EFFECTS OF ELEVATED CARBON DIOXIDE AND TEMPERATURE ON INSECT-PLANT INTERACTIONS - A REVIEW

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ABSTRACT

The information on effects of elevated Carbon dioxide (CO₂) and temperature on insect-plant interactions has been compiled and reviewed. Substantial changes in phytochemistry of plants were mentioned by several workers under elevated CO₂ conditions. Decreased nitrogen (N), tremulacin, increased tannin, starch levels led to reduction in nutritional quality in array of plants exposed. To compensate these changes the consumption rate of larvae increased. Differential response was observed among various guilds of insects. In class Insecta, lepidopterans and homopterans were studied exclusively. Decreased relative growth rate, prolonged development time in lepidoptera (leaf chews), increased abundance and fecundity in homoptera (sap suckers) were reported. The impact of elevated temperature was mentioned.

Human activities have increased the atmospheric concentrations of greenhouse gases and aerosols since the pre-industrial era. Global atmospheric CO₂ concentration has increased by approximately 30% since the industrial revolution and is believed to be responsible for an increase of ∼0.6°C in mean annual global surface temperature (IPCC, 2001). If no climate policy interventions are made, the concentrations of atmospheric CO₂ may increase up to 405-460 ppm, 445-640 ppm and 540-970 ppm by 2025, 2050 and 2100 respectively. It is very likely that 20th century warming contributed significantly to the observed rise in global average sea level and increase in ocean-heat content. Snow covers and ice extent decreased (IPCC, 2001). Apart from the effects mentioned above, agriculture including plants-insect-parasitoid systems is likely to be affected by the climate change. This review summarizes the results from several years of research on the effects of elevated CO₂ and temperature on plant chemistry and subsequent effects on the performance of insect herbivores.

Effect of elevated CO₂

a) Phytochemistry of plants

Among the host plants, forest trees and grasses have been extensively studied for insect-plant interactions under elevated CO₂ (Table 1). Few studies are available on cultivated crops. In majority of studies the elevated CO₂ concentrations ranged from 530 ppm to 1050 ppm.

Nitrogen concentration decreased in European white birch, Betula pendula (Kuokkanen et al., 2003), quaking aspen, Populus tremuloides (Holton et al., 2003), condensed tannins increased in european white birch trees (Kuokkanen et al., 2003), quaking aspen (Agrell et al., 2005), tremulacin levels increased in birch trees (Kopper and Lindroth, 2003) and starch concentration increased in paper birch, Betula papyrifera (Roth and Lindroth, 1995) and pine tree, Pinus taeda (Williams et al., 1997).

As in case of forest trees nitrogen decreased in many of the grasses except annual blue grass in which there was no effect on nitrogen concentration (Bezemer et al., 1998). In erect brome, Brachus erectus, vernal sedge, Carex caryophylla and Fescue, Festuca sps; increased CO₂ resulted in increase in nonstructural carbohydrates and condensed tannins (Goverde et al., 2002). C:N ratio increased in red fesue, Festuca rubra (Mevi-
<table>
<thead>
<tr>
<th>Insect</th>
<th>Common name</th>
<th>Scientific name</th>
<th>Family</th>
<th>Host plant</th>
<th>CO₂ conc. (ppm)</th>
<th>Effect on host plants</th>
<th>Impact on insects</th>
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<td>Lymantria dispar</td>
<td>Lymantriidae</td>
<td>Sesile Oak</td>
<td>Quercus petraea</td>
<td>530</td>
<td>42% increase in stalk, decrease in N. increase in condensed tannins</td>
<td>Relative Growth Rate (RGR) reduced by 30%</td>
<td>Hatterschwieler and Schafellner, 2004</td>
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<td>Lymantria dispar</td>
<td>Lymantriidae</td>
<td>Red maple</td>
<td>Acer rubrum</td>
<td>Ambient + 300</td>
<td>Decreased N and C:N ratio</td>
<td>Reduced larval growth</td>
<td>Williams et al., 2000</td>
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<tr>
<td>Gypsy moth</td>
<td>Lymantria dispar</td>
<td>Lymantriidae</td>
<td>White oak</td>
<td>Quercus alba</td>
<td>Ambient + 300</td>
<td>Decreased N, Higher total non structural carbohydrate: N ratio</td>
<td>Significant growth reduction of early instar larvae</td>
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<td>700</td>
<td>Decrease in N, Increase in condensed tannins</td>
<td>38% smaller pupal mass Declined in relative growth rate</td>
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<td>Malacosoma distria</td>
<td>Lasiocampidae</td>
<td>Quaking aspen</td>
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<td>560</td>
<td>Decreased N, Increased tremulacin levels</td>
<td>No effect on larval performance</td>
<td>Kopper and Lindroth, 2003</td>
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<td>Malacosoma distria</td>
<td>Lasiocampidae</td>
<td>Quaking aspen</td>
<td>Populus tremuloides</td>
<td>642 ± 2</td>
<td>Decreased N, Increased stalk</td>
<td>Fast development time, 20% lowered growth rate</td>
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<td>Small heath</td>
<td>Coenonympha pamphilus</td>
<td>Satyrinae</td>
<td>Red fescue</td>
<td>Festuca rubra</td>
<td>750</td>
<td>Decreased N, Increased C:N Ratio</td>
<td>Larval growth slower</td>
<td>Mext-Schutz et al., 2003</td>
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<td>Coenonympha pamphilus</td>
<td>Satyrinae</td>
<td>Grasses</td>
<td>Bromus erectus</td>
<td>600</td>
<td>Increased lipid concentration in adults, Higher no: of eggs in ovaries of females</td>
<td>Increased lipid concentration in adults, Higher no: of eggs in ovaries of females</td>
<td>Goverde et al., 2002</td>
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<td>Common blue butterfly</td>
<td>Polyommatus icarus</td>
<td>Lycaenidae</td>
<td>Birdfoot trefoil</td>
<td>Lotus corniculatus</td>
<td>600</td>
<td>Decreased N, Increased C:N Ratio and sugar concentration</td>
<td>Increased lipid concentration in adults, Higher no: of eggs in ovaries of females</td>
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<td>Increased carbon based defense compounds</td>
<td>Decreased N, increased stalk and total soluble sugars</td>
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<td>Tobacco caterpillar</td>
<td>Spodoptera litura</td>
<td>Noctuidae</td>
<td>Mung bean</td>
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<td>600 ± 50</td>
<td>Decreased N, increased stalk and total soluble sugars</td>
<td>Increased feeding and growth rate</td>
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<td>Upland cotton</td>
<td>Gossypium hirsutum</td>
<td>900</td>
<td>Decreased N, Increased C:N Ratio</td>
<td>25% increase in consumption Longer development time</td>
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<td>Beta vulgaris</td>
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<td>Increased stalk, soluble carbohydrate content</td>
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<td>Common milkweed</td>
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<td>700</td>
<td>Decreased N, Increased C:N Ratio, Higher above ground biomass</td>
<td>Density decreased, consumption increased and leaf area damaged increased by 33%</td>
<td>Hughes and Bazra, 1997</td>
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<td>Frankliniella occidentals</td>
<td>Thripidae</td>
<td>Common milkweed</td>
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<td>700</td>
<td>Density decreased, consumption increased and leaf area damaged increased by 33%</td>
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<td>Hughes and Bazra, 1997</td>
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<td>Curculionidae</td>
<td>European white birch</td>
<td>Betula pendula</td>
<td>700</td>
<td>Decreased N, flavonol glycosides Increased total phenolics, condensed tannins, (+)-catechin and cinnamoylquinic acids</td>
<td>Increased in stem, leaf total aerial biomass and specific leaf weight, decreased N and phenolics</td>
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<td>Green Leaf Weevil</td>
<td>Phylophorus maculicornis</td>
<td>Curculionidae</td>
<td>European white birch</td>
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<td>Decreased N, flavonol glycosides Increased total phenolics, condensed tannins, (+)-catechin and cinnamoylquinic acids</td>
<td>Increased in stem, leaf total aerial biomass and specific leaf weight, decreased N and phenolics</td>
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<td>Phratora vielliae</td>
<td>Chrysomelidae</td>
<td>Dark leaved willow</td>
<td>Salix myrsinfolia</td>
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<td>Reduced relative growth rate of larvae, increased consumption</td>
<td>Reduced relative growth rate of larvae, increased consumption</td>
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(Contd.)
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<th>CO₂ conc. (ppm)</th>
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<td>Neodiprion lecontei</td>
<td>Lobolly pine</td>
<td>Ambient + 300</td>
<td>Decreased N, Increased starch, Decreased monoterpenes. High starch:N ratios</td>
<td>Overall larval growth higher, consumption lower</td>
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<td>Red-headed pine sawfly</td>
<td>Neodiprion lecontei</td>
<td>Lobolly pine</td>
<td>650</td>
<td>Decreased N, Increased starch, High starch:N ratios</td>
<td>Increased consumption, increase in N utilization efficiency</td>
<td>Williams et al., 1994</td>
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<td>Cotton aphid</td>
<td>Aphis gossypii</td>
<td>Bt cotton</td>
<td>1050</td>
<td>Increased C:N Ratio. Plant height, biomass and leaf area were higher</td>
<td>Aphid fecundity significantly increased</td>
<td>Chen et al., 2005</td>
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<td></td>
<td>Aphididae</td>
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<td>Grain aphid</td>
<td>Stobion avenae</td>
<td>Spring wheat</td>
<td>750</td>
<td>Higher ear starch, sucrose, glucose, total nonstructural carbohydrates, free amino acids and soluble protein. Decreased N</td>
<td>Local populations increased, Alate aphids on sticky traps decreased, alate forms deposited more aphids on plants 20% reduction in nymph survival, delayed development</td>
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<td>Spittle bug</td>
<td>Cercopidae</td>
<td>Heath rush</td>
<td>600</td>
<td>Increased C:N Ratio, Reduced transpiration rates</td>
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<td>Quaking aspen</td>
<td>720</td>
<td>Decreased N, Higher levels of structural compounds</td>
<td>Decrease consumption and assimilation. Growth 15 times slower Slow development, low pupal weight</td>
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<td>Chrysonthemi</td>
<td>Agromyzidae</td>
<td>Common sowthistle</td>
<td>Ambient + 200</td>
<td>High C:N ratio, thicker leaves</td>
<td></td>
<td>Smith and Jones, 1998</td>
</tr>
</tbody>
</table>
schutz et al., 2003).

As in case of forest trees and grasses a nitrogen concentration decreased in cultivated plants like cotton, Gossypium hirsutum (Coviella and Trumble, 2000), mungbean, Vigna radiata (Srivastava et al., 2002), spring wheat, Triticum aestivum (Chen et al., 2004) and birdsfoot trefoil (Goverde et al., 2004). C:N ratio increased in cotton (Chen et al., 2005) and birdsfoot trefoil (Goverde et al., 2004). Starch concentration increased in mungbean (Srivastava et al., 2002), wheat (Chen et al., 2004) and common beet, Beta vulgaris (Caulfield and Bunce, 1994). There was an increase in sugars in mungbean (Srivastava et al., 2002) wheat (Chen et al., 2004) and birdsfoot trefoil (Goverde et al., 2004).

b) Effect on insects
Through host-plant

The impact of elevated carbon dioxide on host plants and insects is comprehensively reviewed and presented in Table 1. Among the orders of class insecta, Lepidoptera was mainly studied with gypsy moth Lymantria dispar and forest tent caterpillar, Malacosoma disstria were studied exclusively.

i) Lepidoptera

Elevated CO₂ had negative effect on larval performance of gypsy moth, which was studied extensively on an array of trees. Relative growth rate (RGR) declined by 30% on sessile oak, Quercus petraea and increased by 29 % on hornbeem, Carpinus betulus (Hattenschwiler and Schafellner, 2004). Decline in RGR was more on yellow birch, Betula allegheniensis compared to gray birch, Betula populifolia. The pupal mass declined by 38 % gray birch while there was no effect on pupal mass on yellow birch. The differential response was attributed to greater decline in nutritional quality of yellow birch than gray birch (Traw et al., 1996). The studies conducted with forest tent caterpillar, M. disstria indicate that larval feeding varies with host plant. Faster development time and 20% decrease in growth rate was observed on quaking aspen (Lindroth et al., 1993). No effect on the performance of the larvae was noticed on white oak, Quercus alba (Williams et al., 1998). Slower larval growth (Mevi-Schutz et al., 2003), increased lipid concentration and higher number of ovaries (Goverde et al., 2002) were observed in small heath, Coenonympha pamphilus feeding on grasses. Increased consumption by common blue butterfly, Polyommatus icarus larvae (Goverde et al., 1999), shorter development time and increased pupal weight (Bazin et al., 2002) were noticed when feeding on birdsfoot trefoil, Lotus corniculatus. Increased consumption by Spodoptera sps was observed on mungbean, Vigna radiata (Srivastava et al., 2002) and upland cotton, Gossypium hirsutum (Coviella and Trumble, 2000). Greater larval survival on common beet, Beta vulgaris (Caulfield and Bunce, 1994) and longer development time was noticed on upland cotton (Coviella and Trumble, 2000) (Table 1).

ii) Homoptera

The family aphididae in this order was widely studied, and mixed response of aphids was reported under elevated CO₂. As is evident from Table 1 Cotton aphid, Aphis gossypii fecundity significantly increased on cotton (Chen et al., 2005). Local populations of grain aphid, Sitobion avenae on spring wheat, Triticum avenae (Chen et al., 2004) and green peach aphid, Myzus persicae on annual blue grass, Poa annua increased under elevated CO₂ (Bezemer et al., 1998). Myzus persicae population on bittersweet (Solanum dulcamara) increased by 120% (Hughes and Bazzaz, 2001). Spittle bug (Neophaeinaeus lineatus) nymphal population was reduced by 20% and delayed development when they were fed with elevated CO₂ grown heath rush (Juncus squarrosus) (Brooks and Whittaker, 1999). Among five aphid-plant interactions tested by
Hughes and Bazzaz (2001) there was no effect of elevated CO₂ on three aphid-host plant interactions. *Aphis nerii* on common milkweed (*Asclepias syriaca*), *Aphis oenotherae* on common evening primrose (*Oenothera biennis*) and *Aulacorthum solani* on white shooting star (*Nicotiana sylvestris*).

**iii) Other Orders**

Red headed pine sawfly (*Neodiprion lecontei*) belonging to order hymenoptera when reared on elevated CO₂ grown loblolly pine (*Pinus taeda*) showed increased consumption, increased N utilization efficiency and overall larval growth (Williams et al., 1994; Williams et al., 1997). Decreased consumption and assimilation, 15 times slower growth of cranefly (*Tipula abdominalis*) belonging to order diptera on elevated CO₂ grown quaking aspen was observed (Tuchman et al., 2002). Chrysanthemum leafminer (*Chromatomyia syngenesiae*) grown on common sowthistle (*Sonchus oleracea*) developed slowly and had low pupal weight (Smith and Jones, 1998). In order Thysanoptera, thrips (*Frankliniella occidentalis*) density decreased, consumption increased and leaf area damage increased by 33% on elevated CO₂ grown common milkweed (Hughes and Bazzaz, 1997) as shown in Table 1.

**Direct effects**

Insects have been shown to respond directly to carbon dioxide concentrations. Wireworm larvae can locate a food source from distances of up to 20 cm and respond to a CO₂ concentration increase as small as 0.002% (Doane et al., 1975). The ability to locate host plants of some herbivores may be affected. Fluctuations in CO₂ density as small as 0.14% or 0.5 ppm were detected by the labial palps of *Helicoverpa armigera* (Stange, 1992). Other insects are able to locate their plant hosts following the plume of slightly higher CO₂ concentrations, as does the moth *Cactoblastis cactorum* (Bergoth) with its host plant *Opuntia stricta* (Stange 1992; Stange et al., 1995). *Diabrotica virgifera virgifera* (Le Conte) uses CO₂ concentrations in soil to locate corn roots (Strnad et al., 1986; Bernklau & Bjostad 1998).

**Effect of elevated temperature**

**a) Plants**

The consequence of rising atmospheric carbon dioxide would be an increase in ambient temperature as pointed by Arrhenius (in Thompson, 1989). But they are usually treated separately because of experimental difficulties of varying both independently (Whittaker, 1999). The effect of temperature on different host plants is reviewed here under.

Differential response was noticed due to elevation of temperature in different species. Temperature caused a decrease in foliar nitrogen in *Q. robur* (Dury et al., 1998; Buse et al., 1998), increased in *Cardamine hirsuta*, *Poa annua*, *Senecio vulgaris* and *Spergula arvensis* (Bezemer et al., 1998) and had no effect on red maple, *A. rubrum* and sugar maple, *A. saccharum* (Williams et al., 2000). The concentrations of Cinnamoylquinic acids decreased and Salidroside decreased in white birch, *Betula pendula* leaves under elevated temperature conditions (Kuoikkaren et al., 2003). Leaf water content of sugar maple leaves declined (Williams et al., 2000) and condensed tannin content increased in *Q. robur* (Dury et al., 1998).

**b) Herbivorous insects**

Temperature is identified as dominant abiotic factor directly affecting herbivorous insects. Temperature directly affects the development, survival and abundance of insects. The influence of elevated temperature on various insect species is presented below.

There was no effect of elevated temperature except early pupation on larvae of winter moth, *Operophthera brumata* feeding on oak leaves, *Q. robur* (Buse et al., 1998).
Larval development and adult fecundity of *O. brumata* was adversely affected by increased temperatures on *Q. robur* (Dury et al., 1998). The long-term exposure to a 3.5°C increase in temperature shortened insect development but had no effect on pupal weight. (Williams et al., 2003). Development time of the beetles *Octotoma championi* and *Octotoma scabripennis* feeding on *Lantana camara* was accelerated by approximately 10-13 days at the higher temperature. There was substantial mortality of the larvae under high temperature/ambient CO₂ treatment due to premature leaf loss by *L. camara* (Johns et al., 2003). The temperature enhancement increased the relative growth rate (RGR) of the larvae of chrysomelid beetle, *Phratora vitellinae* feeding on *S. myrsinifolia* (Veteli et al., 2002).

**DISCUSSION AND CONCLUSIONS**

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. In elevated CO₂ conditions across types of plants viz., forest trees, grasses and cultivated plants the change in phytochemistry of plants was significant. In majority of cases decrease in nitrogen, increase in condensed tannins, tremulin levels, starch, drymatter production and root shoot ratio was observed. These changes in phytochemistry of plants lead to deterioration of nutritional quality of plants.

The majority of the insects studied have been lepidopterans, which are represented by only nine families. Of these, the economically important Noctuidae have received the most attention. Most other orders are represented by only one or two species, nearly all of which are economically important agricultural pests. Remarkably, only three species in two families have been examined in the largest insect order, the Coleoptera, and Diptera is represented by just two species in two families. The above review information on effect of elevated CO₂ on insect pests revealed that the performance of the same insect varied from host to host indicating host species specificity. The effect of elevated CO₂ was significant across various species of lepidopterans. The response of insects varied differently and was not consistent across host plants (e.g., the effects of elevated CO₂ on gypsy moth) while the response of different insects feeding on same host was different (e.g., Differential response of insects feeding on Birch tree). The information on the response of aphids towards elevated CO₂ was of mixed type. All types of response (increase, decrease and no effect) on the population size of the aphids was observed due to elevated CO₂.

The analyzed data on impact of elevated CO₂ on insect pests indicated that the general decreases in foliar nitrogen concentration and increases 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 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 effects upon the pupal weights. The leaf-mining insects could only partially compensate by increased consumption and their 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.

In most of the studies on impact of elevated CO₂ on insect-plant interactions the insects in ambient conditions were fed with detached leaves of host plants grown under elevated CO₂. However, there are a few studies
in which both insects and host plants were exposed to elevated CO₂ but these studies couldn’t pinpoint the direct effects of elevated CO₂ on insects. Hence there is a need to further examine how insects get affected when exposed directly to elevated CO₂ concentrations.

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 increase 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 and Jones, 1998). Geographic distribution of insects will be affected by shifts in host-plant ranges. Scenarios like local extinctions, changes in endangered species status and altered pest status can be predicted (Coviella and Trumble, 1999). Plants and insects exposed to modified environmental conditions may lead to considerable advances in understanding the mechanisms of responses by both insects and plants, they do not necessarily predict the outcome of such interactions in real ecological changes in the open field, where expected change in plant-insect interactions may be buffered by many unknown interactions and other factors (Whittaker, 1999 and 2001).

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 and majority of our studies are from order Lepidoptera followed by Homoptera.

REFERENCES