cases studied indicating a lesser efficiency of conversion of digested food by larvae under elevated CO₂ conditions than ambient CO₂. (Table 7)

Table 6 : Summary of the data included in the meta analysis and corresponding effect sizes (d) – AD of foliage

S.No.	Insect sp.	Order	Host plant	g	d	Study
1	<i>L. dispar</i> ,	L	<i>P. tremuloides</i>	7.18	7.17	Lindroth <i>et al.</i> , 1993
2	<i>M. disstria</i>	L	<i>P. tremuloides</i>	7.48	7.46	Lindroth <i>et al.</i> , 1993
3	<i>L. dispar</i>	L	<i>B. papyrifera</i>	-0.91	-0.91	Roth & Lindroth, 1994
4	<i>L. dispar</i>	L	<i>P. strobus</i>	1.26	1.26	Roth & Lindroth, 1994
5	<i>C. flaveola</i>	L	<i>F. sylvatica</i>	-1.08	-1.01	Lawler <i>et al.</i> , 1997
6	<i>L. dispar</i>	L	<i>P. tremuloides</i>	-4.05	-3.98	Lindroth <i>et al.</i> , 1997
7	<i>L. dispar</i>	L	<i>P. tremuloides</i>	5.34	5.26	Kinney <i>et al.</i> , 1997
8	<i>M. distria</i>	L	<i>P. tremuloides</i>	-0.57	-0.57	Roth <i>et al.</i> , 1998
9	<i>L. dispar</i>	L	<i>Q. alba</i>	0.39	0.31	Williams <i>et al.</i> , 1998
10	<i>M. disstria</i>	L	<i>Q. alba</i>	0.88	0.50	Williams <i>et al.</i> , 1998
11	<i>L. dispar</i>	L	<i>P. tremuloides</i>	1.13	1.11	Lindroth & Kinney., 1998
12	<i>O. leucostigma</i>	L	<i>B. papyrifera</i>	1.11	1.09	Agrell <i>et al.</i> , 2000
13	<i>C. philodice</i>	L	<i>T. pratense</i>	-1.06	-1.04	Karowe., 2007

L : Lepidoptera (Chewer)

Table 7 : Summary of the data included in the meta analysis and corresponding effect sizes (d) – ECD of insect

S.No.	Insect sp.	Order	Host plant	g	d	Study
1	<i>L. dispar</i> ,	L	<i>P. tremuloides</i>	-5.26	-5.25	Lindroth <i>et al.</i> , 1993
2	<i>M. disstria</i>	L	<i>P. tremuloides</i>	-5.19	-5.18	Lindroth <i>et al.</i> , 1993
3	<i>L. dispar</i>	L	<i>B. papyrifera</i>	-0.53	-0.53	Roth & Lindroth ., 1994
4	<i>L. dispar</i>	L	<i>P. strobus</i>	-2.10	-2.09	Roth & Lindroth ., 1994
5	<i>C. flaveola</i>	L	<i>F. sylvatica</i>	-2.13	-2.12	Lawler <i>et al.</i> , 1997
6	<i>L. dispar</i>	L	<i>P. tremuloides</i>	2.05	2.01	Lindroth <i>et al.</i> , 1997
7	<i>L. dispar</i>	L	<i>P. tremuloides</i>	-1.61	-1.58	Kinney <i>et al.</i> , 1997
8	<i>M. distria</i>	L	<i>P. tremuloides</i>	-2.91	-2.90	Roth <i>et al.</i> , 1998
9	<i>L. dispar</i>	L	<i>P. tremuloides</i>	-1.49	-1.47	Lindroth & Kinney, 1998
10	<i>O. leucostigma</i>	L	<i>B. papyrifera</i>	-2.20	-2.18	Agrell <i>et al.</i> , 2000
11	<i>C. philodice</i>	L	<i>T. pratense</i>	0.50	0.49	Karowe, 2007

L : Lepidoptera (Chewer)

Efficiency of conversion of ingested food (ECI)

Effect size was computed for twenty one studies that reported ECI. The ECI values of larvae of insect species under elevated CO₂ were compared with those under ambient CO₂ condition. The effect sizes in the studies ranged from 0.30 to -15.79 with a mean effect size of -3.20. The effect size was found to be significant and negative. It indicates that ECI of insect larvae was 3.20 standard deviations lesser under elevated CO₂ conditions than ambient CO₂. The effect size was negative in eighteen cases out of twenty one cases studied indicating a lesser efficiency of conversion of ingested food by larvae under elevated CO₂ conditions than under ambient CO₂. (Table 8)

Table 8 : Summary of the data included in the meta analysis and corresponding effect sizes (d) – ECI of insect

S.No.	Insect sp.	Order	Host plant	g	d	Study
1	<i>S. eridania</i>	L	<i>M. piperita</i>	-0.43	-0.42	Lincoln & Couvet, 1989
2	<i>L. dispar</i> ,	L	<i>P. tremuloides</i>	-5.29	-5.28	Lindroth <i>et al.</i> , 1993
3	<i>M. disstria</i>	L	<i>P. tremuloides</i>	-6.41	-6.39	Lindroth <i>et al.</i> , 1993
4	<i>N. lecontei</i>	L	<i>P. taeda</i>	-8.34	-8.31	Williams <i>et al.</i> , 1994
5	<i>L. dispar</i>	L	<i>B. papyrifera</i>	-15.83	-15.79	Roth & Lindroth, 1994
6	<i>L. dispar</i>	L	<i>P. strobus</i>	-2.61	-2.60	Roth & Lindroth, 1994
7	<i>S. frugiperda</i>	L	<i>F. arundinacea</i>	-0.87	-0.86	Marks & Lincoln., 1996
8	<i>C. flaveola</i>	L	<i>F. sylvatica</i>	-2.29	-2.28	Lawler <i>et al.</i> , 1997
9	<i>L. dispar</i>	L	<i>P. tremuloides</i>	-0.12	-0.12	Lindroth <i>et al.</i> , 1997
10	<i>L. dispar</i>	L	<i>P. tremuloides</i>	-2.25	-2.22	Kinney <i>et al.</i> , 1997
11	<i>L. dispar</i> ,	L	<i>Q. alba</i>	-2.68	-2.15	Williams <i>et al.</i> , 1998
12	<i>M. disstria</i>	L	<i>Q. alba</i>	0.33	0.19	Williams <i>et al.</i> , 1998
13	<i>L. monarcha</i>	L	<i>P. abies</i>	-2.45	-2.27	Hattenschwiler & Schafellner, 1999
14	<i>P. icarus</i>	L	<i>L. corniculatus</i>	0.27	0.26	Goverde <i>et al.</i> , 1999
15	<i>O. leucostigma</i>	L	<i>B. papyrifera</i>	-2.66	-2.32	Agrell <i>et al.</i> , 2000
16	<i>L. dispar</i>	L	<i>F. sylvatica</i>	0.32	0.30	Henn & Schopf, 2001
17	<i>H. armigera</i>	L	<i>G. hirsutum</i>	-1.63	-1.62	Chen <i>et al.</i> , 2005
18	<i>H. armigera</i>	L	<i>T. aestivum</i>	-9.94	-9.88	Wu <i>et al.</i> , 2006
19	<i>H. armigera</i>	L	<i>G. hirsutum</i>	-0.46	-0.46	Chen <i>et al.</i> , 2007
20	<i>S. litura</i>	L	<i>R. communis</i>	-2.42	-2.40	Srinivasa Rao <i>et al.</i> , 2009
21	<i>A. janata</i>	L	<i>R. communis</i>	-2.56	-2.54	Srinivasa Rao <i>et al.</i> , 2009

L : Lepidoptera (Chewer)

Relative consumption rate (RCR)

RCR parameter was considered in twenty seven studies and was identified for meta analysis. The RCR values of larvae of insect species under elevated CO₂ were compared with ambient CO₂ condition. The effect sizes in the studies included ranged from 20.04 to - 4.13 with a mean effect size of 3.61. The effect size was found to be significant and positive. It indicates that RCR of insect larvae was 3.61 standard deviations higher under elevated CO₂ conditions than ambient CO₂. The effect size was positive in twenty three studies out of twenty seven cases studied indicating a very higher RCR by larvae under elevated CO₂ conditions than ambient CO₂ (Table 9).

Relative growth rate (RGR)

Using the data for RGR reported in thirty seven studies, effect size was computed to bring out the effect of elevated CO₂ on the growth rate of insects. The RGR values of larvae of insect species under elevated CO₂ were compared with those under ambient CO₂ condition. The effect sizes in the studies included ranged from 5.45 to - 8.31 with a mean effect size of -1.072. The effect size was found to be significant and negative. It indicates that RGR of insect larvae were 1.072 standard deviations lesser under elevated CO₂ conditions than under ambient CO₂. The effect size was negative in a twenty two cases out of thirty seven cases studied indicating a lesser RGR of larvae under elevated CO₂ conditions than ambient CO₂ (Table 10).

A total of 88 studies were considered for the analysis. However, not all studies reported all the parameters chosen for meta analysis. We selected eleven parameters related to consumption, performance related indices and biochemical composition. Since not all the studies reported all these parameters, we computed the effect size for each of these parameters based on those studies that reported the parameter concerned. Thus, our effect sizes are in the range of 26 studies for consumption to 61 studies dealing with nitrogen. The effect size was found to be significantly positive in case of two parameters and ranged from 3.430 in case of RCR to 50.353 in case of AD. Thus, elevated CO₂ levels led to significant changes in the biochemical properties, consumption behaviour and growth behaviour of the insects. The null hypothesis that all the studies were homogenous was rejected by a significant Q-statistic indicating that the studies were heterogeneous. The fail safe N, which indicates the number of studies with non-significant results required to reduce the effect size to 0.5, was very high. This shows that the effect sizes are reliable. The details are given in the table 11.

The failsafe N for an effect size of 0.5 in all the cases was found to be considerably high which indicates that there should have been a large number of studies containing non-significant results and were not published and hence could not be included in the analysis. Higher failsafe N indicates more reliability of the effect size computed.

Table 9 : Summary of the data included in the meta analysis and corresponding effect sizes (d) – RCR of insect

S.No.	Insect sp.	Order	Host plant	g	d	Study
1	<i>P. includans</i>	L	<i>G. max</i>	0.70	0.68	Lincoln <i>et al.</i> , 1984
2	<i>S. eridania</i>	L	<i>M. piperita</i>	0.51	0.49	Lincoln & Couvet , 1989
3	<i>M. sanguinipes</i>	O	<i>A. tridentata</i>	0.12	0.12	Jhonson & Lincoln, 1990
4	<i>M. differentialis</i>	O	<i>A. tridentata</i>	-4.21	-4.19	Jhonson & Lincoln, 1991
5	<i>L. dispar</i>	L	<i>P. tremuloides</i>	8.26	8.25	Lindroth <i>et al.</i> , 1993
6	<i>M. disstria</i>	L	<i>P. tremuloides</i>	20.08	20.04	Lindroth <i>et al.</i> , 1993
7	<i>N. lecontei</i>	L	<i>P. taeda</i>	4.90	4.89	Williams <i>et al.</i> , 1994
8	<i>L. dispar</i>	L	<i>B. papyrifera</i>	-1.48	-1.47	Roth & Lindroth , 1994
9	<i>L. dispar</i>	L	<i>P. strobus</i>	3.71	3.70	Roth & Lindroth , 1994
10	<i>S. eridania</i>	L	<i>E. cardamomum</i>	-1.34	-1.16	Arnone <i>et al.</i> ,1995
11	<i>S. frugiperda</i>	L	<i>F. arundinacea</i>	2.58	2.52	Marks & Lincoln, 1996
12	<i>L. dispar</i>	L	<i>P. tremuloides</i>	4.28	4.21	Lindroth <i>et al.</i> , 1997
13	<i>L. dispar</i>	L	<i>P. tremuloides</i>	18.62	18.33	Kinney <i>et al.</i> , 1997
14	<i>L. dispar</i>	L	<i>Q. alba</i>	1.90	1.52	Williams <i>et al.</i> , 1998
15	<i>M. disstria</i>	L	<i>Q. alba</i>	0.97	0.55	Williams <i>et al.</i> , 1998
16	<i>L. dispar</i>	L	<i>P. tremuloides</i>	8.26	8.25	Lindroth & Kinney., 1998
17	<i>M. disstria</i>	L	<i>P. tremuloides</i>	0.63	0.62	Roth <i>et al.</i> , 1998
18	<i>G. viridula</i>	Col	<i>R. obtusifolius</i>	16.51	16.27	Brooks & Whittaker, 1998
19	<i>L. monacha</i>	L	<i>P. abies</i>	2.14	1.97	Hattenschwiler & Schafellner ,1999
20	<i>O. leucostigma</i>	L	<i>B. papyrifera</i>	1.66	1.44	Agrill <i>et al.</i> , 2000
21	<i>L. dispar</i>	L	<i>F. sylvatica</i>	-0.36	-0.35	Henn & Schopf , 2001
22	<i>H. armigera</i>	L	<i>G. hirsutum</i>	1.32	1.31	Chen <i>et al.</i> , 2005
23	<i>H. armigera</i>	L	<i>T. aestivum</i>	5.09	5.06	Wu <i>et al.</i> , 2006
24	<i>H. armigera</i>	L	<i>G. hirsutum</i>	0.78	1.16	Chen <i>et al.</i> , 2007
25	<i>C. philodice</i>	L	<i>T. pratense</i>	0.20	0.19	Karowe ,2007
26	<i>S. litura</i>	L	<i>R. communis</i>	1.70	1.69	Srinivasa Rao <i>et al.</i> , 2009
27	<i>A. janata</i>	L	<i>R. communis</i>	1.52	1.51	Srinivasa Rao <i>et al.</i> , 2009

O : Orthoptera (Chewer), L : Lepidoptera (Chewer), Col : Coleoptera (Chewer)

Table 10 : Summary of the data included in the meta analysis and corresponding effect sizes (d) – RGR of insect

S.No.	Insect sp.	Order	Host plant	g	d	Study
1	<i>P. includans</i>	L	<i>G. max</i>	-0.31	-0.30	Lincoln <i>et al.</i> ,1984
2	<i>S. eridania</i>	L	<i>M. piperita</i>	0.46	0.46	Lincoln & Couvet, 1989
3	<i>M. sanguinipes</i>	O	<i>A.tridentata</i>	0.29	0.28	Johnson & Lincoln, 1990
4	<i>M. sanguinipes</i>	O	<i>A.tridentata</i>	5.48	5.46	Johnson & Lincoln, 1991
5	<i>L. dispar,</i>	L	<i>P. tremuloides</i>	-7.04	-7.02	Lindroth <i>et al.</i> , 1993
6	<i>M. disstria</i>	L	<i>P. tremuloides</i>	-3.00	-2.99	Lindroth <i>et al.</i> , 1993
7	<i>S. exigua</i>	L	<i>B. vulgaris</i>	-5.00	-4.94	Caulfield & Bunce, 1994
8	<i>N. lecontei</i>	L	<i>P. taeda</i>	0.55	0.55	Williams <i>et al.</i> , 1994
9	<i>L. dispar</i> on Birch	L	<i>B. papyrifera</i>	-8.33	-8.31	Roth & Lindroth, 1994
10	<i>L. dispar</i> on Pine	L	<i>P. strobus</i>	-0.34	-0.34	Roth & Lindroth, 1994
11	<i>S. frugiperda</i>	L	<i>F. arundinacea</i>	1.54	1.51	Marks & Lincoln, 1996
12	<i>L.dispar</i>	L	<i>B. populifolia</i>	-3.39	-3.37	Traw <i>et al.</i> , 1996
13	<i>L.dispar</i>	L	<i>P. tremuloides</i>	1.01	0.99	Kinney <i>et al.</i> , 1997
14	<i>L.dispar</i>	L	<i>P. tremuloides</i>	2.29	2.25	Lindroth <i>et al.</i> , 1997
15	<i>P. fagi</i>	H	<i>F. sylvatica</i>	3.64	3.36	Docherty <i>et al.</i> , 1997
16	<i>L.dispar</i>	L	<i>Q. alba</i>	-0.77	-0.61	Williams <i>et al.</i> , 1998
17	<i>M. disstria</i>	L	<i>Q. alba</i>	-0.38	-0.21	Williams <i>et al.</i> , 1998
18	<i>O. brumata</i>	L	<i>Q. robur</i>	4.05	4.02	Buse <i>et al.</i> , 1998
19	<i>L. dispar</i>	L	<i>C.vulgaris</i>	-2.47	-2.43	Kerslake <i>et al.</i> , 1998
20	<i>M.distria</i>	L	<i>P. tremuloides</i>	-3.94	-3.93	Roth <i>et al.</i> , 1998
21	<i>G. viridula</i>	Col	<i>R. obtusifolius</i>	1.13	1.11	Brooks & Whittaker, 1998
22	<i>L. monarcha</i>	L	<i>P. abies</i>	-1.46	-1.35	Hattenschwiler & Schafellner, 1999
23	<i>O. leucostigma</i>	L	<i>B. papyrifera</i>	-1.35	-1.18	Agrell <i>et al.</i> , 2000
24	<i>L. dispar</i>	L	<i>F. sylvatica</i>	0.45	0.44	Henn & Schopf., 2001
25	<i>S. exigua</i>	L	<i>G. hirsutum</i>	1.00	0.99	Coviella <i>et al.</i> , 2002
26	<i>P. vitellinae</i>	Col	<i>S. myrsinifolia</i>	-5.42	-5.39	Veteli <i>et al.</i> , 2002
27	<i>P. xylostella,</i>	L	<i>B. oleracea</i>	-3.09	-3.03	Reddy <i>et al.</i> ,2004
28	<i>S. littoralis</i>	L	<i>B. oleracea</i>	-1.66	-1.63	Reddy <i>et al.</i> ,2004

29	<i>L. dispar</i>	L	<i>Q. petraea</i>	-6.59	-6.54	Hattenschwiler & Schafellner, 2004
30	<i>C. betulaefoliae</i>	H	<i>B. papyrifera</i>	-1.67	-1.33	Awmack <i>et al.</i> , 2004
31	<i>H. armigera</i>	L	<i>G. hirsutum</i>	-0.76	-0.75	Chen <i>et al.</i> , 2005
32	<i>H. armigera</i>	L	<i>T. aestivum</i>	0.00	0.00	Chen <i>et al.</i> , 2005
33	<i>H. armigera</i>	L	<i>T. aestivum</i>	-5.93	-5.89	Wu <i>et al.</i> , 2006
34	<i>H. armigera</i>	L	<i>G. hirsutum</i>	-1.38	-1.38	Chen <i>et al.</i> , 2007
35	<i>C. philodice</i>	L	<i>T. pratense</i>	0.00	0.00	Karowe, 2007
36	<i>S. litura</i>	L	<i>R. communis</i>	5.41	5.36	Srinivasa Rao <i>et al.</i> , 2009
37	<i>A. janata</i>	L	<i>R. communis</i>	-3.53	-3.50	Srinivasa Rao <i>et al.</i> , 2009

O : Orthoptera (Chewer), L : Lepidoptera (Chewer), Col : Coleoptera (Chewer), H : Homoptera (Sucker)

Table 11 : Meta analyses results considering different number of studies (k): common effect size (d_{\pm}), standard error (SE) and fail safe limits

Parameter	k	d_{\pm}	SE	Fail safe N for 0.5
<i>Insect primary parameters</i>				
Total consumption	26	2.94	1.28	3359
Duration	32	0.75	0.38	2674
Population	26	1.01	1.164	353
<i>Insect performance indices</i>				
AD	13	1.28	0.93	3018
RGR	37	-1.072	0.5327	4105
ECI	21	-3.20	0.8707	2308
ECD	11	-1.89	0.6496	2279
RCR	27	3.61	1.139	158
<i>Biochemical constituents</i>				
Nitrogen	61	-2.78	0.602	792
Carbon	8	1.101	0.581	88
C: N	25	5.81	1.089	1169



Coenonympha pamphilus



Spodoptera litura



Orgyia leucostigma

3.4 Biochemical evidences

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 CO₂ per se and CO₂-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 CO₂-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 test plant foliage was carried out.

a. Carbon content : Carbon was estimated in eight studies under elevated CO₂ and was included in the meta analysis. The effect sizes in the studies included ranged from 0.5 to – 3.96 with a mean effect size of -1.101. The effect size was found to be significant and negative. It indicates that carbon was 1.101 standard deviations lesser under elevated CO₂ conditions than under ambient CO₂. The effect size was negative in a five cases out of eight cases studied indicating a lesser carbon content under elevated CO₂ conditions than ambient CO₂ (Table 12).

b. Nitrogen : Sixty one studies were included in the meta analysis where nitrogen content in plant foliage was estimated across elevated and ambient CO₂ conditions. The effect sizes for N in the studies included ranged from 19.79 to – 14.45 with a mean effect size of -2.78. The effect size was found to be significant and negative. It indicates that N values were 2.78 standard deviations lesser under elevated CO₂ conditions than ambient CO₂. The effect size was negative in a fifty two cases out of sixty one cases studied indicating a lesser N in plants under elevated CO₂ conditions than ambient CO₂ (Table 13).

c. C: N ratio : The estimation of C: N ratio in plants grown under elevated CO₂ was conducted in twenty five studies and were included in the meta analysis. The effect sizes in the studies included ranged from 0.37 to 19.89 with a mean effect size of 5.81. The effect size was found to be significant and positive. It indicates that C: N of plants was 5.81 standard deviations higher under elevated CO₂ conditions than ambient CO₂. The effect size was positive in all twenty five cases studied indicating a higher increase under elevated CO₂ conditions than ambient CO₂ (Table 14).

d. Tannins : The quantity of tannins present in plants grown under elevated CO₂ were estimated in twenty three studies and were subjected to metaanalysis. The effect sizes in the studies included ranged from 1.15 to 12.98 with a mean effect size of 3.49. The effect size was found to be significant and positive. It indicates that C: N of plant was 3.49 standard deviations higher under elevated CO₂ conditions than ambient CO₂. The effect size was very positive in all twenty three cases studied indicating a higher increase of tannins under elevated CO₂ conditions than ambient CO₂ (Table 15).

Table 12 : Summary of the data included in the meta analysis and corresponding effect sizes (d) – Carbon content in foliage

S.No.	Insect sp.	Order	Host plant	g	d	Study
1	<i>C. flaveola</i>	Col	<i>E. tereticornis</i>	-4.00	-3.97	Lawler <i>et al.</i> , 1997
2	<i>G. viridula</i>	Col	<i>R. obtusifolius</i>	-3.16	-3.09	Brooks & Whittaker, 1998
3	<i>N. lineatus</i>	H	<i>J. squarrosus</i>	0.37	0.34	Brooks & Whittaker, 1999
4	<i>L. dispar</i>	L	<i>Q. petraea</i>	-0.39	-0.36	Hattenschwiler & Schafellner, 2004
5	Arthropod community		<i>L. japonica</i>	-0.88	-0.79	Sanders <i>et al.</i> , 2004
6	<i>L. dispar</i>	L	<i>P. pseudo-simonii</i>	0.00	0.00	Xiaowei <i>et al.</i> , 2006
7	<i>C. philodice</i>	L	<i>T. pratense</i>	-1.54	-1.51	Karowe, 2007
8	<i>S. litura</i> & <i>A. janata</i>	L	<i>R. communis</i>	0.56	0.51	Srinivasa Rao <i>et al.</i> , 2009

L : Lepidoptera (Chewer), Col : Coleoptera (Chewer), H : Homoptera (Sucker),

Table 13 : Summary of the data included in the meta analysis and corresponding effect sizes (d)– Nitrogen content

S.No.	Insect sp.	Order	Host plant	Parameter	g	d	Study
1	<i>P. includans</i>	L	<i>G. max</i>	N (mg/g)	-2.87	-2.83	Lincoln <i>et al.</i> , 1984
2	<i>T. ni</i>	L	<i>P. lunata</i>	N (mg/g)	0.16	0.16	Osbrink <i>et al.</i> , 1987
3	<i>P. gossypiella</i>	L	<i>G. hirsutum</i>	% N	3.79	3.03	Akey <i>et al.</i> , 1988
4	<i>J. ceonia</i>	L	<i>P. lanceolata</i>	% N	-1.28	-1.25	Fajer <i>et al.</i> , 1989
5	<i>S. eridania</i>	L	<i>M. piperita</i>	N (mg/g)	0.17	0.16	Lincoln & Couvet 1989
6	<i>M. sanguinipes</i>	O	<i>A. tridentata</i>	N (mg/g)	-1.42	-1.39	Jhonson & Lincoln 1990
7	<i>M. differentialis</i>	O	<i>A. tridentata</i>	N (mg/g)	-3.33	-3.20	Jhonson & Lincoln 1991
8	<i>L. dispar</i> , <i>M. disstria</i>	L	<i>P. tremuloides</i>	% N	-5.45	-5.31	Lindroth <i>et al.</i> , 1993
9	<i>S. exigua</i>	L	<i>B. vulgaris</i>	% N	20.0	19.79	Caulfield <i>et al.</i> , 1994
10	<i>N. lecontei</i>	L	<i>P. taeda</i>	N (mg/g)	-8.42	-7.61	Williams <i>et al.</i> , 1994
11	<i>L. dispar</i>	L	<i>B. papyrifera</i>	% N	-1.97	-1.57	Roth & Lindroth 1994
12	<i>L. dispar</i>	L	<i>P. strobus</i>	% N	-1.11	-1.00	Roth & Lindroth 1994
13	<i>S. eridania</i>	L	<i>E. cardamomum</i>	N (mg/g)	-4.18	-2.39	Arnone <i>et al.</i> , 1995
14	<i>S. frugiperda</i>	L	<i>F. arundinacea</i>	N (mg/g)	0.00	0.00	Marks & Lincoln 1996

15	<i>L. dispar</i>	L	<i>B. populifolia</i>	% N	-8.28	-8.14	Traw <i>et al.</i> , 1996
16	<i>N. lecontei</i>	L	<i>P. taeda</i>	N (mg/g)	-4.43	-3.54	Williams <i>et al.</i> , 1997
17	<i>C. flaveola</i>	Col	<i>E. tereticornis</i>	% N	5.22	5.17	Lawler <i>et al.</i> , 1997
18	<i>L. dispar</i>	L	<i>P. tremuloides</i>	% N	-3.35	-3.17	Lindroth <i>et al.</i> , 1997
19	<i>L. dispar</i>	L	<i>P. tremuloides</i>	% N	-4.93	-4.62	Kinney <i>et al.</i> , 1997
20	<i>M. disstria</i>	L	<i>P. tremuloides</i>	% N	-9.33	-8.11	Roth <i>et al.</i> , 1998
21	<i>L. dispar</i>	L	<i>Q. alba</i>	N (mg/g)	-3.28	-2.62	Williams <i>et al.</i> , 1998
22	<i>M. disstria</i>	L	<i>Q. alba</i>	N (mg/g)	-6.32	-5.06	Williams <i>et al.</i> , 1998
23	<i>L. dispar</i>	L	<i>P. tremuloides</i>	% N	-1.11	-1.08	Lindroth & Kinney 1998
24	Defoliators		<i>Q. robur</i>	% N	-2.89	-2.87	Dury <i>et al.</i> , 1998
25	<i>G. viridula</i>	Col	<i>R. obtusifolius</i>	% N	-6.21	-6.08	Brooks & Whittaker, 1988
26	<i>B. brassicae</i>	H	<i>B. oleracea</i>	% N	-5.65	-5.62	Bezemer <i>et al.</i> , 1999
27	<i>N. lineatus</i>	H	<i>J. squarrosus</i>	% N	-1.45	-1.34	Brooks & Whittaker, 1999
28	<i>L. monacha</i>	L	<i>P. abies</i>	% N	-6.56	-6.05	Hattenschwiler & Schafellner, 1999
29	<i>P. icarus</i>	L	<i>L. corniculatus</i>	% N	-0.88	-0.86	Goverde <i>et al.</i> , 1999
30	Leaf miners	L	<i>Q. myrtifolia</i>	% N	-0.13	-0.13	Stilling <i>et al.</i> , 1999
31	<i>S. exigua</i>	L	<i>G. hirsutum</i>	% N	-14.47	-14.45	Coviella <i>et al.</i> , 2000
32	<i>O. leucostigma</i>	L	<i>B. papyrifera</i>	% N	-0.57	-0.50	Agrell <i>et al.</i> , 2000
33	<i>L. dispar</i>	L	<i>A. rubrum</i>	N (mg/g)	-6.73	-5.85	Williams <i>et al.</i> , 2000
34	<i>A. pisum</i>	H	<i>Vicia faba</i>	% N	-4.12	-4.10	Hughes & Bazzaz, 2001
35	<i>D. scariella</i>	L	<i>E. plantagineum</i>	% N	-10.20	-9.77	John and Hughes, 2002
36	<i>S. exigua</i>	L	<i>G. hirsutum</i>	% N	-9.47	-9.35	Coviella <i>et al.</i> , 2002
37	<i>P. vitellinae</i>	Col	<i>S. myrsinifolia</i>	% N	-0.55	-0.55	Veteli <i>et al.</i> , 2002
38	<i>M. persicae</i>	H	<i>B. oleracea</i>	% N	-300.0	-293.3	David & Mark, 2002
39	<i>C. pamphilus</i>	L	<i>Festuca rubra</i>	% N	-8.54	-8.43	Mevischutz <i>et al.</i> , 2003
40	<i>C. pamphilus</i>	L	<i>F. rubra</i>	% N	-8.54	-8.46	Goverde <i>et al.</i> , 2003
41	Leaf miners	L	<i>Q. myrtifolia</i>	% N	-0.73	-0.70	Stilling <i>et al.</i> , 2003
42	Leaf miners	L	<i>Q. myrtifolia</i>	% N	-0.86	-0.69	Cornelissen <i>et al.</i> , 2003

43	<i>L. dispar</i>	L	<i>A. rubrum</i>	% N	-1.18	-1.11	Williams <i>et al.</i> , 2003
44	<i>M. disstria</i>	L	<i>P. tremuloides</i>	% N	-2.26	-2.25	Holton <i>et al.</i> , 2003
45	<i>P. maculicornis</i>	Col	<i>B. pendula</i>	% N	-5.88	-5.56	Kuokkanen <i>et al.</i> , 2003
46	<i>P. xylostella</i>	L	<i>B. oleracea</i>	% N	0.98	0.90	Reddy <i>et al.</i> , 2004
47	<i>S. avenae</i>	H	<i>T. aestivum</i>	N (mg/g)	-0.54	-0.54	Chen <i>et al.</i> , 2004
48	<i>P. icarus</i>	L	<i>L. corniculatus</i>	% N	-4.19	-4.05	Goverde <i>et al.</i> , 2004
49	<i>L. dispar</i>	L	<i>Q. petraea</i>	% N	-2.10	-1.94	Hattenschwiler & Schafellner, 2004
50	Arthropod community		<i>L. japonica</i>	% N	-2.91	-2.63	Sanders <i>et al.</i> , 2004
51	<i>H. armigera</i>	L	<i>G. hirsutum</i>	N (mg/g)	-2.03	-2.02	Chen <i>et al.</i> , 2005
52	Forest pests		<i>R. pseudoacacia</i>	% N	-1.64	-1.63	Knepp <i>et al.</i> , 2005
53	<i>M. disstria</i>	L	<i>B. papyrifera</i>	% N	1.00	0.96	Agrell <i>et al.</i> , 2005
54	<i>A. gossypi</i>	L	<i>G. hirsutum</i>	% N	-3.43	-3.39	Chen <i>et al.</i> , 2005
55	<i>H. armigera</i>	L	<i>T. aestivum</i>	N (mg/g)	-2.31	-2.30	Wu <i>et al.</i> , 2006
56	<i>L. dispar</i>	L	<i>P. pseudosimonii</i>	N (mg/g)	-4.48	-4.14	Xiaowei <i>et al.</i> , 2006
57	<i>A. gossypii</i>	H	<i>T. pratense</i>	% N	4.75	4.75	Awmack <i>et al.</i> , 2007
58	<i>C. philodice</i>	L	<i>T. pratense</i>	% N	-0.47	-0.46	Karowe 2007
59	<i>H. armigera</i>	L	<i>P. sativum</i>	% N	-4.37	-4.28	Coll & Hughes, 2008
60	<i>S. litura</i> & <i>A. janata</i>	L	<i>R. communis</i>	% N	-7.98	-7.21	Srinivasa Rao <i>et al.</i> , 2009
61	<i>H. armigera</i>	L	<i>Z. mays</i>	N (mg/g)	-9.39	-9.35	Yin <i>et al.</i> , 2010

L : Lepidoptera (Chewer), Col : Coleoptera (Chewer), H : Homoptera (Sucker), O : Orthoptera (Chewer)



Achaea janata



Lymantria dispar



Gastrophysa viridula

Table 14 : Summary of the data included in the meta analysis and corresponding effect sizes (d)– C: N ratio

S. No.	Insect sp.	Order	Host plant	g	d	Study
1	<i>P. includans</i>	L	<i>G. max</i>	2.58	2.55	Lincoln <i>et al.</i> , 1984
2	<i>C. flaveola</i>	Col	<i>E. tereticornis</i>	10.01	9.91	Lawler <i>et al.</i> , 1997
3	<i>L. dispar</i>	L	<i>P. tremuloides</i>	4.37	4.09	Kinney <i>et al.</i> , 1997
4	<i>O. brumata</i>	L	<i>C. vulgaris</i>	0.39	0.37	Kerslake <i>et al.</i> , 1998
5	<i>C. syngenesiae</i>	D	<i>S. oleraceus</i>	3.86	3.83	Smith & Jones 1998
6	<i>L. dispar</i>	L	<i>P. tremuloides</i>	2.06	2.02	Lindroth & Kinney, 1998
7	<i>G. viridula</i>	Col	<i>R. obtusifolius</i>	1.83	1.79	Brooks & Whittaker, 1998
8	<i>N. lineatus</i>	H	<i>R. obtusifolius</i>	0.97	0.90	Brooks & Whittaker, 1999
9	Leaf miners	L	<i>Q. myrtifolia</i>	0.47	0.47	Stilling <i>et al.</i> , 1999
10	<i>S. exigua</i>	L	<i>G. hirsutum</i>	2.98	2.97	Coviella <i>et al.</i> , 2000
11	<i>L. dispar</i>	L	<i>A. rubrum</i>	4.96	3.97	Williams <i>et al.</i> , 2000
12	<i>A. pisum</i>	H	<i>V. faba</i>	20.0	19.9	Hughes & Bazzaz, 2001
13	<i>D. scariella</i>	L	<i>E. plantagineum</i>	10.14	9.71	John & Hughes, 2002
14	<i>C. pamphilus</i>	L	Grass sp.	3.29	1.88	Goverde <i>et al.</i> , 2002
15	<i>S. exigua</i>	L	<i>G. hirsutum</i>	6.58	6.50	Coviella <i>et al.</i> , 2002
16	<i>C. pamphilus</i>	L	<i>F. rubra</i>	7.81	7.71	Mevischutz <i>et al.</i> , 2003
17	<i>C. pamphilus</i>	L	<i>F. rubra</i>	7.89	7.82	Goverde <i>et al.</i> , 2003
18	<i>P. icarus</i>	L	<i>L. corniculatus</i>	3.98	3.84	Goverde <i>et al.</i> , 2004
19	Arthropod community		<i>L. japonica</i>	3.15	2.85	Sanders <i>et al.</i> , 2004
20	<i>M. alpina</i>	O	<i>V. uliginosum</i>	4.85	4.65	Roman Asshoff & Hattenschwiler, 2005
21	<i>A. gossypi</i>	L	<i>G. hirsutum</i>	13.83	13.68	Chen <i>et al.</i> , 2005
22	<i>L. dispar</i>	L	<i>P. pseudosimonii</i>	3.93	3.63	Xiaowei <i>et al.</i> , 2006
23	<i>A. gossypii</i>	H	<i>G. hirsutum</i>	-20.00	-19.60	Wu <i>et al.</i> , 2007
24	<i>C. philodice</i>	L	<i>T. pratense</i>	0.54	0.53	Karowe, 2007
25	<i>S. litura</i> & <i>A. janata</i>	L	<i>R. communis</i>	11.14	10.06	Srinivasa Rao <i>et al.</i> , 2009

L : Lepidoptera (Chewer), Col : Coleoptera (Chewer), H : Homoptera (Sucker), O : Orthoptera (Chewer)

Table 15 : Summary of the data included in the meta analysis and corresponding effect sizes (d) – Tannins

S.No.	Insect sp.	Order	Host plant	Parameter	g	d	Study
1	<i>L. dispar</i> ,	L	<i>P. tremuloides</i>	Tannin (% dry mass)	3.15	3.07	Lindroth <i>et al.</i> , 1993
2	<i>L. dispar</i> ,	L	<i>B. papyrifera</i>	Tannin (% dry wt)	2.79	2.23	Roth & Lindroth, 1994
3	<i>M. disstria</i>	L	<i>P. strobus</i>	Tannin (% dry wt)	2.31	2.09	Roth & Lindroth, 1994
4	<i>L. dispar</i>	L	<i>B. populifolia</i>	Tannin (% dry wt)	2.82	2.77	Traw <i>et al.</i> , 1996
5	<i>C. flaveola</i>	C	<i>F.sylvatica</i>	Tannins (mg quebrancho / g)	2.26	2.23	Lawler <i>et al.</i> , 1997
6	<i>L. dispar</i>	L	<i>P.tremuloide</i>	Tannins (% dry wt)	6.61	6.25	Lindroth <i>et al.</i> , 1997
7	<i>L. dispar</i>	L	<i>P.tremuloides</i>	Tannins (% dry wt)	2.38	2.25	Kinney <i>et al.</i> , 1997
8	<i>M. disstria</i>	L	<i>P.tremuloides</i>	Tannins (% dry wt)	5.22	4.54	Roth <i>et al.</i> , 1998
9	<i>L. dispar</i>	L	<i>P.tremuloides</i>	Tannins (% dry wt)	2.33	2.27	Lindroth & Kinney, 1998
10	Defoliators		<i>Q. robur</i>	Tannins (mg/g)	1.44	1.43	Dury <i>et al.</i> ,1998
11	<i>L. monarcha</i>	L	<i>P. abies</i>	Tannins (% dry wt)	2.13	1.97	Hattenschwiler & Schafellner, 1999
12	<i>P. icarus</i>	L	<i>L. corniculatus</i>	Tannin (mg/g)	1.26	1.23	Goverde <i>et al.</i> , 1999
13	<i>O. leucostigma</i>	L	<i>B. papyrifera</i>	Tannins (% dry wt)	1.32	1.15	Agrell <i>et al.</i> , 2000
14	<i>L. dispar</i>	L	<i>A.rubrum</i>	Tannic acid (% dry wt)	2.50	2.00	Williams <i>et al.</i> , 2000
15	<i>P. icarus</i>	L	<i>L. corniculatus</i>	Tannins (mg/g)	5.56	5.54	Bazin <i>et al.</i> , 2002
16	<i>C. pamphilus</i>	L	Grass sp.	Tannins (% dry wt)	3.13	1.78	Goverde <i>et al.</i> , 2002
17	<i>S. exigua</i>	L	<i>G. hirsutum</i>	Tannins (mg/g)	4.17	4.11	Coviella <i>et al.</i> , 2002
18	Leaf miners		<i>Q. myrtifolia</i>	Tannins (mg)	14.75	11.80	Cornelissen, 2003
19	<i>L. dispar</i>	L	<i>A.rubrum</i>	Tannic acid (% dry wt)	13.73	12.98	Williams <i>et al.</i> , 2003
20	<i>M. disstria</i>	L	<i>P. tremuloides</i>	Tannins (% dry wt)	0.63	0.63	Holton <i>et al.</i> , 2003
21	<i>P.maculicornis</i>	C	<i>B. pendula</i>	Tannins (mg/g)	2.45	2.31	Kuokkanen <i>et al.</i> , 2003
22	<i>L.dispar</i>	L	<i>Q. petraea</i>	Tannins (% dry wt)	2.35	2.17	Hattenschwiler & Schafellner, 2004
23	<i>H. armigera</i>	L	<i>G. hirsutum</i>	Tannins (% dry wt)	3.39	3.35	Chen <i>et al.</i> , 2005

L : Lepidoptera (Chewer), Col : Coleoptera (Chewer)

4. Discussion

Most of the literature surveys conducted to synthesize the research results on the impact of elevated CO₂ on the abundance of insect pests resorted to vote-counting method. The number of studies reporting positive, negative and no significant effect was as considered for drawing some generalizations. Such generalizations often tend to be biased and inconclusive as they are based on results that may or may not agree with one another. There are subjective literature reviews that concluded positive effects, negative effects and non-significant effects of elevated CO₂ on pest abundance. A majority of the literature surveys suggest an increased consumption of foliage by insect larvae with extended duration of larvae under elevated CO₂ than under ambient CO₂ conditions. However, such surveys do not consider the experimental methods, sample size and magnitude of the effect while drawing generalizations and will come out with qualitative conclusions only. In this analysis, we attempted to synthesize results from eighty eight (88) experiments on the growth and development of insect pests under elevated CO₂ conditions. Stiling and Cornelissen, 2007 attempted to understand how elevated CO₂ effect plant herbivore interactions through meta analysis. Our analysis includes more number of studies published till 2011 and also some other insect parameters. Our results also indicated an increased consumption under elevated CO₂ with significant positive effect size. It is to be noted however that the studies differed with respect to the crops and pests covered, experimental design, and the nature of treatments. In published literature on effect size, any effect size of about 0.8 is considered as large. The effect sizes observed in this study were much larger than 0.8. For example, the effect size with respect to consumption of foliage by larvae under elevated CO₂ were compared with ambient CO₂ condition. The effect sizes in the studies included ranged from 30.88 to -2.72 with a mean effect size of 2.94. It indicates that the average consumption of insect species was 2.94 standard deviations more or higher under elevated CO₂ conditions than that of ambient CO₂ was larger or higher than 0.8 indicating a strong impact on the growth and behavior of insect larvae. Our meta analysis results indicated significant influence of elevated CO₂ on life history parameters of insect pests. Larval duration was found to be increased significantly under elevated CO₂ compared with ambient CO₂. This increased larval life span and other insect stages was also noticed by various authors. Similar trend was reflected in corresponding effect sizes also.

The impact of elevated CO₂ on the phytochemistry of the plants was well documented. The results indicated that most of the studies have been concentrated on the array of plant species under elevated CO₂ conditions. In majority cases, decrease in nitrogen, increase in carbon, C:N ratio, condensed tannins, tremulacin levels, starch, drymatter production and root:shoot ratio was observed. The changes in phytochemistry of plants lead to deterioration of nutritional quality of plants. The analyzed data on impact of elevated CO₂ on insect pests indicate that the general decreases in foliar nitrogen concentrations and increase in carbohydrate and phenolic based secondary metabolites reported in many individual studies. The consumption by herbivores was related primarily to changes in nitrogen and carbohydrate levels. No differences were found

between CO₂ mediated herbivore responses on woody plants and herbaceous plant species. Leaf chewing insects generally increased their consumption of foliage under elevated CO₂ to compensate for reduced nutritional quality and suffered no adverse effect on pupal weights. The leaf-mining insects could only partially compensate by increased consumption and pupal weights did decline. The phloem-feeding and whole-cell-feeding insects responded positively to elevated CO₂, with increases in population size and decreases in development time. The factors that contribute to increased consumption might be due to compensatory mechanism of larvae.

The following conclusions can be drawn from the present and earlier reviews (Watt *et al.*, 1995; Bezemer and Jones, 1998; Coviella and Trumble, 1999; Whittaker, 1999; Hunter, 2001). Herbivores respond to increased levels of CO₂ 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 such as nitrogen level, C:N ratio, concentration of phenolics. In general, host plant quality declines in elevated CO₂ with leaf nitrogen decreasing and phenolics increasing. Changes in nitrogen content are correlated with changes in food consumption and changes in phenolics with changes in food digestibility. Leaf chewers (14 species) are generally able to compensate for quality of food by increased food consumption (30%) without adverse effects on pupal weight. Leaf miners (4 species) also increased food consumption but insufficiently to prevent a decline in pupal weight. Sap feeders (11 species) are the only functional group to show positive responses to elevated CO₂. (Bezemer & Jones, 1998).

It was observed that majority of insect-plant interactions are from forest trees and grasses. Few studies are available on cultivated plants. There are no studies on important global pest like *Helicoverpa armigera*, which is ubiquitous pest of international importance. As mentioned by Coviella and Trumble (1999) many insect orders have been completely neglected, the situation till date has not changed with majority of our studies are from order Lepidoptera followed by Homoptera.

The present quantified results after metaanalysis showed that insect performance indices of insect species varied significantly under elevated CO₂ than ambient. An increase of about 10-15 % of AD was observed and reflected in effect sizes of various larvae under elevated CO₂ than ambient. Reduction of ECI, ECD and RGR under elevated CO₂ than ambient was noticed in several studies. Within each elevated CO₂ level also increased AD (about 1-6%) and RCR (13-15%) were observed. Larvae consumed more foliage grown under elevated CO₂ 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.

The impact of elevated CO₂ on the phytochemistry of the plants was well studied. In this study also, nitrogen concentration in plants decreased by about 10-25 per cent when plants were grown under elevated CO₂ 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. Since nitrogen is the chief constituent of proteins, this suggests that plants grown under elevated CO₂ 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 CO₂ conditions. Similar trend in effect sizes was obtained with respect to carbon, Nitrogen and C: N ratio. 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.

5. Limitations of Meta analysis

Meta analysis is a useful tool to integrate research results from different studies. There is however certain limitations that needs to be considered. First, critics say that integrating studies that differ widely with respect to the experimental design and statistical analysis as meta analysis does may not be appropriate. However, by carefully defining the selection criteria, as we attempted here, one can minimize the consequences of inappropriate integration. Second, only the published results are considered leaving the unpublished results out of the analysis. Since it is the non-significant results that usually do not get published the effect sizes may be, in reality, overestimates of the population effect sizes. The 'fail-safe N' addresses this problem to some extent. Another limitation arises when a single study reports more than one effect size as they study the behaviour of different pests in different situations and at different points of time. Including all the results from a single study may result in bias as the sample size gets artificially inflated. Various insect parameters were selected for meta analysis from same study to understand the exact effect of elevated CO₂ on these. Selecting one effect size from a given study is one option to overcome with this limitation but the choice of the one effect remains a subjective question. It is to be mentioned here that these limitations are also relevant to the subjective literature reviews and meta analysis as a tool is prone to be misused, as is the case with any other statistical tool. It is therefore helpful to be aware of these limitations while conducting meta analysis or while accepting results of a meta analysis.

6. Conclusions

Considering the potential impacts of elevated CO₂ on various insect stages of several crops, forest trees, grasses to understand the mechanism, several studies looked into the relationship between elevated CO₂ and growth and development of insects. In order to consolidate the understanding, attempts were made to synthesize such information. Qualitative literature reviews have been the most popular means of putting together research results to draw some generalizations on the research question at hand. These qualitative reviews suffer from the fact that they do not consider the quantitative information contained in the individual studies and hence the generalizations or conclusions that emerge cannot be given any statistical validity. We

have attempted here a quantitative synthesis, also called meta analysis, of studies dealing with growth and behavior of insects under elevated CO₂ condition. Results based on the effect size, one of the frequently used measures in meta analysis, showed that the effect of elevated CO₂ on the growth and development of insect pests was significant and relatively large. The effect size was positive meaning that the consumption of foliage by larvae was more; duration was extended under elevated CO₂ conditions than the corresponding ambient CO₂ conditions. Among various biochemical constituents, nitrogen is known to be a most important limiting factor influencing the growth and development of herbivorous insects and thus a slight reduction in foliar nitrogen content would have profound effects on their performance. In majority of studies nitrogen content was reduced under eCO₂ and mean effect size was also got reduced. The studies included in the meta analysis were also observed to differ in terms of crops and pests dealt with, experimental methods, etc which was reflected in the range of effect sizes for different studies. It can be concluded that meta analysis can be most useful for drawing quantitative inferences especially when confronted with conflicting evidences.

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Polydrusus sericeus



Melanoplus differentialis



Aphis gossypii



Myzus persicae

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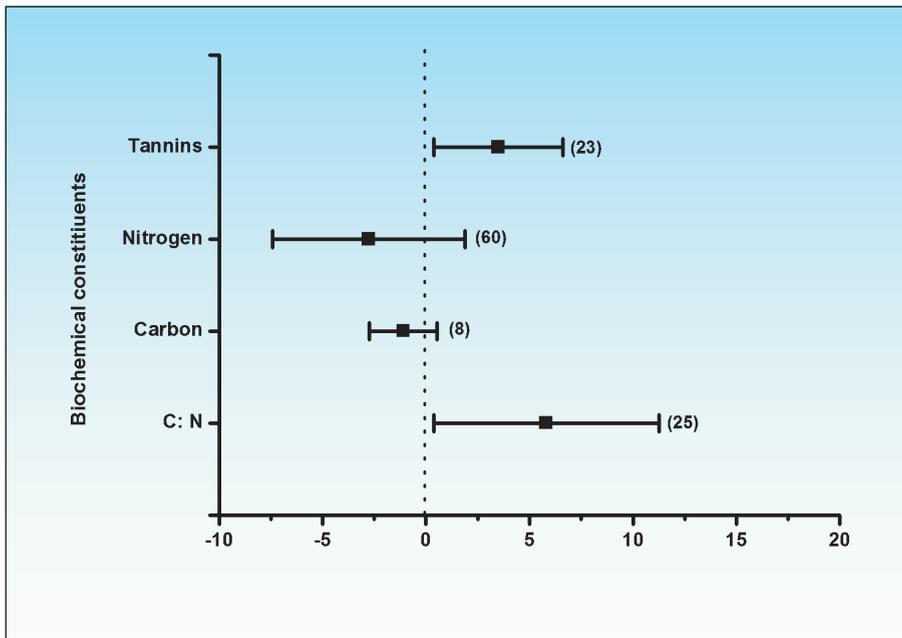
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9. Annexure

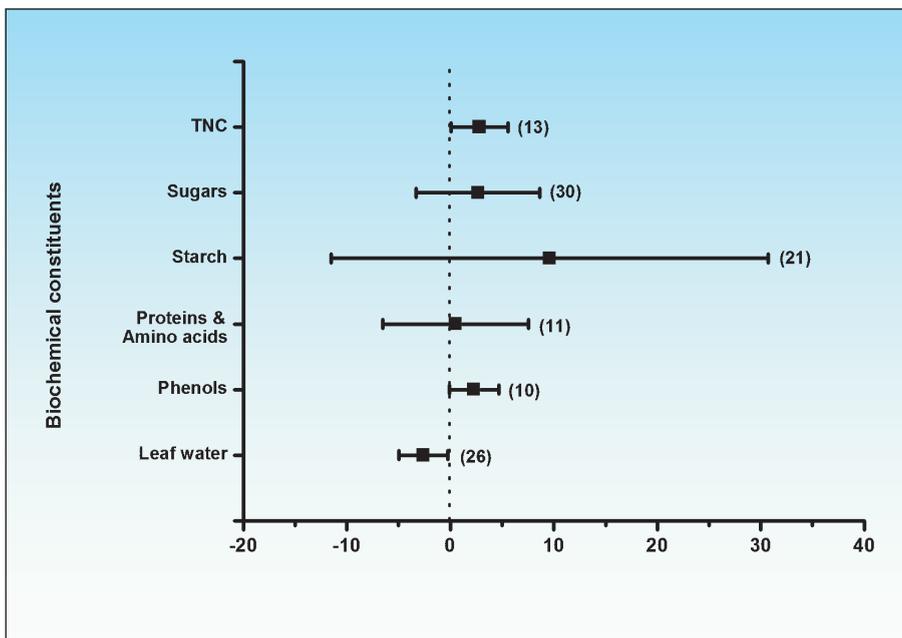
List of Insect herbivores and host plants included in the Meta analysis studies

INSECT HERBIVORE	
Common name	Scientific name
Soybean looper	<i>Pseudoplusia includans</i>
Cabbage looper	<i>Trichoplusia ni</i>
Pink bollworm	<i>Pectinophora gossypiella</i>
Buckeye butterfly	<i>Junonia ceonia</i>
Southern armyworm	<i>Spodoptera eridania</i>
Grasshopper	<i>Melanoplus sanguinipes</i>
Grasshopper	<i>Melanoplus differentialis</i>
Gypsy moth	<i>Lymantria dispar</i> ,
Forest tent caterpillar	<i>Malacosoma disstria</i>
Beet armyworm	<i>Spodoptera exigua</i>
Pine saw fly	<i>Neodiprion lecontei</i>
Fall armyworm	<i>Spodoptera frugiperda</i>
Leaf beetle	<i>Gastrophysa viridula</i>
Beech aphid	<i>Phyllaphis fagi</i>
Chrysomelid beetle	<i>Chrysophtharta flaveola</i>
Western flower thrips	<i>Franklinealla occidentalis</i>
Potato aphid	<i>Aulacorthum solani</i>
Winter moth	<i>Operophtera brumata</i>
Chrysanthemum leaf miner	<i>Chromatomyia syngenesiae</i>
Green peach aphid	<i>Myzus persicae</i>
Grass foam Spittle	<i>Neophileanus lineatus</i>
Nun moth	<i>Lymantria monarcha</i>
Common blue butterfly	<i>Polyommatus icarus</i>
Aphid	<i>Rhopalosiphum padi</i>
White-marked tussock moth	<i>Orgyia leucostigma</i>
Two-spotted spider mite	<i>Tetranychus urticae</i>
Pea aphid	<i>Acyrtosiphon pisum</i>
Sap feeding aphid,	<i>Chaitophorus stevensis</i>
Echium leaf miner	<i>Dialectica scariella</i>
Satyr butterfly	<i>Coenonympha pamphilus</i>
Chrysomelid beetle	<i>Phratora vitellinae</i>
Tobacco caterpillar	<i>Spodoptera litura</i>
Cabbage aphid	<i>Brevicoryne brassicae</i>
Cotton leafworm	<i>Spodoptera littoralis</i>
Acorn weevil	<i>Phyllobius maculicornis</i>
Diamond back moth	<i>Plutella xylostella</i> ,
Grain aphid	<i>Sitobion avenae</i>
Aphid	<i>Cepegillettea betulaefoliae</i>
Green mountain grasshopper	<i>Miramella alpina</i>
Cotton bollworm	<i>Helicoverpa armigera</i>
Potato aphid	<i>Macrosiphum euphorbiae</i>
Cotton aphid	<i>Aphis gossypii</i>
Sulfur butterfly	<i>Colias philodice</i>
Castor semi looper	<i>Achoea janata</i>
Green immigrant leaf weevil	<i>Polydrusus sericeus</i>

HOST PLANT	
Common name	Scientific name
Soybean	<i>Glycine max</i>
Lima beans	<i>Phaseolus lunata</i>
Cotton	<i>Gossypium hirsutum</i>
Narrow leaf plantain	<i>Plantago lanceolata</i>
Peppermint	<i>Mentha piperita</i>
Sagebrush	<i>Artemisia tridentata</i>
White pine	<i>Pinus strobus</i>
Quaking aspen	<i>Populus tremuloides</i>
Sugar beet	<i>Beta vulgaris</i>
Loblolly pine	<i>Pinus taeda</i>
Birch	<i>Betula papyrifera</i>
Cardamom	<i>Elettaria cardamomum</i>
Tall fescue	<i>Festuca arundinacea</i>
Gray birch	<i>Betula populifolia</i>
Broad leaved dock	<i>Rumex obtusifolius</i>
Beech	<i>Fagus sylvatica</i>
Milk weed	<i>Asclepias syriaca</i>
Bean	<i>Vicia faba</i>
Common heather	<i>Calluna vulgaris</i>
Pedunculate Oak	<i>Quercus robur</i>
Smooth sow thistle	<i>Sonchus oleraceus</i>
White Oak	<i>Quercus alba</i>
Red clover	<i>Trifolium pratense</i>
Brussels sprout	<i>Brassica oleracea</i>
Heath rush	<i>Juncus squarrosus</i>
Spruce	<i>Picea abies</i>
Bird's foot trefoil	<i>Lotus corniculatus</i>
Myrtle oak	<i>Quercus myrtifolia</i>
Kidney bean	<i>Phaseolus vulgaris</i>
Sugar maple	<i>Acer saccharum</i>
White clover	<i>Trifolium repens</i>
Paterson's curse	<i>Echium plantagineum</i>
Dark leaved willow	<i>Salix myrsinifolia</i>
Mung bean	<i>Vigna radiata</i>
Red fescue	<i>Festuca rubra</i>
Spring wheat	<i>Triticum aestivum</i>
Sessile Oak	<i>Quercus petraea</i>
Japanese honeysuckle	<i>Lonicera japonica</i>
Alpine Blueberry	<i>Vaccinium uliginosum</i>
Black locust	<i>Robinia pseudo-acacia</i>
Climbing nightshade	<i>Solanum dulcamara</i>
Corn	<i>Zea mays</i>
Poplar	<i>Populus pseudo-simonii</i>
Garden pea	<i>Pisum sativum</i>
Castor	<i>Ricinus communis</i>
Ecotron community	<i>Cardamine hirsuta,</i> <i>Poa annua, Senecio</i> <i>vulgaris, Spargula arvensis</i>



Mean effect size of biochemical constituents under eCO₂



Mean effect size of other biochemical constituents under eCO₂



हर कदम, हर डगर
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