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Chen, C.

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Summary

Plants play a central role in mediating species interactions within and between trophic levels. Plants quality and quantity can affect the behavior and development of insect herbivores. Furthermore, these effects may cascade up to higher trophic levels, such as parasitoids and hyperparasitoids, through bottom-up processes. However, in nature, these biotic interactions are inevitably influenced by their complex abiotic environment. Understanding abiotic-biotic interactions is becoming increasingly important in a rapidly changing world. The aim of my thesis was to explore how these climate-related factors impact interactions involving plants, insect herbivores, predators, parasitoids and hyperparasitoids. I first investigated effects of simulated wind and rain on the performance of insect herbivores feeding on their host plants. Secondly, I examined the impact of simulated heatwaves on interactions between parasitoids and hyperparasitoids.

In a greenhouse experiment (chapter 2), I studied direct and plant-mediated effects of simulated wind on the performance of two insect herbivores, *Plutella xylostella* and *Pieris brassicae*, feeding on black mustard plants, *Brassica nigra*. Plants were exposed to four different wind treatments that allowed me to separate direct and indirect effects of wind exposure on herbivores. Morphological and chemical traits of plants and developmental parameters of insect herbivores were measured. The results showed that adults of *P. brassicae* grew larger under conditions of direct wind-exposure, but adults of *P. xylostella* did not. Development time of both herbivores was longer. I further conducted a choice experiment to study effects of wind exposure on the preference of an avian predator (*Parus major*) for caterpillars of *P. brassicae* in an observation room. I found that caterpillars on plants without wind exposure had a higher predation risk than caterpillars on plants with wind exposure. I conclude that *P.*

brassicae can perceive lower predation risk under windy condition, and extends its developmental program by prolonging its larval development to achieve a larger adult body size. Using the same model plant and insect species, I tested the effects of simulated heavy rain on the performance of the two herbivores on plants (chapter 3). Rainfall regimes were set either as a single long or as three short rain showers per day. I found that rain exposure extended the development time of both herbivores and had a strong negative effect on the survival of *P. xylostella*, but not on that of *P. brassicae*. Effects of rain exposure on adult body mass depended on species and rainfall frequency. Overall, plant-mediated effects of rain exposure on the herbivores were generally small. The results suggest that changes in the duration and frequency of rainfall may alter the population dynamics of insects and insect community structure.

In a lab experiment (chapter 4), I examined the effects of different temperature regimes on reproduction and functional responses of two hyperparasitoid species, *Gelis agilis* and *Acrolyta nens*. Host cocoons of two different ages were exposed to three different temperature regimes that represent cool, normal and warm conditions in the Netherlands. I found that temperature had stronger negative effects on the reproduction of *G. agilis* (a less fecund species) than on *A. nens* (a more fecund species). Host cocoons of *C. glomerata* developed faster under warmer conditions. Therefore, I conclude that exposure to simulated heatwaves may change community structure at higher trophic levels. Using the same temperature regimes, I further tested the effects of simulated heatwaves on intrinsic competition between two hyperparasitoids, *Lysibia nana* and *A. nens* (chapter 5). I showed that *L. nana* benefited in competition under warmer conditions. Higher temperature enhanced the competitive advantage of the superior competitor. The results indicate that heatwaves associated with global warming may have the potential to reduce species coexistence in the fourth trophic level.

In conclusion, abiotic factors (wind, rainfall, temperature) had important impacts on the plant-herbivore and parasitoid-hyperparasitoid multitrophic interactions that I tested in this thesis. Wind and rainfall exposure clearly affected the performance of insect herbivores. An extended developmental program was observed in *P. brassicae* as a result of a reduction in predation risk under windy condition. Overall, plant-mediated effects of wind and rainfall exposure were generally small. Exposure to simulated heatwaves differentially influenced reproduction and functional responses of two hyperparasitoid species. Moreover, simulated heatwaves negatively affected fitness of species and species coexistence at the terminal end of food chain. Future studies integrating various climate-related abiotic factors into multitrophic interactions at global scale are urgently needed to mitigate the ecological effects of climate change.

Samenvatting

Planten spelen een centrale rol in het reguleren van interacties tussen verschillende organismes binnen en tussen verschillende trofische niveaus. De kwaliteit en kwantiteit van waardplanten kan het gedrag en de ontwikkeling van herbivore insecten sterk beïnvloeden. Als gevolg kunnen deze effecten ook hogere trofische niveaus, zoals parasitaire en hyperparasitaire sluipwespen beïnvloeden, door middel van ‘bottom-up’ processen. In natuurlijke omgevingen worden deze processen onvermijdelijk beïnvloed door de complexe abiotische omgeving. Begrijpen hoe abiotische en biotische interacties functioneren in een snel veranderende wereld is erg belangrijk. Het doel van dit proefschrift, was te onderzoeken hoe deze klimaat-gerelateerde factoren interacties tussen waardplanten, herbivoren, sluipwespen en hypersluipwespen beïnvloeden. Eerst onderzocht ik hoe gesimuleerde wind en regen plant-herbivoor interacties beïnvloedden. Vervolgens onderzocht ik de effecten van gesimuleerde hittegolven op de interacties tussen sluipwespen en hypersluipwespen.

In een kasexperiment (hoofdstuk 2), bestudeerde ik de directe en plant-gereguleerde effecten van wind op de groei van twee herbivore insecten, *Plutella xylostella* en *Pieris brassicae*, voedend op zwarte mosterd, *Brassica nigra*. Planten werden blootgesteld aan vier verschillende windbehandelingen, waardoor ik directe en indirecte effecten van wind op herbivoren kon onderscheiden. Plant morfologische en chemische kenmerken en ontwikkelingsparameters van de rupsen werden gemeten. De resultaten toonden aan dat *P. brassicae* rupsen groter groeiden onder de directe invloed van wind, terwijl dit niet zo was voor *P. xylostella*. De ontwikkelingstijd was langer voor beide herbivoren. Daarna voerde ik een keuze-experiment uit, om de effecten van wind op de voorkeur van een vogel-predator (*Parus major*), voor rupsen van *P. brassicae*

te testen in een observatie-volière. Ik nam waar dat rupsen zonder wind een groter risico liepen op predatie dan de rupsen onder de wind behandeling. Ik concludeer dat rupsen lagere predatie risico's ervaren onder wind omstandigheden, waardoor ze hun larvale stadia uit kunnen rekken om zo een grotere biomassa te vergaren.

Met hetzelfde waardplant modelsysteem en dezelfde insecten, testte ik de effecten van gesimuleerde zware regenval op de groei van de twee insecten op de waardplanten (hoofdstuk 3). Regenval werd gesimuleerd als een enkele langdurige periode van regenval, of als drie kortere regenbuien per dag. Ik bevond dat regenval de ontwikkeling van de rupsen vertraagde en dat regenval een sterk negatief effect had op de overleving van *P. xylostella*, maar niet op *P. brassicae*. De effecten van regenval op de adulte biomassa was afhankelijk van de herbivoor en van de regen-behandeling. De effecten op herbivoren, via de plant, waren over het algemeen klein. Deze resultaten suggereren dat veranderingen in de duur en frequentie van regen de populatiedynamica van insecten en de structuur van insecten gemeenschappen zouden kunnen veranderen.

In een laboratoriumexperiment (hoofdstuk 4), bestudeerde ik de effecten van verschillende temperatuurbehandelingen op de functionele respons van twee hypersluiswespen; *Gelis agilis* en *Acrolyta nens*. Gastheer-cocons van twee verschillende leeftijden werden blootgesteld aan drie verschillende temperatuurschema's die koude, normale en warme condities in Nederland reflecteerden. Ik bevond dat temperatuur een sterker effect had op de voortplanting van *G. agilis* (een minder productieve soort) dan op *A. nens* (een erg productieve soort). Gastheer-cocons van *Cotesia glomerata* ontwikkelden sneller onder warme omstandigheden. Hierdoor concludeer ik dat gesimuleerde hittegolven de structuur van hogere trofische niveau's zouden kunnen veranderen.

In een experiment met dezelfde temperatuur-schema's, testte ik de effecten van gesimuleerde hittegolven op intrinsieke competitie tussen twee hypersluipwespen, *Lysibia nana* en *A. nens* (hoofdstuk 5). Ik toonde aan dat *L. nana* een competitief voordeel ondervond onder warme omstandigheden. Hogere temperaturen versterkten de competitieve voorsprong van de superieure tegenstander. Deze resultaten laten zien dat hittegolven die worden geassocieerd met opwarming van de aarde, potentieel het samenleven van soorten binnen het vierde trofische niveau zouden kunnen beïnvloeden.

Ik concludeer dat abiotische factoren (wind, regen, temperatuur) belangrijke effecten hebben op plant-herbivoor en sluipwesp-hypersluipwesp multitrofische interacties die werden getest in dit proefschrift. Wind en regen hadden duidelijke effecten op de groei van herbivore insecten. Een verlengde larvale ontwikkeling werd waargenomen binnen larven van *P. brassicae*, als gevolg van een verlaagde predatiedruk onder wind omstandigheden. De effecten van regen en wind, via de plant, op herbivoren waren over het algemeen klein. Blootstelling aan gesimuleerde hittegolven had verschillende effecten op twee soorten hypersluipwespen. Bovendien hadden hittegolven een negatief effect op 'fitness' van soorten, evenals op de mogelijkheid tot samenleven van verschillende soorten in het hoogste trofische niveau. Studies die de effecten van verschillende klimaat-gerelateerde abiotische factoren integreren binnen multitrofische interacties zijn nodig om de ecologische effecten van klimaatverandering te verminderen.

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