

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

M. Sreenivasa Rao, M.A. Masood Khan, K. Srinivas,
M. Vanaja, G.G.S.N. Rao and Y.S. Ramakrishna

Central Research Institute for Dryland Agriculture (CRIDA)
Santoshangar, Hyderabad, A.P. - 500 059, India

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 chewers), 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 upto 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, *Brumus 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 fescue, *Festuca rubra* (Mevi-

Table 1. Impact of elevated CO₂ on insect-plant interactions

Insect		Host plant		CO ₂ conc. (ppm)	Effect on host plants		Impact on insects	Reference
Common name	Scientific name	Common name	Scientific name		CO ₂ conc. (ppm)	Effect on host plants		
Lepidoptera Gypsy moth	<i>Lymantria dispar</i>	Sessile Oak	<i>Quercus petraea</i>	530	42% increase in starch, decrease in N, increase in condensed tannins	Relative Growth Rate (RGR) reduced by 30%	Haitenschwiler and Schafellner, 2004	
Gypsy moth	<i>Lymantria dispar</i>	Red maple	<i>Acer rubrum</i>	Ambient + 300	Decreased N and C:N ratio	Reduced larval growth	Williams et al., 2000	
Gypsy moth	<i>Lymantria dispar</i>	White oak	<i>Quercus alba</i>	Ambient + 300	Decreased N, Higher total non structural carbohydrate: N ratio	Significant growth reduction of early instar larvae	Williams et al., 1998	
Gypsy moth	<i>Lymantria dispar</i>	Gray birch	<i>Betula populifolia</i>	700	Decrease in N, Increase in condensed tannins	38% smaller pupal mass Declined in relative growth rate	Traw et al., 1996	
Forest tent caterpillar	<i>Malacosoma distria</i>	Quaking aspen	<i>Populus tremuloides</i>	560	Decreased N, Increased tremulacin levels	No effect on larval performance	Kopper and Lindroth, 2003	
Forest tent caterpillar	<i>Malacosoma distria</i>	Quaking aspen	<i>Populus tremuloides</i>	642 ± 2	Decreased N, increased starch.	Fast development time, 20% lowered growth rate	Lindroth et al., 1993	
Small heath	<i>Coenonympha pamphilus</i>	Red fescue	<i>Festuca rubra</i>	750	Decreased N, Increased C:N Ratio	Larval growth slower	Meyr-Schutz et al., 2003	
Small heath	<i>Coenonympha pamphilus</i>	Grasses	<i>Bromus erectus</i>	600	Decreased N, Increased non structural carbohydrates and condensed tannins	Increased lipid concentration in adults, Higher no: of eggs in ovaries of females	Goverde et al., 2002	
Common blue butterfly	<i>Polyommatus icarus</i>	Bird'sfoot trefoil	<i>Lotus corniculatus</i>	600	Ratio and sugar concentration	Marginal negative effect on larval mass gain	Goverde et al., 2004	
Common blue butterfly	<i>Polyommatus icarus</i>	Bird'sfoot trefoil	<i>Lotus corniculatus</i>	700	Increased carbon based defense compounds	Greater pupal weight, shorter development time	Bazin et al., 2002	
Tobacco caterpillar	<i>Spodoptera litura</i>	Mung bean	<i>Vigna radiata</i>	600 ± 50	Decreased N, Increased starch and total soluble sugars	Increased feeding and growth rate	Srivastava et al., 2002	
Beet armyworm	<i>Spodoptera exigua</i>	Upland cotton	<i>Gossypium hirsutum</i>	900	Decreased N, Increased C:N Ratio	25% increase in consumption	Coviella and Trumble, 2000	
Beet armyworm	<i>Spodoptera exigua</i>	Common beet	<i>Beta vulgaris</i>	700	Increased starch, soluble carbohydrate content	Longer development time Greater larval survival	Caulfield and Bunce 1994	
Thysanoptera Western Flower Thrips	<i>Frankliniella occidentalis</i>	Common milkweed	<i>Asclepias syriaca</i>	700	Decreased N, Increased C:N Ratio, Higher above ground biomass	Density decreased, consumption increased and leaf area damaged increased by 33%	Hughes and Bazzaz, 1997	
Coloptera Green Leaf Weevil	<i>Phyllotribus maculicornis</i>	European white birch	<i>Betula pendula</i>	700	Decreased N, flavonyl glycosides increased total phenolics, condensed tannins, (+)-catechin and cinnamoylquinic acids	Weevils preferred leaves grown under elevated CO ₂ given a choice between treatments	Kuokkanen et al., 2003	
Willow beetle	<i>Phratora vitellinae</i>	Dark leaved willow	<i>Salix myrsinifolia</i>	700	Increase in stem, leaf total aerial biomass and specific leaf weight, decreased N and phenolics	Reduced relative growth rate of larvae, increased consumption	Veteli et al., 2002	

(Contd.)

Insect		Family		Host plant		CO ₂ conc. (ppm)	Effect on host plants	Impact on insects	Reference
Common name	Scientific name	Common name	Scientific name	Common name	Scientific name				
Hymenoptera Red-headed pine sawfly	<i>Neodiprion lecontei</i>	Diprionidae	Loblolly pine	Pinus taeda	Pinus taeda	Ambient + 300	Decreased N, Increased starch, Decreased monoterpenes, High starch:N ratios	Overall larval growth higher, consumption lower	Williams et al., 1997
Red-headed pine sawfly	<i>Neodiprion lecontei</i>	Diprionidae	Loblolly pine	Pinus taeda	Pinus taeda	650	Decreased N, Increased starch, High starch:N ratios	Increased consumption, increase in N utilization efficiency	Williams et al., 1994
Homoptera Cotton aphid	<i>Aphis gossypii</i>	Aphididae	Bt cotton	<i>Gossypium hirsutum</i>		1050	Increased C:N Ratio, Plant height, biomass and leaf area were higher	Aphid fecundity significantly increased	Chen et al., 2005
Grain aphid	<i>Sitobion avenae</i>	Aphididae	Spring wheat	<i>Triticum aestivum</i>		750	Higher ear starch, sucrose, glucose, total nonstructural carbohydrates, free amino acids and soluble protein, Decreased N	Local populations increased, Alate aphids on sticky traps decreased, alate forms deposited more aphids on plants	Chen et al., 2004
Spittle bug	<i>Neophilaenus lineatus</i>	Cercopidae	Heath rush	<i>Juncus squarrosus</i>		600	Increased C:N Ratio, Reduced transpiration rates	20% reduction in nymph survival, delayed development	Brooks and Whittaker, 1999
Diptera Crane fly	<i>Tipula abdominalis</i>	Tipulidae	Quaking aspen	<i>Populus tremuloides</i>		720	Decreased N, Higher levels of structural compounds	Decrease consumption and assimilation, Growth 15 times slower	Tuchman et al., 2002
Chrysanthemum leafminer	<i>Chromatomyia syngenesiae</i>	Agromyzidae	Common sowthistle	<i>Sonchus oleraceus</i>		Ambient + 200	High C:N ratio, thicker leaves	Slow development, low pupal weight	Smith and Jones, 1998

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 hornbeam, *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, *Polymmatius 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 (*Neophilaenus 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 crane fly (*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 oleraceus*) 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 (Kuokkanen *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, *Operophtera 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, tremulacin 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 (eg. The effects of elevated CO₂ on gypsy moth) while the response of different insects feeding on same host was different (eg. 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 with majority of our studies are from order Lepidoptera followed by Homoptera.

REFERENCES

- Agrell, J. *et al.* (2005). *Glob. Change Biol.*, 11(4): 588-599.
 Bazin, A. *et al.* (2002). *Ecol. Ent.*, 27: 271-278.
 Bernklau, E.J. and Bjostad, L.B. (1998). *J. Econ. Ent.*, 91: 444-456.
 Bezemer, T.M. *et al.* (1998). *Oecologia.*, 116: 128-135
 Bezemer T.M. and Jones T.H. (1998). *Oikos.*, 82: 212-222.
 Brooks, G.L. and Whittaker, J.B. (1999). *Glob. Change Biol.*, 5: 395-401.
 Buse, A. *et al.* (1998) *Func. Ecol.*, 12: 742-749.
 Butler, G.D. Jr. *et al.* (1986). *Env. Ent.*, 15: 61-63.
 Caulfield, F. and Bunce, J.A. (1994). *Env. Ent.*, 23: 999-1005.
 Chen, F.J. *et al.* (2004). *J. Appl. Ent.*, 128: 723-730.
 Chen, F. *et al.* (2005). *Env. Ent.*, 34(1): 37-46.
 Coviella, C.E. and Trumble, J.T. (2000). *Biocontrol.*, 45: 325-326.
 Coviella, C.E. and Trumble, J.T. (1999). *Cons. Biol.*, 13(4): 700-712.
 Doane, J.F. *et al.* (1975). *Canad. Ent.*, 107: 1233-1252
 Dury, S.J. *et al.* (1998). *Glob. Change Biol.*, 4: 55-61.

- Goverde, M. *et al.* (1999). *Func. Eco.*, **13**: 801-810.
- Goverde, M. *et al.* (2002). *Ecology.*, **83**: 1399-1411.
- Goverde, M. *et al.* (2004). *Oecologia.*, **139**: 383-391.
- Hattenschwiler, S. and Schafellner C. (2004). *Glob. Change Biol.*, **10**: 1899-1908.
- Holton, K.M. *et al.* (2003). *Oecologia.*, **137**: 233-244.
- Hughes, L. and Bazzaz F.A. (2001). *Ent. Exp. Appl.*, **99**: 87-96.
- Hughes, L. and Bazzaz, F.A. (1997). *Oecologia.*, **109**: 286 -290.
- Hunter, M.D. (2001). *Agri. and Forest Ent.*, **3**: 153-159.
- IPCC (2001). *Climate Change 2001: Intergovernmental Panel on Climate Change*, Geneva.
- Johns, C.V and Hughes, L. (2002). *Glob. Change Biol.*, **8**: 142-152.
- Johns.C.V. *et al.* (2003). *Ent. Exp. Appl.*, **108**: 169-178.
- Kopper, B.J. and Lindroth, R.L. (2003). *Oecologia.*, **134**: 95-103.
- Kuokkanen, K. *et al.* (2003). *Agri. and Forest Ent.*, **5**: 209-217.
- Lindroth, R.L. *et al.* (1993). *Ecology*, **74**(3): 763-777.
- Mevi-Schutz, J. *et al.* (2003). *Behav. Ecol. Sociobiology*, **54**: 36-43
- Roth, S.K. and Lindroth, R.L. (1995). *Glob. Change Biol.*, **1**: 173-182
- Smith, P.H.D. and Jones, T.H. (1998) *Glob. Change Biol.*, **4**: 287-291
- Srivastava, A.C. *et al.* (2002). *Curr. Sci.*, **82**(9): 1148-1150.
- Stange, G. *et al.* (1995). *Oecologia.*, **102**: 341-352.
- Stange, G. (1992). *J. Comp. Phys. A: Sensory Neural and Beh. Phys.*, **171**: 317-324.
- Strnad, S.P. *et al.* (1986). *Env. Ent.*, **15**: 839-842.
- Thompson, R.D. (1989). *Progr. Physic. Geogr.*, **13**: 315-347.
- Traw, M.B. *et al.* (1996). *Oecologia.*, **108**: 113-120.
- Tuchman, N.C. *et al.* (2002). *Glob. Change Biol.*, **8**: 163-170.
- Veteli T.O. *et al.* (2002). *Glob. Change Biol.*, **8**(12): 1240-1252.
- Watt, A.D. *et al.* (1995). In: *Insects in a Changing Environment* (Harrington, R. and Stork, E. eds), Symp. Royal Ent. Soc. Acad. Press, London, pp. 198-217.
- Whittaker, J.B. (2001). *J. Ecol.*, **89**: 507-518.
- Whittaker, J.B. (1999). *Eur. J. Ent.*, **96**: 149-156.
- Williams, R.S. *et al.* (2003). *Oecologia.*, **137**: 114-122.
- Williams, R.S. *et al.* (2000). *Glob. Change Biol.*, **6**: 685-695.
- Williams, R.S. *et al.* (1998). *Glob. Change Biol.*, **4**: 235-246.
- Williams, R.S. *et al.* (1997). *Env. Ent.*, **26**(6): 1312-1322.
- Williams, R.S. *et al.* (1994). *Oecologia.*, **98**: 64-71.