Neotropical Entomology

ISSN: 1519-566X

journal homepage: www.scielo.br/ne

FORUM

Climate Change and Its Effects on Terrestrial Insects and Herbivory Patterns

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Keywords
Elevated CO_2, insect-plant relationships, trophic interaction

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Edited by Fernando L Cônsoli – ESALQ/USP

Received 24 February 2011 and accepted 12 March 2011

Abstract

Climate change and extreme weather events affect plants and animals and the direct impact of anthropogenic climate change has been documented extensively over the past years. In this review, I address the main consequences of elevated CO_2 and O_3 concentrations, elevated temperature and changes in rainfall patterns on the interactions between insects and their host plants. Because of their tight relationship with host plants, insect herbivores are expected to suffer direct and indirect effects of climate change through the changes experienced by their host plants, with consequences to population dynamics, community structure and ecosystem functioning.

Introduction

Climate change and extreme weather events affect plants and animals and the direct impact of anthropogenic climate change has been documented on every continent, in every ocean, and in most major taxonomic groups (Parmesan 2006 and references therein). As a consequence of recent human activities and its effects on global climate, plants will face new environmental conditions in the near future, such as elevated CO_2 and O_3 concentrations, elevated temperature and UV radiation, and changes in rainfall patterns over the seasons. Insects represent almost half of the biodiversity so far described (Speight *et al* 1999) and are central pieces on ecosystem structure and function (Crawley 1983). Because of their tight relationship with host plants, insect herbivores are expected to suffer direct and indirect effects of climate change through the changes experienced by their host plants.

Global climatic changes are expected to impact insect-plant interactions in several ways. They might affect insects directly, through changes in physiology, behavior and life history parameters, as well as indirectly, through changes experienced by host plants in their morphology (Barnes *et al* 1988, Morrison & Morecroft 2006, Lake & Wade 2009), biochemistry (e.g., Yuan *et al* 2009), physiology (Gifford *et al* 1996, Yadugiri 2010) and patterns of richness, diversity and abundance (Thuiller *et al* 2005, Kazakis *et al* 2007). Insects play important roles in ecosystem services, acting as herbivores, pollinators, predators and parasitoids, and changes in their abundance and diversity have the potential to alter the services they provide (Hillstrom & Lindroth 2008). The number of studies reporting climate change effects on insects has rapidly increased during the past 20 years. A keyword search for “climate change” and “insects” in the Science Citation Index Expanded (1991-2010) resulted in almost 500 references, with a sharp increase over the past five years (277 studies from 2006 to 2010, compared with 102 references from 2001 to 2005). As a result, a great body of literature has accumulated and several other authors reviewed the topic, both qualitatively (e.g., Watt et al 1995, Lindroth 1996, Bezemer & Jones 1998, Parmesan 2006, Tylianakis *et al* 2008) and quantitatively, using meta-analytical techniques (e.g., Zvereva & Kozlov 2006, Stiling & Cornelissen 2007, Wu *et al* 2011).

In this review, I aim to address the main changes herbivorous insects will face with the expected changes in host plant abundance, chemistry, physiology and/or morphology after global climatic changes such as those already experienced by terrestrial plants. These include changes in the concentration of gases such as CO_2 and O_3, as well as changes in temperature, rainfall patterns and radiation, and changes in the synchrony between insects and host plants that might be caused by any of the aforementioned changes. This review focuses only on terrestrial insects, although it has been acknowledged that aquatic insects have also experienced changes in abundance, diversity and feeding patterns due to changes in resources on aquatic environments such as temporary ponds, lakes and rivers (e.g., Brown *et al* 2007, Hering *et al* 2009, Woodward *et al* 2010).

Effects of Elevated CO_2 on plant Chemistry and Herbivore Performance

Currently, there is great concern for the effects of elevated carbon dioxide concentrations since CO_2 concentration rose about 30% from pre-industrial concentration, and CO_2 level is continuously increasing because of anthropogenic activities. The expected concentration of CO_2 in the year of 2100 ranges from 540 to 970 ppm compared to about 280 ppm in the pre-industrial era (Stiling *et al* 1999), and changes in plant quality due to elevated CO_2 may affect herbivory patterns and insect richness, abundance and/or diversity. Many studies have now addressed effects of CO_2 enrichment on herbivores mediated by changes in host plant characteristics and how herbivores respond to these altered conditions (reviewed by Stiling & Cornelissen 2007). Enriched atmospheric CO_2 influences plant physiology, with direct consequences for plant productivity and biochemical composition. Plant chemical composition influences positive and negative trophic interactions, as well as decomposition, which will then feedback to atmospheric CO_2 concentrations (Lindroth 2010).

Although the effects of enriched CO_2 on plants are variable and not universal, plants growing under elevated CO_2 conditions often exhibit enhanced photosynthetic activity, increased productivity and increased leaf area or biomass (e.g., Hughes & Bazzaz 1997, Owensby *et al* 1999). Elevated CO_2 might also alter plant primary and secondary metabolism. The increase in carbon availability for plant tissues and the consequent changes in the C/N ratio impact nitrogen levels in plant tissues, causing a "nitrogen dilution effect". This low nitrogen concentration, coupled with a high C/N ratio and its potential effects on plant secondary metabolism, means a lowered concentration of leaf protein and therefore reduced nutritive value to herbivores (Lincoln *et al* 1986). Elevated CO_2 conditions are also expected to cause changes in plant secondary chemistry due to an increased carbon supply and allocation to the production of carbon-based secondary and structural compounds.

How do herbivorous insects respond to these changes in host plants? In a recent meta-analytical study, Stiling & Cornelissen (2007) reviewed the evidence for the indirect effects of elevated CO_2 on several aspects of insect life history parameters and herbivory patterns from 75 studies that generated 405 independent comparisons. It was previously suggested that herbivores would respond to altered plant primary and secondary metabolism under elevated CO_2 by increasing food consumption to compensate for the plant lowered nutritional quality (e.g., Fajer 1989, Marks & Lincoln 1996), by reducing their growth rates and prolonging their development time (e.g., Smith & Jones 1998, Goverde & Erhardt 2003), and by reducing food conversion efficiency (e.g., Lawler *et al* 1997, Brooks & Whittaker 1998). These reductions in herbivore performance under CO_2 enrichment would have the potential to increase mortality imposed by natural enemies (e.g., Fajer 1989, Stiling *et al* 2003), ultimately reducing herbivore abundance, richness and diversity if compared to ambient CO_2 conditions (Fig 1).

But, by how much are insects affected by elevated CO_2 conditions? In general, the results of the meta-analysis of Stiling & Cornelissen (2007) demonstrated strong responses of herbivores to elevated CO_2 conditions, such as 1) a decline in insect abundance of almost 22.0% in elevated as compared to ambient CO_2 conditions, 2) an increase of almost 17.0% in consumption rates, 3) an increase of almost 4.0% in development time, 4) a decrease of 9.0% in relative growth rate and of 5) 5.0% in pupal weight. When results for the effects of CO_2 were partitioned into feeding guilds (e.g., chewers, miners, gallers), stronger and significant effects of elevated CO_2 were observed for chewers compared to other feeding guilds. However, the vast majority of studies so far conducted to address effects of elevated CO_2 on herbivores have been biased to free-feeding herbivores (chewers represented 60% of the comparisons reviewed by Stiling & Cornelissen 2007) and many more studies are necessary to obtain a clearer pattern of CO_2 effects on other guilds of herbivores. For sap-sucking insects such as aphids, for example, it has been demonstrated that despite the studies carried out to evaluate aphid responses to changes in CO_2 concentrations in the atmosphere, it is not yet possible to establish general rules nor to predict responses of aphid species, populations or even clones to global climatic changes (Hullé *et al* 2010).

Effects of Increased O_3 in the Troposphere

Besides elevated CO_2, another change plants - and indirectly insects - will face in the near future is elevated ozone (O_3) concentration in the troposphere. Tropospheric ozone is recognized as the most damaging and widespread pollutant affecting agricultural and

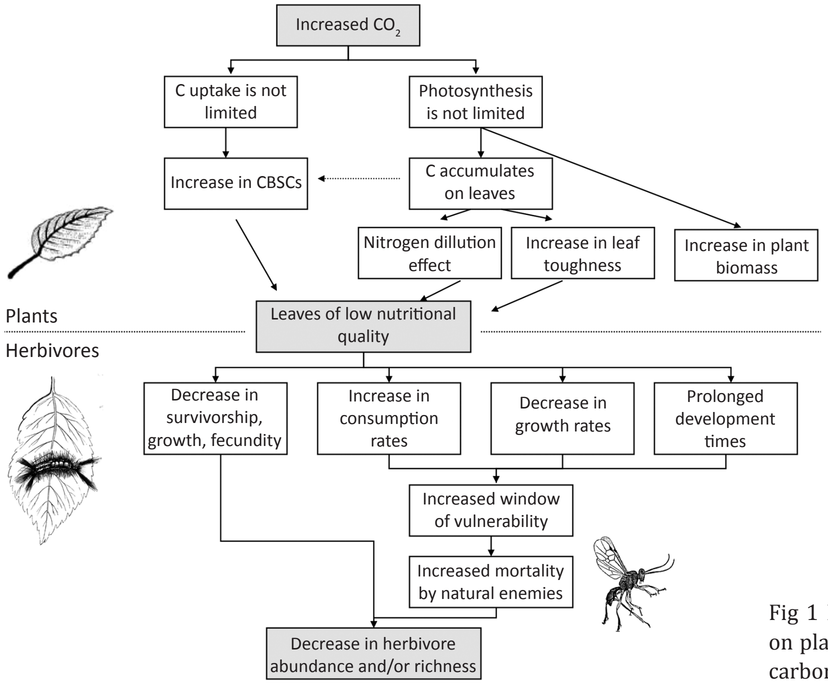

Fig 1 Predicted effects of elevated CO_2 conditions on plants and insect herbivores (C: carbon, CBSCs: carbon-based secondary compounds).

forested ecosystems in North America and Europe (Witting *et al* 2009, Lindroth 2010). Concentrations of O_3 have increased almost 40% since the pre-industrial era (Lindroth 2010) and are expected to directly impact plant species and indirectly impact herbivorous insects.

O_3 elicits a cascade of damaging physiological consequences in plants, compromising photosynthesis and decreasing the supply of carbohydrates in the entire plant (Wittig *et al* 2009, Lindroth 2010). Although elevated CO_2 stimulates plant productivity and growth, O_3 tends to exhibit deleterious effects on plants, typically causing decreased growth and lowered leaf nutritional quality. This change in plant quality has the potential to increase herbivory levels due to insect overcompensation for poor nutritional quality of the tissues. In general, plants growing under increased O_3 conditions exhibit decreased photosynthetic rates, decreased leaf area, premature leaf abscission and weakened branch and root growth (Isebrands *et al* 2001). For insects, the effects of elevated O_3 are likely to be indirect and will depend upon the magnitude of change in host plant quality (bottom-up factors) and/or natural enemy impact (top-down factors). Elevated O_3 might change natural enemy population via shifts in the diversity, abundance and quality of preys or changes in natural enemy behavior that might affect host-finding (Hillstrom & Lindroth 2008).

Elevated O_3 decreased nitrogen and phenolic glycoside levels on the quacking aspen *Populus tremuloides*, but increased the concentrations of starch and tannins (Holton *et al* 2003). The authors suggested that enriched O_3 atmospheres result in increased activity of defense-related plant enzymes, increasing the production of phenolics controlled by the shikimic acid pathway, such as tannins, and decreasing the production of glycosides, due to competition between branches of the pathway for substrates. This study, however, also showed that the forest tent caterpillar *Malacosoma disstria* (Hubner) (Lepidoptera: Lasiocampidae) reared on plants grown under increased O_3 conditions were larger and developed faster, a result probably related to the decreased concentration of phenolic glycosides, known to negatively affect this species. The parasitoids *Compsilura concinnata* (Meigen) (Diptera: Tachinidae), on the other hand, exhibited decreased survivorship on hosts of *M. disstria* reared under elevated O_3 conditions, revealing a complex relationship between aspen chemistry, herbivore performance and parasitoid attack.

Using yellow sticky traps, Hillstrom & Lindroth (2008) evaluated the effects of elevated CO_2 and O_3 on the abundance and diversity of herbivores, predators and parasitoids on forested communities in a Free Air CO_2 Enrichment (FACE) facility in Wisconsin, USA. Elevated CO_2 reduced the abundance of phloem-feeders and ants, and increased the abundance of chewing herbivores and parasitoids, but elevated O_3 reduced the *total* abundance of insects by 17% compared to ambient O_3 conditions, with prominent effects on parasitoids like Ichneumonidae (reduced by 41%), Brachonidae (reduced by 33%) and Chalcidoidea (reduced by 26%). Arthropod family richness was not affected by treatments, but the authors observed shifts in arthropod community composition over a four-year period. Results like the ones listed here and others (e.g., Holton *et al* 2003, Dermody *et al* 2008) show that insect communities in the 21st century will be different from current ones due to elevated CO_2, elevated

O_3 and the combination of both factors. Forests exposed to elevated ozone, for example, may have significantly fewer parasitoids (Hillstrom & Lindroth 2008) with potential effects on host population dynamics and biological control programs. These changes in insect abundance and/or diversity are a combination of changes in bottom-up, top-down and abiotic factors, and predicting the results of these changes in community composition and ecosystem function, both at larger scales as well as for other biomes, still represents a challenge for insect ecologists.

Combined Effects of CO_2 and O_3

CO_2 and O_3 are considered the most important and ubiquitous gases affecting forest vegetation worldwide (Lindroth 2010). A recent meta-analysis demonstrated that when plants are simultaneously exposed to CO_2 and O_3, enriched CO_2 atmospheres tend to counteract changes caused in plant physiology caused by enriched O_3 (Valkama *et al* 2007). Lindroth (2010), on the other hand, suggests that effects of CO_2 and O_3 might work in additive or interactive ways, depending on particular plant species.

How do insects respond to atmospheres enriched by both CO_2 and O_3? Plant selection by insects is influenced by both CO_2 and O_3 concentrations due to their indirect effects on plant quality for herbivores and natural enemies. Few studies so far, however, addressed the combined effects of CO_2 and O_3 on insect host plant selection and insect performance (but see Awmack *et al* 2004, Peltonem *et al* 2006, and the studies reviewed meta-analytically by Valkama *et al* 2007) and the studies so far conducted have shown no significant interactions between both factors (Lindroth 2010) for temperate insects in forested ecosystems.

Increased Temperature

Global warming is one of the major changes that terrestrial ecosystems will experience in the forthcoming years. The Intergovernmental Panel on Climate Change IPCC (Team *et al* 2007) predicted an increase of the air temperature at the order of 1.1 to 6.4^{o}C by the year of 2100. Due to their ectothermic nature, insects are very likely to respond quickly to increased temperatures (Robinet & Roques 2010), and rising temperatures have the potential to affect most life history parameters of terrestrial insects, altering their ecological roles, as well as intra- and inter-specific interactions. Effects of global warming on insects can be direct, through impacts on physiology and behavior, or indirect, especially through impacts on host plants and/or natural enemies. Although the effects of elevated CO_2 and O_3 have been intensively studied, especially in temperate ecosystems, the effects of experimentally elevated temperature on plant features that might *indirectly* affect herbivory have been neglected in the scientific literature. According to Zvereva & Kozlov (2006), the few case studies available do not allow to draw general conclusions.

Direct effects of temperature on insect life history parameters, on the other hand, have been addressed in the literature and are likely to be larger and more important than any other factor on insect life history and physiology (Bale *et al* 2002). Studies have shown that increased temperature tends to have positive effects on insects (Bale *et al* 2002), especially multivoltine insects in temperate ecosystems. Climate can act directly on an insect either as a mortality factor or by determining insect growth rate and/or development. Temperature can alter insect life-cycle duration, voltinism, population density, size, genetic composition, extent of host plant exploitation (both in time and space) and geographical distribution (Bale *et al* 2002). Many insect species, for example, are predicted to expand their geographical range to higher latitudes and altitudes – where climatic factors will be less harsh with global warming – as already documented for several butterflies, beetles, dragonflies and grasshoppers (e.g., Parmesan *et al* 1999). As climatic isotherms have moved northwards 120 km during the past century, ≈ 60% of non-migratory butterflies in Europe have extended their distributions by 35-240 km northwards. Although most studies regarding how increased temperatures might shift species range polewards and towards higher elevations have been conducted in temperate biomes, a study by Colwell *et al* (2008) showed that this trend might also be true for tropical insects (geometrid moths and ants). Using data collected for 1,902 species of insects and plants along an altitudinal transect in Costa Rica, they showed that a high proportion of tropical species analyzed (≈53%) may be faced with range-shift gaps and might face extinction with a 1000m range shift in isotherms.

One of the major aspects of climate change and increased temperature is the associated advancement in the phenology of life history events for many plant and animal species (Memmott *et al* 2007) with the potential to disrupt synchrony between interacting pairs. For many insect herbivores, synchronization to plant phenology is crucial, as development outside the period of optimal conditions often has severe fitness consequences (VanAsch & Visser 2007). Global warming has advanced, for example, bud burst and the first flowering date of plants, disrupting interactions with herbivores and flower visitors. But, an important point in the understanding of the immediate impacts of climate change is the *extent* to which species will alter their phenologies, in response to altered temperatures, leading to both temporal and spatial mismatches between, for example, plants and herbivores, plants and pollinators, and hosts and parasitoids. Successful life-cycle completion in many specialist insects requires a very tight synchrony with host plant phenology. As changes in phenological states of either insects or plants are expected under rising temperatures, they have the potential to disrupt ecological and evolutionary relationships between these two groups.

For plants and insect herbivores, the use of ecological-niche models under several global change scenarios demonstrated a pronounced spatial mismatch between the monophagous butterfly *Boloria titania* (Esper) (Lepidoptera: Nymphalidae) and its larval host plant *Polygonum bistorta* due to differential range expansion of each species in response to changes in climate and land use (Schweiger *et al* 2008). This result shows that increased temperatures and other human-altered factors have the potential to disrupt trophic interactions between insects and plants due to species-specific responses to climate change issues. The winter moth *Operophtera brumata* (L.) (Lepidoptera: Geometridae) is another example of the effects of rising temperature in generating asynchrony between insects and their food sources. A study by Visser & Holleman (2001) showed that winter moth eggs tend to hatch before the leaves of their host *Quercus robur* is available and in some years more than 90% of the eggs hatch before oak bud burst. In a more recent study, Both *et al* (2009) showed unequal phenological changes across four trophic levels within a European mixed woodland food web. Oaks are food for moth caterpillars, which are, in turn, preyed upon by songbirds, which are the food source of hawks. Data from a long-term study (17 years) have shown advancement over time for tree budburst, peak of caterpillar biomass, as well as passerines and hawks hatching dates. However, differences in the strength of this advancement (stronger for caterpillars, weaker for birds) have the potential to cause mismatches in the timing of breeding and food availability that could lead to declines in predators and outbreaks of herbivores, which are released of the top-down pressure caused by birds.

Although most studies regarding effects of global warming on trophic interactions have focused on negative interactions involving insects (e.g., herbivory studies listed above), Memott *et al* (2007) addressed how climate change will disrupt or even eliminate mutualistic interactions among species, such as pollination and seed dispersion. Using simulations based upon a real network of interactions between 1,419 species of pollinating insects on 429 plant species, they demonstrated that between 17% and 50% of all pollinators analyzed will suffer a reduction in food supply with a phenological advance of two weeks of their floral resources. This reduction will be even more drastic for specialist pollinators. Data on the impacts of climate change on synchrony of host-parasitoid interactions are not as common as plant-herbivore and predator-prey interactions (Klapwijk *et al* 2010), but recent studies have shown that effects of climate change on parasitoid and host asynchrony might be direct or indirect through changes on host plants. Klapwijk *et al* (2010), studying the relationship between the host *Euphydrias aurinia* (Rottermburg) (Lepidoptera: Nymphalidae) and its specialized Braconidae parasitoid *Cotesia bignellii* (Marshal) observed that experimental increases of temperature and shading were enough to decrease developmental times for the host. However, no significant effects of altered temperatures were observed for the parasitoid, indicating that parasitoid development was independent of the microenvironment, and changes in temperatures might not alter the dynamics of this host-parasitoid system. The paucity of studies like this, however, impairs any generalization about the effects of warming in such a diverse group and in tri-trophic interactions.

Combined Effects of CO_2 and Temperature

Another expectation raised by the IPCC (2007) is that global changes in several climatic factors will not occur alone. As such, one should expect to see combined effects of climatic change factors in both terrestrial and aquatic ecosystems, with detectable effects on different organisms and ecosystem processes.

Not only carbon dioxide concentrations, but also globally averaged surface temperatures are expected to increase during the 21st century (Zvereva & Kozlov 2006). How will the combined effects of these two abiotic factors on plant physiology and growth modify plant-insect interactions? In a meta-analytical review of 42 studies that *simultaneously* increased carbon dioxide and temperature conditions compared to ambient conditions, Zvereva & Kozlov (2006) showed that nitrogen concentration in plants was reduced under both elevated CO_2 and elevated temperature conditions, and this decrease was stronger for woody compared to herbaceous plants. Ratios of C:N in plants, on the other hand, exhibited the opposite trend, increasing under elevated CO_2 and temperature treatments, but carbon-based secondary compounds did not show a significant response to increases in either factors. Because herbivore performance – measured as survival, pupal weight, relative growth rate and fecundity – was negatively affected by elevated CO_2 alone, but positively affected by elevated temperature; when acting simultaneously, these two factors had no detectable effects on insect performance.

Similar to conclusions reached by previous studies, their meta-analytical review also revealed the scarcity of studies on insect performance under both elevated CO_2 and temperature, i.e., conditions that are believed to mimic the environment of 2050-2080 (Zvereva & Kozlov 2006). Only six studies (Williams *et al* 2000, Veteli *et al* 2002, John & Hughes 2002, Johns *et al* 2003, Williams *et al* 2003, Chong *et al* 2004) addressed combined effects of elevated carbon dioxide and temperature on insect parameters, and all of them were conducted in temperate regions with different insect guilds, revealing therefore gaps in our general knowledge of insect response to simultaneously changing climatic factors.

Changes in Rainfall Patterns

Precipitation and extreme events such as flooding and hurricanes are also predicted to increase due to global climatic changes, although there is less certainty about the magnitude of these changes (Bale *et al*. 2002) and how they will affect ecosystem functioning and the ecological role of species. Abiotic changes caused for example by increased precipitation and wind during hurricanes can have profound effects on vegetation structure and the availability of resources for plants (Pickett & White 1985, Hunter & Forkner 1999, Spiller & Agrawal 2003). Hurricanes influence, for example, the availability of light and nutrients for surviving trees, affecting the allocation of compounds to plant nutrition and defense. This, in turn, might affect insect feeding and performance.

Few studies so far have addressed the effects of hurricanes and floodings in insect-plant interactions, especially due to the difficulties to obtain before and after data that would enable comparisons of herbivory patterns, insect abundance and/or community composition. The four available studies do not allow any generalizations at this moment. Using data from plants on hurricane-damaged sites and undamaged sites in North Carolina, Hunter & Forkner (1999), for example, showed that oak and maple trees in damaged sites exhibited higher concentrations of tannins, but were also more defoliated by insect herbivores, indicating that increased levels of plant defenses following disturbances were not enough to protect the trees from insect attack. Similar results were found for trees damaged by hurricane Lili, which hit the Bahamas in 1986. Using controlled experiments, Spiller & Agrawal (2003) showed that surviving shrubs of *Conocarpus erectus* (Combretaceae) that were sprouting after the hurricane storm were more susceptible to herbivory by Lepidoptera than new foliage on undamaged shrubs, indicating that changes in leaf features induced by hurricane had profound effects on herbivory patterns with potential to affect food web dynamics in island conditions.

Two other studies, on the other hand, showed opposite results. Koptur *et al* (2002) evaluated herbivory patterns for eight plant species after hurricane Andrew caused severe damage at the Everglades National Park, in Florida, and reported lower herbivory rates in newly produced foliage, indicating that the hurricane might have eliminated most herbivores from the studied sites. The study by Angulo-Sandoval *et al* (2004) was conducted in Puerto Rico and analyzed leaf production and herbivory by comparing post-hurricane data with pre-hurricane data collected before hurricane Georges struck their studied sites. They found increased leaf production after hurricane damage for eight understory plant species, but herbivory levels on these plants were much lower (2.03%) compared to pre-hurricane conditions (16.05%). They suggested a number of reasons to explain lower levels of herbivory after hurricane damage, including changes in leaf chemistry caused by changes in leaf availability as well as changes in herbivore abundance and/or pressure exerted by natural enemies.

Effects of Climate Change on Plant Volatile Compounds

Considering that global CO_2 and O_3 concentrations as well as temperature have been increasing over the past decades (Team *et al* 2007) and that the production and emission of plant volatile organic compounds (VOCs) can be affected by changes in these abiotic factors, it is expected that global climate changes could influence how insects perceive and use plant VOCs in intra- and inter-specific interactions (Penuelas & Staudt 2010). VOCs are involved in a series of interactions between insects and plants, ranging from positive (e.g., pollination and seed dispersal) to negative ones (e.g., defenses against herbivory), and are expected to be affected by changes in temperature, rainfall patterns and atmospheric concentration of gases through plant-mediated effects.

Global climatic changes might make the world more ‘fragrant’, as it is expected that plants under a changing environment will emit greater levels of fragrant chemicals. This, in turn, will alter how plants interact with one another through the processes of competition and allelopathy, and how they defend themselves against pests, including insects, viruses and pathogens.

Although considerable few studies have been conducted to address the effects of changing temperature and gas concentration on the metabolism and expression of VOCs, some patterns have arisen in the literature (reviewed by Penuelas & Llusia 2003, Yaun *et al* 2009, Penuelas & Staudt 2010). Under higher temperatures, it is expected that plants would produce higher concentrations of VOCs and for longer periods of time (Penuelas & Staudt 2010), altering therefore their ecological role in insect-plant interactions. Monoterpene emissions, for example, are highly temperature-sensitive (Constable *et al* 1999), exhibiting a 2-3 fold increase for each 10°C increase in temperature. Therefore, the production and emission of higher concentrations of VOCs that act as plant signaling against insect attack – such as methyl jasmonate or methyl salicylate – might put neighboring plants in a steady state of alert against natural enemies, with the potential to reduce future herbivory rates. On the other hand, positive interactions might also be disrupted if pollinators and seed dispersers get confused with a more fragrant atmosphere, causing reduction in plant reproduction and fitness.

Under high CO_2 concentrations, VOCs are expected to increase due to positive relationship between carbon availability and VOC production (Yuan *et al* 2009). It has been hypothesized that increased CO_2 concentrations should increase monoterpenes and sesquiterpenes emissions to the atmosphere based upon the resource allocation theory (Lerdau *et al* 1994). According to this hypothesis, there is an increased production of C-based plant secondary compounds when there is an excess of carbon compared to what is required for plant growth. Increased production of some C-based VOCs under elevated CO_2 conditions has been demonstrated for conifers (Constable *et al* 1999), oaks (Togneti *et al* 1998, Loreto *et al* 2001) and for cultivated plants (Jasoni *et al* 2004). Similar increases of VOC production are expected under higher O_3 concentrations, as demonstrated for homoterpenes in lima beans (Vuorinen *et al* 2004), and limonenes in Mediterranean plant species (Llusia *et al* 2002).

Although changes in patterns of VOC emission under changing environments have been investigated, none of the abovementioned studies have addressed how insects – pollinators, herbivores and/or parasitoids – respond to these changes, impairing the complete understanding of herbivore response to changes in host plants triggered by climatic changes.

Concluding Remarks

Responses of organisms to global changes will be species-specific and might occur at different rates, potentially altering community structure and the ecological roles of several species in maintaining ecosystem processes and services. As shown here, the vast majority of research on plant and insect responses to altered climatic factors has focused on agricultural and forest species in temperate ecosystems, with a strong bias to leaf chewer insects, especially defoliators. Studies regarding native, tropical species are still very incipient (if not completely absent), and interactions between insect herbivores and plants in tropical, moist forests are supposed to be stronger as rates of herbivory are higher, plants are better defended and herbivores tend to exhibit more specialized diets. Predicted scenarios for tropical biomes suggest that herbivory rates might increase by 2-4 fold in a world of increasing CO_2 and drought, and the frequency of insect outbreaks are expected to be higher (Coley 1998), with negative consequences to plant growth and development. Also, changes in natural enemy pressure might increase or decrease herbivore abundance, with consequences for community structure and composition.

Because changes in global climate will not occur alone, a complete understanding of the effects of these changes on the interactions between insects and their host plants will be achieved only after controlled, factorial experiments can be designed and followed over longer periods of time to predict future trends.

Acknowledgements

This research was partially supported by grants to the author from CNPq and FAPEMIG.

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