Effects of abiotic factors on plant-insect multitrophic interactions

Chen, C.

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Chapter 6

General discussion

Introduction

In terrestrial ecosystems, plants are in constant interactions with other organisms in different trophic levels. Plants have evolved a range of morphological and chemical traits that may directly or indirectly influence their antagonists (e.g. herbivores, pathogens) as well as organisms that they can potentially benefit from (e.g. parasitoids, predators). For example, plant morphological traits such as trichomes on leaves or stems may protect them from herbivore attack (Agren & Schemske, 1993; Dussourd & Eisner, 1987). On the other hand, these traits can also hinder the searching behavior of natural enemies (e.g. predators, parasitoids) (Fordyce & Agrawal, 2001; Romeis, Shanower, & Zebitz, 2003). Furthermore, plants produce a variety of secondary metabolites which may be constitutively present, or induced after plant tissue damage (Karban & Baldwin, 2007; Schoonhoven et al., 2005). These chemical traits can significantly reduce survival or performance (e.g. body size, development rate) of insect herbivores (Schoonhoven et al., 2005; Van Dam, Hadwich, & Baldwin, 2000), but also affect interactions at higher trophic levels, for instance by altering the quality, susceptibility or availability of herbivores to their natural enemies.

In nature, abiotic factors also influence the interaction between species, such as interactions between plants and herbivorous insects, or between insect hosts and their parasitoids. These abiotic factors may disrupt plant multitrophic interactions when plants and higher trophic-level organisms respond differently to abiotic factors, e.g. with respect to their rate of development or timing of life history events (Both, Van Asch, Bijlsma, Van Den Burg, & Visser, 2009; Visser & Holleman, 2001; Voigt et al., 2003). Although plant-insect interactions have been well studied in recent decades (Ali & Agrawal, 2012; Ehrlich & Raven, 1964; Mello & Silva-Filho, 2002), the effects of abiotic factors, such as rainfall and wind, on these interactions have received less attention in the empirical literature. Climate change may affect plant-herbivore-parasitoid-hyperparasitoid multitrophic interactions by altering a range of eco-physiological characteristics of plants, which subsequently affect plant-herbivore interactions as well as interactions amongst organisms at higher trophic levels such as herbivores and their natural enemies, which themselves may also directly respond to changes in abiotic factors. The main aim of my thesis was to examine the effects of abiotic factors on the performance of plants, insect herbivores and their natural enemies, as well as on their interactions. In the first part of this discussion, I summarize the main findings of this thesis; in the second part, I discuss the results in a broader context of climate change and multitrophic interactions.

First, in a greenhouse experiment, I tested whether wind exposure could directly or indirectly affect the performance of two insect herbivores, *Plutella xylostella* and *Pieris brassicae*, feeding on *Brassica nigra* plants (chapter 2). In order to separate the effects of direct and indirect wind exposure on herbivores, I exposed plants to different simulated wind regimes before and after plants were infested with caterpillars. I found that wind exposure affects plant morphological and chemical traits. However, plant-mediated effects of wind on herbivore performance were generally small. Development time of both herbivores was extended and adult biomass of *P. xylostella* was marginally reduced. In contrast, adult *P. brassicae* butterflies were significantly larger under windy conditions. Based on these results, I conducted a behavioral experiment to test whether wind exposure alters the preference of an avian predator (*Parus major*) for the last instar of *P. brassicae* caterpillars on plants (chapter 2). I showed that caterpillars on still plants had a higher predation risk than on wind-exposed plants. These results suggest that wind exposure may be perceived by *P. brassicae* and that in response, it alters its developmental program by extending development time, allowing it to achieve a larger body mass under windy conditions that are associated with a lower predation risk.

Second, using the same plant and herbivore species, I examined the effects of rainfall on the performance of two insect herbivores on plants (chapter 3). Plants in rainfall treatments were exposed to different rainfall regimes, applied either as a single long or as multiple short rain events per day. I found that direct rainfall exposure negatively affected the survival of the micro-moth *P. xylostella*, but not that of the macro-butterfly *P. brassicae*. Direct rainfall exposure extended the development time of both herbivores, whereas effects on body mass depended on herbivore species and rainfall frequency. Indirect effects of rainfall on the herbivores were generally small. These results suggest that changes in precipitation can directly and indirectly influence plant-herbivore interactions, which may in turn alter the population dynamics of insect herbivores and community structure.

Third, in an incubator experiment, I investigated the effects of an elevated temperature on reproduction and functional responses of two species of hyperparasitoids (*Gelis agilis* and *Acrolyta nens*) at the fourth trophic level that parasitize a host species (*Cotesia glomerata*) at the third trophic level (parasitoid cocoons) (chapter 4). I exposed the parasitized host cocoons to three different day and night temperature regimes (low, medium and high) that reflect cool, normal and hot conditions in the Netherlands. I found that host cocoons developed faster under warmer conditions. However, the effects of an increased temperature markedly differed between the two hyperparasitoid species. Temperature and host quality had a much stronger effect on early reproduction in the less fecund hyperparasitoid *G. agilis*, than on the more fecund species *A. nens*. These results indicate that exposure to higher temperatures influences the ability of species at the fourth trophic level to exploit finite resources at the third trophic level whose suitability is temperature-dependent. Consequently, this may have the potential to change community structure and trophic cascades.

Lastly, using the same temperature treatments, I studied the effects of an elevated temperature on intrinsic inter-specific competition between two hyperparasitoid wasps, *Lysibia nana* and *A. nens* in host cocoons of a primary parasitoid, *C. glomerata* (chapter 5). I exposed singly parasitized and multiparasitized host cocoons to the same temperature conditions as described above. I found that higher temperature decreased survival to eclosion, reduced development time and led to the production of smaller adult wasps in both species. *L. nana* usually won most contests when it oviposited first, irrespective of the time interval, whereas *A. nens* only dominated when it had a 24 h or longer head start. Moreover, *L. nana* in particular benefited in competition at higher temperatures, perhaps due to an increase in the metabolic rate and more rapid egg and/or larval development. These results suggest that heat waves may negatively affect life history traits (survival and body size) in (hyper)parasitoids and intensify intrinsic competition.

Effects of wind and rainfall on plant-herbivore interactions

Plant-herbivore interactions have been extensively studied for decades both in terrestrial and aquatic ecosystems (Ali & Agrawal, 2012; Awmack & Leather, 2002; Carmona, Lajeunesse, & Johnson, 2011; Ehrlich & Raven, 1964; Gregory, 1983; Hay & Fenical, 1988; Wittstock et al., 2004). The outcome of these interactions is affected by a variety of biotic and abiotic factors. Wind and rainfall are very important climate-related factors that may directly and indirectly (plant-mediated) influence herbivore performance. In particular, AGW is an important driver of changes in other abiotic factors such as wind and rainfall (IPCC, 2014; Lenderink & van Meijgaard, 2008; Vautard, Cattiaux, Yiou, Thépaut, & Ciais, 2010). Consequently, these changes may have profound effects on interactions between plants and herbivores through direct and/or indirect (both bottom-up and top-down control) ecological process.

Direct wind exposure negatively affected the survival of *P. xylostella*, but not that of *P. brassicae* (chapter 2). Similar results were found when caterpillars were directly exposed to rainfall (chapter 3), indicating that the two herbivore species respond differently to physical disturbance of their feeding behavior by these two abiotic factors. The two species differ in size and life history strategies (Capinera, 2000; Feltwell, 1982). Larvae of *P. brassicae* are gregarious and feed in clusters during their first three instars. By contrast, larvae of *P. xylostella* are solitary and are much smaller than *P. brassicae* in their final instar. Indeed, small and active species such as *P. xylostella* are generally more susceptible to physical disturbance than larger and less motile species such as *P. brassicae* (Vogel, 1994).

Several studies have reported that the abundance of insect herbivores is associated with the two climatic factors wind and rainfall (Barton, 2014; Shure, Mooreside, & Ogle, 1998; Zhu et al., 2014). In our studies, wind and rainfall differentially affected the development of the two studied insect herbivores. Both factors extended their development time, but for biomass the effect depended on exposure condition as well as herbivore species. Interestingly, wind exposure was perceived by the herbivore *P. brassicae* and resulted in a plastic change in its development program, leading to an increase in its adult biomass, whereas heavy rainfall events resulted in a reduction of its biomass. For herbivores, there are costs and benefits associated with feeding on plants under abiotic stress conditions. We speculate that in response to wind exposure, *P. brassicae* initiates an adaptive developmental program, prolonging its development time to increase its adult biomass in response to the reduced predation risk observed under windy conditions. By contrast, the response of both insect herbivores to heavy rain exposure may reflect a consequence of the difficulty to produce a large pupa or adult under these conditions either as a direct consequence of exposure to rain (physical disturbance) or because of the concomitant drop in local temperature. Although rainfall may also create “enemy-free space” by reducing the risk of predation that can incur benefits for insect herbivores (Gols et al., 2005; Jeffries & Lawton, 1984; Stamp, 2001), we speculate that *P. brassicae* has not evolved a similar response to heavy rain, perhaps because heavy rain imposes greater costs through disturbance of feeding or a decrease in temperature, which in turn negatively influences larval development (chapter 3).

Overall, indirect (plant-mediated) effects of wind and rainfall exposure on performance of the two insect herbivores were generally small (chapter 2 and chapter 3). Plant primary and secondary metabolism plays an essential role in regulating growth and defense of plants against herbivores (Hartmann, 1996; Schoonhoven et al., 2005; Scriber & Slansky, 1981). However, both herbivore species used in the experiments are specialist and well adapted to the plants in the Brassicaceae family and the defense chemicals that they produce (Gols et al., 2009; Ratzka, Vogel, Kliebenstein, Mitchell-Olds, & Kroymann, 2002). Although specialists are less affected by secondary metabolites than by primary metabolites, the latter are probably not strongly modified by the abiotic factors. This may be the reason why wind and rainfall-mediated changes in plant chemistry only marginally affected the performance of the herbivores.

The results from chapter 2 and chapter 3 emphasize the importance of wind and rainfall in studies of plant-herbivore and predator-prey interactions. Changes in these patterns may have the potential to disrupt species interactions and ecosystem function (Barton & Ives, 2014; Cherry & Barton, 2017; Wade, Karley, Johnson, & Hartley, 2017).

Effects of climate warming on species interactions at higher trophic levels

Climate warming is one of major threats to biodiversity and ecosystem function across all trophic levels (Parmesan & Yohe, 2003; Thomas et al., 2004; Van der Putten, Macel, & Visser, 2010; Walther et al., 2002). Many studies have shown that warming is likely to disrupt interactions between species in the first three trophic levels, such as plant-herbivore, and plant-herbivore-predator/parasitoid interactions (Gillespie, Nasreen, Moffat, Clarke, & Roitberg, 2012; Sentis, Hemptinne, & Brodeur, 2013; Visser & Holleman, 2001). However, thus far few studies have been performed on the impact of warming and heat waves on species interactions further up the food chain, such as parasitoid-hyperparasitoid interactions. Importantly, temperature is a key factor that can affect resource availability and life-history traits of species, especially for ectotherms as they are very sensitive to temperature variability (Atkinson, 1994; Kharouba, Vellend, Sarfraz, & Myers, 2015; Masson, Valente, Fox, & Copp, 2014).

One of the life-history traits that has the potential to affect the impact of climate warming on trophic interactions is the degree of host specificity of parasitoids. In chapter 4, I found that warming had more negative effect on a generalist than on two specialist hyperparasitoids. This finding contradicts results from previous studies using second trophic level organisms that focused on effects of warming on herbivores, showing that specialist butterflies are more susceptible to climate change than generalist butterflies (Menéndez, 2007; Warren et al., 2001). The abundance of specialist herbivores mostly relies on a narrow range of host plants with phylogenetically conserved secondary metabolites. In contrast, generalist species are able to exploit a broader spectrum of plant species (Loxdale & Harvey, 2016). This is not supported by our findings for hyperparasitoids. One of the possible explanations for the discrepancy between the effects of warming observed in these studies is that (hyper)parasitoids have less options for responding to warming-induced changes in their hosts (parasitoids) than herbivores have for responding to warming-induced changes in their hosts (plants). This is because generalist herbivores can be buffered against reduced availability of host plant species by exploiting another host plant species that is less affected by climate change, whereas generalist hyperparasitoids cannot easily switch to another host because all of their hosts share a similar response to climate change, i.e. faster development that shortens the critical time window for exploitation (chapter 4). Thus, the temporal window for herbivores to exploit their hosts under warmer conditions is much broader than for hyperparasitoids.

In nature, many species coexist in the same habitat with shared resources (Ayala, 1972; Harvey, Poelman, & Tanaka, 2013). In a changing world, an important ecological question is what species will have a greater chance to win the competition under warmer conditions. In chapter 5, I showed that warming negatively influences competitive ability of superior species in the competition between two hyperparasitoid wasps at the end of the food chain. Species coexistence can be impaired if climate warming reduces trait diversity in communities or favors only one or a few species from a community (Le Lann et al., 2014; Traill, Lim, Sodhi, & Bradshaw, 2010). For instance, the parasitoids *Diadegma semiclausum* and *Cotesia vestalis* are important biological control agents of the pest *P. xylostella*, occurring in different thermal regions (Furlong, Wright, & Dosdall, 2013), the latter being more adapted to warmer climatic conditions. Thus, *C. vestalis* may displace *D. semiclausum* if temperature continues to rise in cooler regions. Other studies have also provided evidence that interspecific interactions of invertebrates and ectothermic vertebrates are likely affected by differences in thermal tolerance (Juliano, O'Meara, Morrill, & Cutwa, 2002; Llewelyn, Shine, & Webb, 2005; Medley, 2010).

The results from chapter 4 and chapter 5 demonstrate that climate warming may disrupt interactions between the third and fourth trophic level. Consequently, these effects may indirectly alter species interactions at lower trophic levels through altering top-down control across the trophic cascade (Kratina, Greig, Thompson, Carvalho-Pereira, & Shurin, 2012; Schmitz, Hambäck, & Beckerman, 2000), which in turn may change the composition and structure of communities.

Effects of climate change on multitrophic interactions

Climate change drives multitrophic interactions through changes in bottom-up control and top-down control. Plant quality and quantity generally play an important role in determining the performance of species at higher trophic levels (Awmack & Leather, 2002; Fei, Gols, Zhu, & Harvey, 2016; Price et al., 1980). Climate-induced changes in plant primary and secondary metabolites may influence insect herbivore performance, which in turn affects host quality and availability for species at third and higher trophic levels (Harvey, Van Dam, & Gols, 2003; Harvey, Wagenaar, & Bezemer, 2009; Ode, 2006). In this thesis, I found that abiotic factors such as wind and precipitation affected a range of plant traits. However, changes in these morphological and chemical traits had little impact on insect herbivores. As discussed above, this might have been due to the fact that the herbivore species that I used in the experiments are specialists that tend to be less affected by plant defensive traits than generalist herbivores. When we place this in a multitrophic context, we can thus speculate that (generalist) natural enemies of generalist herbivores are also more likely influenced by abiotic factors than the (generalist) enemies of specialist herbivores through changes in plant quality.

Climate change may directly affect the performance and behavior of insects at various trophic levels. Temperature is the major abiotic factor influencing development, survival and population dynamics of insect herbivores and higher trophic levels (Bale et al., 2002; Hance, van Baaren, Vernon, & Boivin, 2007; Harvey, 2015). For example, higher temperatures increase development rates of herbivores and parasitoids, potentially resulting in more generations within a year (Hance et al., 2007; Nealis, Jones, & Wellington, 1984; Pollard & Yates, 1994). However, species at higher trophic levels are predicted to be more sensitive to climate change than lower trophic levels (Voigt et al., 2003). For instance, it has been shown that warming more negatively affected predator (spiders) than their prey (grasshoppers) as a result of a decrease in spatial overlap (Barton, 2010). Likewise, in my thesis, I showed that hyperparasitoid fitness correlates (survival, body masss) were more negatively affected at higher temperatures than parasitoid (pupal) survival. This was probably because of different physiological responses by the two trophic levels to elevated temperature. There is evidence that communities with longer chains of trophic levels embedded in them are more resilient to climate change than communities with shorter trophic chains (Sentis et al., 2013; Wilmers & Post, 2006). Hence, multitrophic interactions involving plants, herbivores, parasitoids and hyperparasitoids may be disrupted if species at the end of longer food chains are more vulnerable in response to AGW.

Changes in other abiotic factors, such as wind and precipitation, may also have a profound impact on multitrophic interactions (Barton, 2014; Wade et al., 2017) because organisms at different and/or same trophic levels may also respond differently to these aspects of climate change, i.e. through differential effects on phenology, life history traits or development rate. Therefore, not only warming, but also other abiotic stresses may result in asynchrony between any pairs of interacting species and may disrupt the structure of food webs.

Predicting the effects of climate change on biodiversity is one of biggest challenges in ecology. In nature, species do not live in isolation, but interact with one another in often highly complex ways. The complexity of biotic interactions is vital to maintain the stability of ecological communities. Insect communities are dependent on primary producers (host plants). An important question is how plant-herbivore-parasitoid-hyperparasitoid multitrophic interactions as a whole are affected by climate change. Climate change may change the phenology, development, behavior and physiology of individual species at each trophic levels (Tylianakis et al., 2008). For example, climate warming may promote plant growth resulting in faster development of herbivores (Bale et al., 2002). Insect herbivores are more likely to escape from their natural enemies under these conditions. However, higher trophic levels, such as hyperparasitoids, may be more constrained by a narrower temporal window of host availability under warmer conditions. Consequently, insect herbivore outbreaks are predicted to be more frequent in a warming world.

In natural systems, it is difficult to predict which climate-related factors drive community composition and changes in ecosystem functions. Although empirical and theoretical studies often emphasize the impact of AGW, other aspects of climate change such as heat waves, the duration and intensity of precipitation and wind and integrated factors are also likely to play an important role in shaping ecosystem structure and functioning. For example, a recent field study has reported that larval weight and survival of the heather beetle decreased dramatically when three abiotic factors (warming, drought and elevated CO_2) were combined (Scherber et al., 2013). Another recent study comparing databases on parasitism rate from 15 geographical regions between southern

Canada and central Brazil revealed a dramatic decrease in parasitism by parasitoids under conditions of increased climatic variability (Stireman et al., 2005). Many parasitoids are highly specialized natural enemies of insect herbivores, and it appears that they may be less able to track host populations under rapidly changing climatic conditions. At larger scales, we may expect the decoupling of (multi)trophic interactions as a result of multiple abiotic stressors to have consequences for the structure and function of food webs, and ultimately ecosystem functioning (Bale et al., 2002; Coley, 1998; Davis, Jenkinson, Lawton, Shorrocks, & Wood, 1998; Davis, Lawton, Shorrocks, & Jenkinson, 1998; Emmerson et al., 2004; Voigt et al., 2003).

The complex interactions between multiple abiotic and biotic factors make it even more difficult to predict ecological consequences of climate change for communities and ecosystems. In my thesis, I mainly explored the impact of single abiotic factors in isolation on bitrophic species interactions. It is important to scale the results of these pairwise interactions between species up to the entire food chain and beyond to include entire food webs, communities and ecosystems (McCann, 2007). Nevertheless, theoretical studies have shown that many predictive models can be improved by incorporating biotic interactions (Heikkinen, Luoto, Virkkala, Pearson, & Körber, 2007; Palacio & Girini, 2018; Raath, le Roux, Veldtman, & Greve, 2018). More empirical research is urgently needed to better understand the various potential negative impacts of AGW on multitrophic interactions and ecosystems.

Broader implications

Current anthropogenic global warming represents a severe threat to biodiversity across all levels of organization, from primary producers to the terminal end of food chains. The magnitude of observed and predicted changes in climate for the 21th century are comparable to the largest warming episode in at least the past 65 million years near the Cretaceous-Tertiary boundary, or even earlier, to the Permian-Triassic boundary 270 million years ago (Diffenbaugh & Field, 2013; Kemp, Eichenseer, & Kiessling, 2015; Lewis & Maslin, 2018). Climate warming, and attendant extreme events such as floods, hurricanes and heat waves, is emerging as a major threat to not only to ecosystems but also to humans around the world. Given that insects are the most abundant and diverse group in the animal kingdom, they play an important role in ecological processes such as bottom-up and top-down control in ecosystems. Numerous studies have reported that AGW is the main driver of collapsing insect populations across a wide geographical range (Conrad, Warren, Fox, Parsons, & Woiwod, 2006; Goulson, Nicholls, Botías, & Rotheray, 2015; Kerr et al., 2015). For example, in Puerto Rico, arthropod abundance declined by 98% in a tropical rainforest between 1976 and 2012, leading to collapses in the abundance of insectivorous vertebrates such as birds and anolis lizards (Lister & Garcia, 2018). Moreover, other anthropogenic stresses still challenge the biodiversity all over the world, from environmental pollution and over-harvesting to land-use change, habitat loss and invasive species (Tylianakis et al., 2008).

Importantly, the mechanisms of decline in insect populations driven by climate change are unclear. One potential driver behind this is physiological damage under conditions of heatwaves. A recent study showed that exposing beetles to a 5-day heatwave reduced males reproduction (through sperm death) by more than half, whereas female reproduction was not affected (Sales et al., 2018). In my thesis, I also found that heatwaves can negatively affect the reproductive success of hyperparasitoids. These results have important implications for insect populations if males of many species are not able to adapt to heatwaves in a warming world. Furthermore, insects in nature are likely to experience multiple stressors. For example, drivers of bee population declines encompass multiple factors, including climate change, pesticides and anthropogenic disturbances (Goulson et al., 2015). My thesis suggests that several climatic factors (wind, precipitation, temperature) may have profound effects on the population dynamics of insects via bottom-up and top-down control. However, the question as to which abiotic and/or biotic factors generate population and biodiversity declines in the real world and which mechanisms underlie such effects need to be addressed. Therefore, more mechanistic studies are urgently needed to better understand the impacts of AGW on biodiversity.

Concluding remarks and future directions

In this thesis, I have addressed how species interactions can be affected by abiotic factors including temperature, wind and precipitation. To fully understand the impact of climate change on plant-based multitrophic interactions, some important aspects of research need more attention in the future. First, I only studied the effects of rainfall and wind on plant-herbivore interactions in a greenhouse experiment. Barton & Ives, (2014) demonstrated that drought influences herbivores across a food chain involving other herbivores and predators. Thus, climate change may indirectly influence herbivores through complex interactions with communities within the same trophic level and/or at different trophic levels. It is important to examine these net effects on food webs in the field. Second, plants and herbivores are important food resources for consumers at higher trophic levels. Future studies should incorporate the whole food chain to provide more insight into the community-level effects of climate warming. Third, plants are known to be able to produce volatile blends that can be used by herbivores, parasitoids and predators as cues to locate their host (Amo, Jansen, van Dam, Dicke, & Visser, 2013; De Moraes, Lewis, Pare´, Alborn, & Tumlinson, 1998; Paré & Tumlinson, 1999). The emission of plant volatiles is influenced by a variety of biotic and abiotic factors, such as temperature and herbivore attack (Holopainen & Gershenzon, 2010). Consequently, warming and attendant changes in drought, precipitation and wind may influence plant volatiles qualitatively and quantitatively, thereby disrupting biotic interactions among species. This is a potentially interesting area for future research. Lastly, other factors, such as changes in CO_2, land use and biological invasions, often influence various antagonistic and mutualistic interactions across trophic levels (Tylianakis et al., 2008). Moreover, increasing climatic variability can weaken top-down control of herbivores, resulting in an increase in the frequency and intensity of herbivore outbreaks (Stireman et al., 2005). Thus, the combined effects of multiple abiotic and biotic factors need further examination.