

Impacts of Climate Change on Plant-Herbivore-Natural Enemy Interactions

Chandra Kanta Dash[1,2,3,4,5,6] Bamisope Steve Bamisile [1,2,3,4,5] Sangeeta Mitra[7]
Muhammad Qasim[1,2,3,4,5] Mubasher Hussain[1,2,3,4,5] Muhammad Salman Hameed[1,4]
Liande Wang [12345*]
1. Plant Protection College, Fujian Agriculture and Forestry University, Fuzhou 350002, China
2. Key Laboratory of Integrated Pest Management for Fujian-Taiwan Crops, Ministry of Agriculture, Fuzhou 350002, China
3. Key Laboratory of Biopesticide and Chemical Biology, Ministry of Education, Fuzhou 350002, China
4. Institute of Applied Ecology and Research Centre for Biodiversity and Eco-Safety, Fujian Agriculture and Forestry University, Fuzhou 350002, China
5. State Key Laboratory of Ecological Pest Control for Fujian and Taiwan Crops, Fujian Agriculture and Forestry University, Fuzhou 350002, China
6. Faculty of Agriculture, Sylhet Agricultural University, Sylhet 3300, Bangladesh
7. College of Horticulture, Fujian Agriculture and Forestry University, Fuzhou 350002, China

Abstract
Over the last century, the global climate has been changing rapidly. Numerous anthropogenic activities have caused an unprecedented increase in the concentrations of atmospheric CO_2 with other gases which consequently resulted in increased temperature and altered precipitation. In agriculture ecosystem, insect population dynamics are regulated by top-down forces i.e. predators and parasitoids feed on them and bottom-up forces where host plants regulate herbivore population. Climate change may directly affect all the organism in the trophic system at the same time changes in the first trophic level may subsequently bring changes in the following trophic levels which may further have implications on ecosystem services. Understanding of the way climate change factors may affect tri-trophic interactions may help farmers to adopt future pest management strategies. This review focuses on direct and mediated effects of climate change on plant-herbivore-natural enemy interactions as well as provides some suggestions for future research direction on predicting adverse effects of climate change on tri-trophic interactions.
Keywords: global warming, carbon di oxide, temperature, Ozone, predator, parasitoid

1. Introduction

Since the beginning of nineteenth century, the concentration of greenhouse gases, particularly carbon dioxide (CO_2), has increased in the atmosphere which has also increased temperature, causing a wide range of changes to the environment at a global scale (IPCC 2013). For example, the atmospheric carbon dioxide (CO_2), has been increased to ~400 ppm in 2011 from ~310 ppm in 1950 and which is estimated to reach at levels of 421–936 ppm by the end of twenty-first century (IPCC 2013). The quantities of other gases, like ozone (O_3) and nitrogen dioxide (NO_2), have also increased because of human interventions (Karnosky *et al.* 2007).

Climate change can significantly affect living communities in trophic chain directly and indirectly which has been documented over the years. It can affect the physiology, phenology and distribution of living species in any trophic level directly and at the same time it can cause further changes in diversity and composition at upper trophic levels interlinked with each other. For example, in agriculture ecosystem, herbivore population is regulated by "top down" force by natural enemies like, predators and parasitoids which consume herbivores, thereby benefit first trophic level which is known as trophic cascade (Hairston *et al.* 1960; Oksanen *et al.* 1981). Another force is "bottom up" which focuses on management of first trophic level to impair the performance of herbivores on them.

In this review, we highlight the effects of climate change on plant-insect and multi-trophic interactions. Specifically, we address the direct and mediated effects of climate change in the form of increased CO_2, O_3 and temperature on plants, herbivores and natural enemies. Firstly, we discuss the direct and mediated effect on plant-insect interactions and secondly, we confer how higher trophic level organism can be affected directly and indirectly in the light of climate change. Finally, we provide some suggestions and future research directions on this topic need to be addressed.

2. Direct and mediated effect of climate change on plant-insect interactions

Climate change can directly affect crop plants through modification of physiology, morphology, growth, development, phenology and chemistry which have been reviewed by many authors (Fuhrer 2003; Garrett *et al.* 2006; Aguilar-Fenollosa & Jacas 2014). Increased photosynthesis, increased water use efficiency have been reported under elevated CO_2 (von Tiedemann & Firsching 2000). Additionally, plant biomass (e.g. leaves, branches) also increased when plants are exposed to increased CO_2 (Pritchard *et al.* 1999). The food quality for insects on plants depends on the of primary metabolites concentration, especially nitrogen, carbohydrates which act as feeding stimulants as well as secondary metabolites like allelochemicals that can deter feeding. Elevated CO_2 effect plants by increasing C:N ratio in leaf tissue with increased growth rate and lower nutritional value (DeLucia *et al.* 2012).These can result in higher crop productivity with plant biomass which can lead increased herbivory (Robinson *et al.* 2012; Dyer *et al.* 2013; Zavala *et al.* 2013). Increased consumption of plant foliage has been documented by chewing insects under elevated CO_2 (Bezemer *et al.* 1998). Due to decrease in the nutritional quality in foliage insect consume more food to meet the critical nutrient limitations is known as "compensatory feeding" which can cause greater damage to crops (Cornelissen 2011). The effects of increased CO_2 on sap-feeders however vary according to the type of plant tissue they feed on (Bezemer *et al.* 1998). A review by Holopainen (2002) points increased, decreased, or unchanged performance of aphid when reared on plants under elevated CO_2 compared with ambient CO_2 levels. Generally, development time of aphid is reduced when reared under elevated CO_2 conditions (Bezemer *et al.* 1998). Many studies so far have addressed the effects of elevated CO_2 on herbivore mediated by host plant changes due to climate change (Stiling & Cornelissen 2007a). In a meta-analysis reported the effects of elevated CO_2 on insect pests and their feeding patterns from 75 studies with 405 independent comparisons. They showed significant responses of insect pests to increased CO_2 with a 22% decline in insect abundance, 17% increase in consumption rate, 4% increase in development time, 9% decrease in relative growth rate and 5% reduction in pupal weight.

Besides increased CO_2 another climate change element is elevated tropospheric ozone (O_3) concentration. Tropospheric O3 has substantial impact on agricultural and forest ecosystem (Lindroth 2010). O_3 enters into leaves through stomata, which creates reactive oxygen species and oxidative stress, thereby decreasing photosynthesis, plant growth and biomass production (Ainsworth *et al.* 2012). O_3 also influence plant-insect interactions through modifying the biosynthetic pathway of secondary metabolites (Holopainen 2002), thereby changing plant volatile cues and consequently affecting the host locating by phytophagous insects (Pinto *et al.* 2010). Natural enemies use this secondary plant metabolites as synomones to find insects pests (L E M Vet & Dicke 1992)which can be obstructed due to modification in O_3 concentrations in the atmosphere (Bidart-Bouzat & Imeh-Nathaniel 2008; Lindroth 2010; Pinto *et al.* 2010).

Since temperature has direct influence on plant and insect physiology, fluctuation of temperature may results marked changes in the interaction between plant and herbivore. For instance, changes in temperature may lead to mismatches between plant and insects. An increase in winter temperature can cause phonological mismatch between the winter moth and its host plant (Dewar & Watt 1992).There are few studies on how elevated temperature influence the secondary metabolites in plants and how these may affect plant-herbivore interactions. Studies assessed the effects suggest that the outcome depends on plant species and chemical types. Variable results have been obtained in terms of phenolic compounds, glucosinolates and volatile organic compounds like terpenes (Snow *et al.* 2003; Hansen *et al.* 2006; Velasco *et al.* 2007). For example, phenolics have been observed to decline whereas, terpenoids generally increased when plant exposed under elevated temperature (Bidart-Bouzat & Imeh-Nathaniel 2008). Increased temperature has been recorded to influence glucosinolates production in broccoli (*Brassica oleracea* var. *italica*) and *Arabidopsis thaliana* (Matusheski *et al.* 2004). There is a dearth of information on potential effect of elevated temperature in production of plant secondary metabolites and subsequent effect on herbivore. It is hypothesized that increased temperature results increased production of secondary metabolite which can adversely affect herbivore performance (Dury *et al.* 2010).

Direct effect of climate change on herbivores has been well studied and documented (Stiling & Cornelissen 2007b; Lindroth 2010; Ainsworth *et al.* 2012; Aguilar-Fenollosa & Jacas 2014). Arthropods as poikilothermic organisms, their body temperature is highly dependent on the ambient temperature. For these, many of the key processes such as life-history parameters, physiology, metabolic rate, development times, behavior, reproduction, survival, voltinism etc. are mediated by temperature (Clarke 2003; Beveridge *et al.* 2010; Romo & Tylianakis 2013). Metabolic rate of insect is highly sensitive to temperature, which doubles with an increase of 10°C in temperature (Berggren *et al.* 2009; Ainsworth *et al.* 2012). Higher metabolic rate cause higher consumption, development rates and higher growth. Faster development rate, consequently may lead to increased population with reduced generation time thereby decreased exposure to natural enemies. Global warming has substantial effects on voltinism of the herbivores which is the number of generations can be completed in a single season. Warm temperature accelerates insect development reducing cue that triggers for the initiation of diapause. Fluctuations in the voltinism patters have been reported due to increased temperature (Altermatt 2010).

Limited research have been carried out on the direct effect of elevated CO_2 on insects (Guerenstein & Hildebrand 2008). Insects such as moths, flies, and hematophagous insects use atmospheric CO_2 to find food sources and oviposition sites which can be directly affected by elevated CO_2 (Guerenstein *et al.* 2004; Guerenstein & Hildebrand 2008). Oviposition behavior of herbivores can the influenced by CO_2 (Stange 1996; Stange 1999). For example, fruit flies use respiratory CO_2 for the oviposition in the fruit skin (Stange 1999).

Combined effect of climate change factors in agricultural ecosystem is another issue of concern raised by the IPCC. Not only CO_2, but also surface temperature, O_3 and other gas in combination can affect different organism in trophic level. In a meta-analysis (Zvereva & Kozlov 2006) showed 42 studies that used increased CO_2 and temperature and found reduced nitrogen concentration under both increased CO_2 and increased temperature conditions. C: N ratio on the other hand increased under increased CO_2 and increased temperature treatments, but carbon-based compound did not show any significant change to increase in both factors. Insects survival, growth rate, fecundity were negatively and positively affected by individual increase in CO_2 and temperature. However, when exposed to two factors simultaneously, these two factors did not show any significant change in the performance. Few studies have been conducted so far addressing simultaneous effects of CO_2 and O_3 (Elena *et al.* 2010). When plants were exposed to both CO_2 and O_3 there was interaction among the changes caused when plants were exposed individually. (Elena *et al.* 2010). Plant selection by herbivore is influenced by CO_2 and O_3. Studies so far conducted have concluded no difference between both factors for insects from forest ecosystem in temperate zone.

3. Effect of climate change on multi-trophic interactions

Predator and parasitoid efficiency in a tri-trophic interaction may be altered by climate change drivers (Sun *et al.* 2011b). It has been well established that plant exposed to elevated CO_2 could alter the production of plant primary metabolites, as well as secondary metabolites (Klaiber *et al.* 2013b) which have an important role in plant defense against herbivore (Bennett & Wallsgrove 1994). Parasitoids could also be affected by plant mediated changes in herbivore host (Ode 2006; Harvey *et al.* 2011; Kos *et al.* 2012). Although there are many publications on how climate change effects plant and herbivore interaction, very few research work has been conducted on climate change effect on higher trophic level because of the difficulty in assessing the multiple factors together. Additionally, mediated effect of climate change on the higher trophic level can affect plant performance and thereby ecosystem functions via trophic cascades. For instance, direct positive or negative effects of predator and parasitoid on herbivore can lead to indirect positive or negative effect on plants.

Elevated CO_2 affects insect-plant interactions through changing food consumption and development rates of herbivore with positive, negative or neutral effect which can affect natural enemies via cascade effects. For instance, development period of aphid parasitoid *Lysiphlebia japonica* Ashmead was significantly increased under elevated CO_2 although for two out of three tested genotypes(Sun *et al.* 2011a). Similar effects were also recorded on *Cotesia plutellae* (Kurdjumov), a Lepidopteran parasitoid (Vuorinen *et al.* 2004). Increased parasitism rate under elevated CO_2 concentrations has been recorded for the parasitoid *Aphidius picipes* (Nees) on the grain aphid *Sitobion avenae* (F.) with decreased abundance of newly emerged adult parasitoids(Chen *et al.* 2007). On the other hand no difference in the rate of parasitism was observed for the parasitoid *Aphidius matricariae* Haliday under elevated and ambient CO_2 (Bezemer *et al.* 1998). However, a decrease parasitism rate was recorded for *Diaretiella rapae (Mc'Intosh)* with short-lived emerging adult parasitoid under elevated CO_2 concentrations (Klaiber *et al.* 2013a).

Several studies indicated that secondary metabolites production by the plants could be altered when plants are exposed and grown under elevated CO_2 (Klaiber *et al.* 2013a; Klaiber *et al.* 2013c) thereby affecting plant's defense against herbivores. Natural enemies could also be affected by this alteration through their host (Harvey *et al.* 2011; Kos *et al.* 2012), although very few studies have been conducted on this interaction. Recently (Klaiber *et al.* 2013a) studied the effect of elevated CO_2 on the tri-trophic interaction between *Brassica*, aphid and parasitoid *D. rapae. Brassica* plants were exposed to elevated CO_2 for about ten weeks. Glucosinolate content was found to be increased in the plants grown under elevated CO_2 which is the main secondary metabolite in *Brassica.* When aphid was exposed to that plants, attained reduced size when feed on plant grown elevated CO_2. Alongside, suppression of the aphid by parasitoid *D. rapae* was reduced as aphid host fed on glucosinolate-rich plants was recorded smaller in size.

Few studies have been conducted on predators in comparison to parasitoids to know the effects of climate change on higher trophic level and the results are highly variable. For example, development time of aphidophagous predatory beetle *Propylaea japonica* (Thunberg) and *Leis axyridis* (Pallas) (Coleoptera: Coccinellidae) were significantly enhanced under elevated concentrations of CO_2 (Chen *et al.* 2005; Gao *et al.* 2008) whereas, development time and predatory efficacy of lacewing *Chrysopa sinica* (Tjeder) (Neuroptera: Chrysopidae) were significantly decreased under elevated concentrations of CO_2 (Gao *et al.* 2010). All of above mentioned studies indicate the variation in the parasitism rate under elevated CO_2. All of these above-mentioned studies represents the major variability in the performance of natural enemies under elevated CO_2.

In ecosystem, predator, parasitoids, and pathogens play a significant role in regulating populations of insect herbivore (Kapari *et al.* 2006). Climate change can affect these higher trophic level organisms. For example, similar to insects herbivore, the elevated temperature may increase the metabolic rate and development of predators and parasitoid with increased generation time per year (Hance *et al.* 2007). Likewise, efficacy of entomopathogens could be influenced due to increased temperature and precipitation which is important biocontrol agent against herbivore. For example, a fungal pathogen *Entomophaga maimaiga* Humber, Shimazu et Soper, which regulates gypsy moth (*Lymantria dispar* (L.) is believed to be influenced by available temperature and water (Siegert *et al.* 2009).

In general, plants grown under elevated CO_2 become nutritionally poor with decreased nitrogen which leads to increased foliage consumption by the herbivore. However, increased consumption do not necessarily compensate the reduced food quality as it can decrease the development of herbivore feeding on them. For example, it has been observed that insect size is reduced when they feed on plants grown under elevated CO_2 (Kuokkanen K 2001), and take longer time to develop with decreased fecundity and increased mortality. Performance of natural enemies may decrease as the quality of their host become poor (Hansen *et al.* 2006). Although predators and parasitoid also can increase their consumption to compensate this to improve pest control (Chen *et al.* 2005). On the other hand, predator and parasitoid may need more time to search for their prey host due to increased foliage of the plants. The efficacy of natural enemies may decrease when they have to feed on poor quality host and also prey hosts are difficult to locate. Conversely, natural enemy performance might be increased as because prey size is smaller and increase development time of prey which make hosts longer time available for the prey for predation and parasitism. All of these observation illustrates the complexity of the climate change on tri-trophic interaction to predict especially when increased temperature and CO_2 coupled with lower precipitation and other factors of climate change.

Plants constitutively release blends of volatile organic compound (VOCs) (Stange 1997) and under herbivore attack plants release more diverse and larger quantity of those compounds (Stange 1999) which attracts wide range of predators and parasitoids to find their prey host. This is known as indirect defense for the plants. Such chemicals are mainly green leaves volatiles, terpenoids, aldehydes, alcohol and their derivatives (Stange 1992). Elevated temperature and CO_2 can affect the production of these compound thereby affecting the indirect plant defense. For example, Brassicaceae release glucosinolate compounds constitutively and release of this compounds are far increased when plant is under attack by herbivore (Blande *et al.* 2004). These compounds release rate is reported to increase under elevated CO_2 (Bidart-Bouzat & Imeh-Nathaniel 2008) which can be positive for the natural enemies but at the same time, higher temperature and other air-pollutants can result in modification and degradation in concentration and attraction for natural enemies (Elena *et al.* 2010).

4. Conclusion

Several above-cited examples clearly demonstrated that climate change represents a major challenge to biodiversity and can affect the living organisms across the trophic level. As because, atmospheric CO_2 and other gases including temperature can directly influence higher trophic levels i.e. predator and parasitoids also indirectly through climate change mediated effect on host plants and insect herbivores, it is therefore very crucial to study the impact of climate change on complete trophic system including plant, insect and natural enemies. But such studies are very few. Only limited number of studies have been carried out on trophic interactions including three or more levels of a food chain. Rather, the main focus has been on two trophic level interactions, little attention has been paid to member of higher trophic level organism. It is relatively well understood how elevated CO_2 and temperature independently affect primary chemistry in plant leaves however, little is known about the effect on secondary chemistry in plants which have direct implication in tritrophic interactions. Recent studies on the effect of elevated CO_2 and temperature on hormonal signaling modulation and its consequence on plant defense improve our understanding to predict how climate change will affect plant-herbivore interactions. So far few studies have investigated the combined effects of two or more climate change drivers like CO_2 and temperature simultaneously. Several authors have concluded that temperature does not influence the response of plant and herbivore to elevated CO_2, while others showed strong influence of CO_2 and temperature. Studies reporting the impact of increased CO_2 under elevated temperatures are much more common but this is of limited importance as temperature can strongly modify the response to increased CO_2. For example, it is generally accepted that, one of the common impact of elevated CO_2 on herbivores is prolonged development of insect pests with increased exposure to predators and parasitoids, which can be further minimized by elevated temperature through decreasing the development time. Therefore, more emphasis should be given on assessment of multiple environmental factors simultaneously to get a comprehensive picture of how tritrophic interactions can be affected by the climate change which have implications on pest management and ecosystem service.

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