Impact of climate change on vegetable pest insects - *Aleyrodes proletella* as a model organism

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Abstract

The cabbage whitefly *Aleyrodes proletella* is a serious pest in cabbage. The importance of this species increased in the last 30 years with an enormous increase in the last ten years (Loomans et al. 2002; van Alebeek 2008). The population increase might be a consequence of the climate change and the increase in the average temperature in the last decades. Therefore we investigated experiments to test the influence of climate change on the cabbage whitefly. It has been assumed that the temperature will increase about 2 °C in Lower Saxony in the next century and that extreme events like heat waves will occur more often (Hartmann et al. 2013). Repeated heat waves were modeled in climate chambers to study the effect of this slowly increasing hot temperature on the mortality and development on *A. proletella*. The whiteflies were exposed to the heat waves in all developmental stages either in Petri dishes or on plants. The experiments showed that the temperature and the duration of the heat waves had no influence on the mortality or the developmental success. The only effect was a speeding up of the development from egg to larvae.

An increase in temperature can also effect the plant nutrients and the secondary plant compounds. To test the influence of repeated heat waves on secondary compounds and to investigate if a change in the population density might be caused by them, the glucosinolates in plants exposed to heat waves were analyzed. The heat waves had no significant effect on the amount and composition of glucosinolates, while the sucking of the whitefly increased the amount of glucosinolates, especially sinigrin and progroitin threefold.

Next to the temperature also the precipitation regime will change with an increase in heavy rains in summer, but also more dry spells from spring to autumn. To test the influence of heavy rain a rain arena was constructed where whiteflies were exposed to medium (0.6 l/min*m^2), heavy (2 l/min*m^2) and torrential (6 l/min*m^2) rain. Our experiments showed that the rain had no negative effect on the larvae and the adults were only negatively influenced under torrential rain, whereas half of the egg clutches were destroyed by all rain intensities. Also the egg-laying decreased, if the females had faced a torrential rain shower.

To test the influence of droughts Brussels sprout plants were either water-stressed (water holding capacity > 80%) or drought-stressed (water holding capacity <15%). Plants growing under a normal water holding capacity (40-50%) served as control. The plants grown under drought-stress were significantly smaller compared to the other plants. Under drought stress also the C/N-ratio decreased. Heavy droughts led to a decrease in the egg-laying and the insects which developed under these circumstances were significantly smaller. The water-stress had no significant effect on both plants and whiteflies.

In the last part of the project the influence of mild winters in comparison to cold winters was examined to study the mortality and development of the whiteflies. Furthermore the synchronization between the cabbage whitefly and its natural enemy, the parasitoid *Encarsia tricolor* should be studied. *E. tricolor* is a common parasitoid in Lower Saxony, which is however not able to control the whitefly successfully in the field today. Therefore greenhouses were built, half of them with heating devices, representing semi-field conditions. In autumn Brussels sprout plants, which were infested with *Aleyrodes proletella* in all developmental stages and additional parasitoids were brought into the houses. Our results showed that the adults survived best in the unheated houses while none of the larvae survived. In February the surviving adults laid eggs and the population development was much faster in the heated houses compared to the unheated ones. No parasitoids survived the winter in the greenhouses.

Due to the results of our experiments we assume that the cabbage whitefly will gain in importance in the next years and might become one of the major pests in cabbage.

Keywords: climate change, *Aleyrodes proletella*, heat waves, glucosinolates, drought, simulated rain

Zusammenfassung

Die Kohlmottenschildlaus *Aleyrodes proletella* ist einer der brisantesten Kohlschädlinge. Die Bedeutung dieser Art hat in den letzten 30, ganz besonders aber in den letzten zehn Jahren zugenommen (Loomans et al. 2002; van Alebeek 2008). Dieses Populationswachstum könnte eine Folge des Klimawandels und des Anstiegs der Durchschnittstemperaturen in den letzten Jahren sein. Aus diesem Grund haben wir Experimente entwickelt, um den Einfluss des Klimawandels auf die Kohlmottenschildlaus zu untersuchen. Die Durchschnittstemperaturen werden sich in Niedersachsen bis zum Ende des Jahrhunderts um 2 °C erhöhen und Extremereignisse wie Hitzewellen werden sich häufen (Hartmann et al. 2013). Um den Einfluss von extremen Temperaturen auf die Mortalität sowie die Entwicklung von *Aleyrodes proletella* zu testen, wurden wiederholte Hitzewellen in Klimakammern modelliert. Die Kohlmottenschildläuse wurden der Hitze in all ihren Entwicklungsstadien, entweder in Petrischalen oder aber an Rosenkohlpflanzen, ausgesetzt. Die Ergebnisse zeigen, dass weder die Höchsttemperaturen der Hitzewellen, noch die Dauer des Hitzeereignisses einen Einfluss auf die Mortalität oder den Entwicklungserfolg haben. Einzig die Entwicklungszeit der Eier war positiv beeinflusst.

Der Anstieg der Durchschnittstemperatur kann ebenso die Nährstoffe in Pflanzen und die sekundären Pflanzeninhaltsstoffe beeinflussen. Um die Wirkung der Hitzewellen auf sekundäre Pflanzeninhaltsstoffe zu testen und festzustellen, ob diese einen Einfluss auf die Populationsänderungen von *Aleyrodes proletella* haben, wurden Rosenkohlpflanzen der Hitze ausgesetzt und die Glucosinolate in diesen geprüft. Die Hitzewellen hatten keinen signifikanten Effekt auf die Menge und Zusammensetzung der Glucosinolate, wohingegen die Saugaktivität der Kohlmottenschildläuse, besonders das Sinigrin und Progroitin, um das Doppelte bis Dreifache erhöhte.

Neben der Temperatur wird sich auch das Niederschlagsregime ändern. Es ist eine Zunahme von Starkregenereignissen im Sommer zu erwarten, unterbrochen von länger anhaltenden Trockenperioden. Um den Einfluss dieses Starkregens zu testen, konstruierten wir eine Regenarena, in der die Kohlmottenschildläuse mittlerem (0,6 l/min*m²), starkem (2 l/min*m²) und sintflutartigem (6l/min*m²) Regen ausgesetzt waren. Die Ergebnisse zeigen, dass der Regen keine negativen Auswirkungen auf die Larven von *A. proletella* hatte und lediglich der sintflutartige Regen die Adulten negativ beeinflusste, wohingegen circa die

Hälfte der Eigelege unter allen Regenintensitäten zerstört wurden. Ebenso nahm die Eiablage ab, nachdem die Weibchen einem sintflutartigem Regenschauer ausgesetzt waren.

Um den Einfluss von Trockenperioden zu testen, wurden Rosenkohlpflanzen entweder durch Trockenheit (Wasserkapazität des Bodens <15%) oder durch Überflutung (Wasserkapazität des Bodens >80%) gestresst. Pflanzen in normal feuchten Böden (Wasserkapazität des Bodens 40-50-%) dienten als Kontrolle. Die Pflanzen, die unter Trockenstress wuchsen, waren signifikant kleiner und das C/N-Verhältnis in den Blättern war geringer als bei den Kontrollpflanzen. Derartig starke Trockenheit führte zu einer Verringerung der Eiablage und die Tiere, die sich unter diesen Bedingungen entwickelten, waren kleiner. Das Überangebot an Wasser hatte keine signifikanten Auswirkungen, weder auf die Pflanzen, noch auf die Kohlmottenschildläuse.

Im letzten Teil des Projekts wurde die Auswirkung von milden Wintern im Vergleich zu kalten Wintern auf die Mortalität und die Entwicklung von *A. proletella* untersucht. Darüber hinaus sollte die Synchronisation zwischen der Kohlmottenschildlaus und ihres natürlichen Gegenspielers, der Schlupfwespe *Encarsia tricolor* getestet werden. *E. tricolor* ist eine parasitische Wespe, die natürlicherweise in Niedersachsen vorkommt, unter den heutigen klimatischen Umständen aber nicht in der Lage ist, die Kohlmottenschildlaus erfolgreich zu kontrollieren. Für die Winterversuche wurden Minigewächshäuser konstruiert, in denen es möglich ist, die Insekten unter Semifreilandbedingungen zu untersuchen; die Hälfte der Häuser wurde dazu mit einer Heizung ausgestattet. Rosenkohlpflanzen, die mit Kohlmottenschildläusen in allen Entwicklungsstadien befallen waren, wurden in die Gewächshäuser gebracht. Zusätzlich wurden Mumien der Schlupfwespe in die Gewächshäuser eingebracht. Die Ergebnisse zeigen, dass die adulten Kohlmottenschildläuse am besten in den ungeheizten Häusern überlebten, wohingegen eine hohe Mortalität bei den Larven zu beobachten war. Im Februar legten die überlebenden Tiere Eier, wobei sich die Populationen in den geheizten Häusern deutlich schneller entwickelten als in den ungeheizten. Es fanden sich keine Parasitoide, weder in den geheizten noch in den ungeheizten Gewächshäuser.

Aufgrund der Ergebnisse unserer Versuche nehmen wir an, dass die Bedeutung der Kohlmottenschildlaus in den nächsten Jahren weiter zunehmen und sie zu einem der signifikantesten Schädlinge im Kohlanbau werden wird.

Schlüsselworte: Klimawandel, *Aleyrodes proletella*, Hitzewellen, simulierter Regen, Glucosinolate, Trockenheit

Contents

1 General Introduction

The worldwide climate has changed in the last century due to human impact and it is likely that these changes will continue in the next years. Global scenarios predict an increase in average temperature of about 2-4 °C (0.3- 4.8 °C) and a change in the precipitation regime (Hartmann et al. 2013). But these changes will vary between different continents and regions. It has been forecast that the precipitation in the Sahel zone for example will decrease, while it is going to increase in polar regions, and that the changes in temperature will be more relevant in the higher latitudes than in the equatorial region (Hartmann et al. 2013). It is also likely that the temperature changes will occur mainly in the cold extremes leading to warmer winters and warmer nights (Hartmann et al. 2013). Also more weather extremes like heavy storms, heat waves or extreme rain intermediated by longer dry spells, are to be expected (Hartmann et al. 2013).

Due to these variations in change it is important to predict the regional or even local climate changes. For Lower Saxony a temperature increase of 2 °C till the year 2100 is expected. Lower precipitation in the middle of Lower Saxony concerning the region around Hanover, and little increase in precipitation in the Northern and Southern region are expected due to the fact that the temperature has increased in this region 2-3 °C in the last 50 years and the precipitation has decreased in this region (Haberlandt & Hölscher 2010). Overall we expect more extreme events as forecast worldwide. These changes will have an important influence on our life and especially on agriculture, forestry and water management.

To explore the expected changes and mainly the influence they will have on the ecosystems the KLIFF-Network was incorporated. *“The aim of the research co-operation KLIFF, is to increase the knowledge base of the consequences of climate change at regional and local scales, in order to develop sustainable adaptation strategies”*(Beese 2012). The network is organized in five divisions with different working groups concerning, agriculture and horticulture, forestry and water management. The working group (Pflanzenproduktion - crop production) within which this thesis was preformed, focuses on the influence of the climate change on selected species in some of the most important horticultural crops in Lower Saxony. Agriculture and horticulture are prominent economic sectors in Lower Saxony and it is of utmost relevance to study how key pest species will behave under a changing CO_2-level, warmer temperatures and a changed precipitation regime.

Worldwide, the CO_2-levels will rise with consequences for all creatures including insects. Via the plants, the increased CO_2 will have direct and indirect effects on insects (Bale et al. 2002; Pritchard et al. 2007). Plants generally react positive to increased CO_2: It offers added protection against ozone and increases resistances against pests and viruses while also stimulating growth due to increased photosynthesis (Fuhrer 2003). It also leads to a higher wax layer on leaves and more carbon-based secondary plant compounds (Bezemer et al. 1999; Pritchard et al. 2007; Hillstrom & Lindroth 2008). On the other hand it is leading to a decreased amount of nitrogen in the leaves (Holton et al. 2003). In the experiment of Vuorinen (2004) generalists were able to find the plants regardless of CO_2-level, while specialists were not able to detect the plants under elevated CO_2-concentrations

Other indirect effects of elevated CO_2-levels may be a higher surface temperature of leaves (Fuhrer 2003; Dermody et al. 2008), which might increase growth rate of leaf settling populations. It also leads to a changing C/N-ratio in the leaves due to the faster growth (Williams et al. 2000; Fuhrer 2003) resulting in higher herbivory (Pritchard et al. 2007; Guerenstein & Hildebrand 2008; Thomson & Hoffmann 2010), whereas various species react differently to the changed circumstances. Some aphids reproduce better under increased CO_2, some worse and many aphids do not react to a change in the CO_2-concentration and (Coviella & Trumble 1999; Hughes & Bazzaz 2001; Stacey & Fellows 2002; Newman 2005; Pritchard et al. 2007). The reasons for that may be (a) other plant parameters which are more important for the insects, (b) the change in the nitrogen-sugar-rate is more important than the total amount of nitrogen or (c) a changed sucking behaviour based on a different location on the plant (Hughes & Bazzaz 2001).

But the CO_2 may also have direct effects. Awmack et al. (1997) found that *Aulacorthum solani*, grown under elevated $CO_{2,}$ produce less or no alarm pheromones, therefore making them more vulnerable to predators. Many insects use the carbon dioxide to find their egg laying spaces, because plants assimilate CO_2 manly during the night and CO_2-concentration near the leaf surface is about 80 ppm higher compared to the surrounding concentration (Guerenstein & Hildebrand 2008). A change in the concentration will have direct effects on them (DeLucia 2008). But the increase in the CO_2-concentration in all experiments was very fast, in nature the increase will be slower, giving the insects time to adapt to the new circumstances (Whittaker 2001).

Besides carbon dioxide the amount of ozone and UV radiation will increase as well (Hartmann et al. 2013). There are different findings regarding the effect of O_3 on the plant compounds. Fuhrer (2003) found that an increased amount of O_3 increases nitrogen, sugar and starch in the leaves, while Holton et al. (2003) could show that nitrogen and phenolic glucosides are decreasing and starch and tannins are increasing. The ozone has mainly indirect effects on insects, as it for example can lead to an increase of VOCs (Yuan et al. 2009). As to the CO_2- concentration insects react species-dependent on an increase in O_3 (Holton et al. 2003). The survival rate of a caterpillar (*Malacosoma disstria*) increased under elevated O_3-levels, while the fitness of its parasitoid was decreased (Holton et al. 2003) or even no reaction was detectable (Dermody et al. 2008).

The UV radiation will increase (Fuhrer 2003), but it will have mainly indirect influences on insects. Plants protect themselves against UV with an increasing level of jasmonic acid in the leaves (Foggo et al. 2007). Studies could show that enhanced UV radiation induces resistance to herbivores in plants. Enhanced UV-B leads to an increase in flavonoids, reducing herbivory (Lavola et al. 1998; Rousseaux et al. 2004). On plants grown under enhanced UV-B radiation not only the herbivory, but also the growth rate of herbivores is decreased and their mortality increased (McCloud & Berenbaum 1999; Zavala et al. 2001; Warren et al. 2002). Increased UV radiation not only influences herbivores, it also affects the third trophic level for example parasitoids because plants send the same signals under enhanced UV radiation as under herbivore attack. Therefore parasitoids prefer plants grown under enhanced UV (Foggo et al. 2007). Nevertheless it seems that aphids and whiteflies are more abundant under plants grown under elevated UV (Kuhlmann & Müller 2009).

Increasing temperatures will have several effects on weather events like warmer winters, warmer nights, early snow melting leading to less days with snow cover and longer growing periods, more heat extremes and more days with temperatures at the upper developmental level (Juroszek & Tiedemann 2012). A change in the average annual temperature can result in a changed geographical distribution (increased risk of pest invasion, range expansion), changed seasonal phenology (earlier emergence in spring) or changed population development (decreased winter mortality, faster development) (Juroszek & Tiedemann 2012). The warmer temperatures will have ambivalent effects on insects. Warmer temperatures can promote insects in leading to a faster development, decrease the winter mortality and may boost insects with low frost resistance (Netherer & Schopf 2010). It can also lead to an earlier arrival of the pest in spring making it possible to build up bigger populations and reach the host in an earlier, more vulnerable stage (Juroszek & Tiedemann 2012). But it can be disadvantageous for species that need the cold for their diapause or to increase their frost resistance (Netherer & Schopf 2010). Heat extremes and temperatures near the upper thermal tolerance can also raise insect mortality. Higher temperatures in spring and winter can also lead to an asynchronisation of pests and their natural enemies (Cannon 1998; Parmesan 2006; Hance et al. 2007). Most pest species are temperature-triggered, so that they occur earlier after a mild winter. The breaking of diapause of most parasitoids in contrast is triggered by the photoperiod (Tobin et al. 2008). An earlier emergence of the pest hence cannot be controlled by the natural enemy. Such asynchronism between prey and parasitoid can already be observed with a decrease in parasitism on caterpillars in a more variable climate (Stireman et al. 2005). But there is also evidence that high temperatures in spring can break the diapause independent of photoperiod avoiding the problem of asynchronism (Tobin et al. 2008).

The temperature also indirectly affects herbivores due to changed secondary plant compounds. Glucosinolates are a major group in Brassicaceae which are important in the plants' defence system. The glucosinolates can be found in the cell vacuole separated from the enzyme myrosinase. In the event of herbivory and damage of the plant tissue, the myrosinase can hydrolyze the glucosinolates to volatiles. Different groups of herbivorous insects react differently to glucosinolates. Generalists are repelled by the substances, whereas specialists are attracted and able to metabolise the toxic substances.

The changes in the precipitation regime (more rain in winter, more precipitation in winter with rain instead of snow, less rain in summer, more heavy rains in summer, more frequent droughts) and their effects on insect herbivores are not well understood. Rain has mainly negative effects on insects resulting in a higher mortality due to direct impacts and lower developmental rate due to (a) higher mortality of eggs and larvae and (b) less favourable conditions like cooler temperatures. But also a lack of humidity can influence the insects directly as they might lack humidity essential for egg laying, or indirectly, by fostering the plants with an adequate water ability or impair them with droughts (Bale et al. 2002; Harvell et al. 2002). The plant stress hypothesis predicts that plants suffering drought stress are more vulnerable to herbivore attack and that herbivory and drought will have synergetic negative effects (English-Loeb et al. 1997; Grinnan et al. 2013). This hypothesis is supported by the fact that in tropical forest under extraordinary dry conditions after El Niño events, mass outbreaks of several lepidopteran pest are observed (Van Bael et al. 2004). Especially generalist herbivores benefit from the drought stress, because drought stress reduces the plants defence (Gutbrodt et al. 2011). The plant vigor hypothesis in contrast predicts that insects will prefer fast-growing vigorous plants. In an experiment with soybeans, Grinnan et al. (2013) could show that drought decreased herbivory, which supports the plant vigor hypothesis. Nevertheless it is likely that drought will have mainly negative effects on plants, either through reduced growing or increased herbivory.

In an "old field community climate and atmosphere manipulation experiment" Engel et al. (2009) could show that the impact of the changed temperature eclipsed the effects of the elevated $CO_{2.}$ Hence the influence of CO_2 is not included in this study.

The first part of this thesis will evaluate which pest species in the most important vegetable crops might become important under a changing climate. We also evaluated how the species which are already important in vegetable crops may behave under changed climatic conditions. This will be done by assembly and comparison of developmental thresholds of the different herbivore species in literature to compile a compendium of the most important insect species in horticulture in Lower Saxony.

The effects of climate change may become already visible as they appear to lead to a changed plant community and the appearance of new species. One of those species with gaining importance is the cabbage whitefly *Aleyrodes proletella*. In the 70s this species was found only seldom in private gardens (Loomans et al. 2002), but in the last ten years its distribution and population size increased rapidly (van Alebeek 2008). Nowadays it is one of the most important pest species in cabbage in Central Europe. It is likely that the population increase is a consequence of a changing climate and the altered surroundings with a higher amount of oil rape providing optimal overwintering habitats for the whitefly (Richter 2010). *Encarsia tricolor* on the other hand is a parasitoid that naturally occurs in Lower Saxony and that is specialised in whiteflies like *Aleyrodes proletella*. The species is common to Lower Saxony, yet is not able to fully control the whitefly population here in the field. Schultz et al. (2010) could show that they can be used successfully under agricultural foil, indicating that they have the potential to become an important beneficial against the cabbage whitefly under certain conditions.

In the past, mainly effects of cold and increased temperatures, still ranging within the optimum of the insects temperature thresholds, were studied while extremely high temperatures were merely studied as singular heat events lasting for a short time. Additionally, effects of altered rain patterns are studied rarely, although precipitation is crucial for plant and insects development. Therefore, we performed experiments with the cabbage whitefly as a model organism to answer the following questions.

1. How does a selected study species (*Aleyrodes proletella*) react to very high temperatures and repeated heat waves?
2. How does the glucosinolates in the plant react to repeated heat waves?
3. How does the same species react to heavy rain?
4. How does it (*Aleyrodes proletella*) reacted to drought stress of the plants?
5. How do the selected species and its natural enemy (*Encarsia tricolor*) react to a mild winter compared to a cold winter?

2 Review: Impact of climate change on vegetable pest insects ‒ A case study for Lower Saxony, Germany

2.1 Magnitudes of climate change: on the global and regional scale (Lower Saxony)

Due to human impact the global climate has already changed drastically. Air CO_2 levels increased rapidly (from 280 pm at the beginning of the century to 390.5 ppm nowadays) during the last century, with consequences for temperature and precipitation averages (Gleick 1987). During that time global average temperature increased by 0.74 °C and the distribution of precipitation changed dramatically (Hartmann et al. 2013). Until the end of this century, a further CO_2 increase by factors 2-3 (540-970 ppm) is to be expected and will result in a temperature increase of another 2-4 °C (0.3-4.8 °C) (Hartmann et al. 2013). In general, the continuation of today’s climate changes, i.e. warmer winters and nights as well as further changes in precipitation regime are very likely. Rainfall will move to higher latitudes and although frequencies of storms might drop, their intensity will increase. Generally, different world climate scenarios predict that all kinds of extreme weather events will become more frequent in the future, while regions in higher latitudes are affected the most (Hartmann et al. 2013).

On a regional scale, climate change effects will show in correlation to those expected globally. Yet, due to their nature, they can prove far more difficult to predict, as for example with quickly evolving cloud patterns (Juroszek & Tiedemann 2012). The reason behind is that most prognostic models are developed for a global scale on a grid of 10 x 10 km, without any intention to predict local weather events. Therefore it is likely, that regional weather effects will display high variability and low predictability (Juroszek & Tiedemann 2012).

For Northern Germany, i.e. Lower Saxony, the regional scenarios predict milder winters, warmer summers as recorded in the summer heat waves of 2003 and 2010, which reached temperatures up to more than 40 °C in Germany (38 °C in Lower Saxony) (DWD). A shift of precipitation from the summer to the winter half-year, increased CO_2 levels, and more frequent extreme weather events, like droughts, thunderstorms, heavy rain etc. will complement this.

2.2 Research areas in KLIFF

As a consequence of a changing climate and the lack of knowledge about the reaction of natural recourses in smaller regions like Lower Saxony, the KLIFF-Network (KLImaFolgenForschung in Niedersachsen, Climate impact and adaptation research in Lower Saxony) was founded and funded by the Niedersächsisches Ministerium für Wissenschaft und Kultur (Ministry for Science and Culture of Lower Saxony). It is the aim of the KLIFF-Network to study the influence of the expected climate change on a regional scale. Therefore, several research groups have formed, studying the impact of a changing climate on agriculture, divided in plant- and animal production, forestry and water management inland and the coast respectively. In the working group "plant production" most sub-groups deal with cereal crops and their pests or diseases. The aim of our subgroup (Klimaänderungen: Auswirkungen auf Schadinsekten und Nützlinge im Freilandgemüsebau - Climate Change: Impact on pest and natural enemies on horticulture) is to identify pests which might become more important in the future and study how they behave under a changing climate to help growers to develop adaptation strategies to these threats.

2.3 Impact of climate change on production systems: in general and in Lower Saxony

Climate change will have direct impact (crop selection; growing period; changed temperature, precipitation regime and higher CO_2-level; N availability on assimilation efficacy of specific crops) and indirect effects (pests, diseases) on most production systems (Bale et al. 2002). Field crops will be more affected than crops under protected cultivation due to the fact that in greenhouses temperatures and water supply are regulated. Basically, growers will select crop species based on climatic conditions, market demands and economic value (Tuck et al. 2006). Under climate change conditions it is likely that growers will pay more attention to resistant varieties regarding drought and pest and the selection of new crop species which prefer warmer climates (Seo & Mendelsohn 2008; Olesen et al. 2011). The relevance of protected cultivation might increase since unforeseen weather extremes were not to endanger growth. Additionally there will be an inverse trend insofar today's greenhouse crops will find agreeable conditions in the open field of tomorrow. The most important climate change impact will be expanded growing periods and in consequence the intensification of land use (Olesen & Bindi 2002). The challenge for growers will be to comply with the growing period earlier in the year, thereby increasing the number of cropping cycles. In consequence, supply of nutrients and water has to be adjusted and new crop rotation regimes as well as plant protection strategies have to be adapted (Olsen & Bindi 2002). Finally, policies will have a tremendous effect on the production system, though only within the range of crops that are suitable for specific climatic conditions (Vasil 2003; Stone 2013). For example, the market and subsidies for energy plants in combination with a loss of subsidies for land set-aside made their extensive cultivation highly attractive (Tuck et al. 2006). Consequently, biodiversity (and conservation biological control) in the agricultural landscape is largely affected (Opdam & Wasch 2004). Further incentives and shifts on the crop markets due to political decisions are hard to predict.

In Lower Saxony it is likely that climate change will affect the production systems in a way as outlined above. At the moment the area under cultivation in Lower Saxony is about 2.6 million hectare, of which 35% are agricultural, 30% are meadows and pastures, 16% are energy plants like maize and rapeseed, and only 1.5% horticultural crops are grown. Among the horticultural crops vegetable- (18,712 ha) and fruit-growing (13,515 ha) are most important. Fruit-growing is mainly focused on apples and strawberries, while field vegetable growing is devoted to asparagus (22%), green salad (17%), cabbage (18%), onions (11%) and carrots (9%) (Niedersächsisches Landesamt für Statistik 2011). There is a trend of increasing fruit and vegetable growing over the last 20 years (**Fig. 1**).

In the future, the relevance of different crop groups might follow the trend recognised in the last years, i.e. increasing horticultural growing areas. Trends towards other crop species have not been recognised so far, but i.e. peaches, apricots, and grapevines are already part of the grower's portfolio in Lower Saxony. A peek at other regions where the expected climatic conditions for Lower Saxony are already a reality, i.e. Brittany, France, underlines the further rise of field vegetable crops. Brittany today is one of the most important vegetable producers in Europe and the largest one in France (http://www.invest-in-bretagne.org). Vegetables are grown on more than 80% of the agricultural area, with cauliflower, artichoke, shallot, and broccoli as most widespread crops. Of their land under cultivation, they even yield more than 50% to cabbage (Institut national de la statistique at des études économiques). This might be an indication that vegetable growing will increase substantially in Lower Saxony under future climatic conditions.

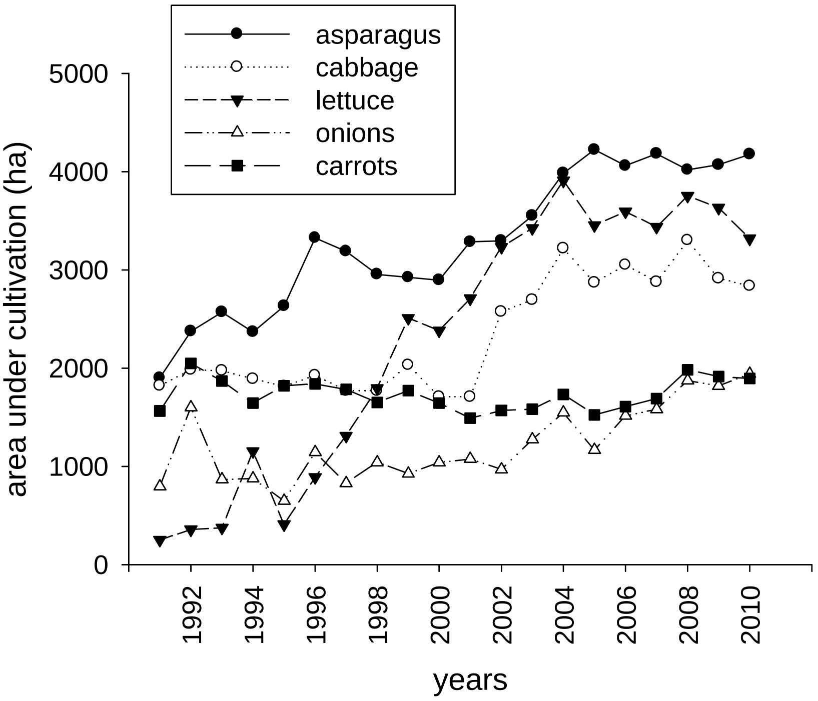

Fig. 1: Area under cultivation of the most important horticultural crops in Lower Saxony (data from Niedersächsischem Landesamt für Statistik).

2.4 Impact of climate change on pest insects and plant protection

Climate change will not only influence crops and cropping systems, but also pest insects and their natural enemies in many ways (Cannon 1998; Bale et al. 2002). It is known that all expected climate changes (CO_2, temperature, precipitation, etc.) influence insects directly and indirectly. By increasing CO_2 levels, insects are influenced to a minor extent directly as well as even more indirectly via the altered nutritional quality of the host plant (Awmack et al.

1997). Among other abiotic factors, temperature is the most important one and influences development times, reproduction and survival rates (Finch et al. 1996; Bale et al. 2002; Morsello et al. 2008). To a wide extent, the relationship between development and temperature is linear, with faster development at higher temperatures, limited only by upper and lower threshold temperatures (Grassberger & Reiter 2002; Kontodimas et al. 2004). The number of developing generations per year will increase and thereby on the evolutionary timescale also the speed of adaptations (Altermatt 2010). In the same way, temperature has a huge impact on locomotion and related behavioural activities. The impact of rain on insects is less understood, but most likely population growth (survival, reproduction) and locomotory activities are impaired. Indirectly, pest insects and natural enemies might be influenced by the host plant nutritional quality and the host's location processes (visual and olfactorial) (Himanen et al. 2008).

Having in mind the predictions for Lower Saxony, i.e. milder winters, warmer summers, a shift in precipitation (from summer to winter), and more frequent extreme weather conditions, the impact of climate change on pest insects and their natural enemies can be summarised briefly by three major effects: Thus, (a) mild winter conditions enhance survival rates, (b) warmer spring, summer and autumn conditions lead to faster development and therefore more generations per year and (c) extreme weather events, like heat waves or heavy rainfall, cause additional mortality and therefore reduce pest numbers. The same pattern can be expected for natural enemies, with the difference that they have different thresholds for development which may lead to shifts towards non-synchronous development with their hosts (Doi et al. 2008).

But under the predicted climate changes, plant protection strategies not only have to cope with changing population dynamics of already important pest species. So far, minor pest species might become key pest species in the future, if their optimal developmental conditions align with future climate conditions or as secondary pests. Additionally new pest species will arrive, either due to range expansion or as invasive species (Warren et al. 2002; Parmesan 2006). Such range expansions can already be observes by the mountain pine beetle (*Dendroctonus ponderosae*) in North Columbia, a species which distribution expanded north- and eastwards in the last decades due to a climate warming (Carroll et al. 2003). In Europe such northward range expansions can be noticed, for example for the winter moth (*Operophtera brumata*) in Fennoscandia (Jepsen et al. 2008). Also the common butterflies European Peacock (*Inachis io*) and the Small Tortoiseshell (*Aglais urticae*) might change their area of distribution. The species survive far better at temperatures of less than 10 °C in winter. With climate warming they will likely migrate northwards (Bale et al. 2002). A range expansion also brings the hazard of new disease. In Canada Ogden et al. (2006) could observe that the tick *Ixodes scapularis* is enlarging its range northwards and will continue to do this boosting the risk of Lyme disease in these regions. In both cases, the predicted climatic conditions might be favourable not only for survival but also for mass development of a new species to gain pest status.

In summary it is likely, that in the future the number of relevant pest species in vegetable crops will increase mainly due to better living conditions and new crop species. Therefore, adequate plant protection strategies have to be adopted.

It is likely that the pest spectrum will change under a changing climate as species, which prefer warmer conditions will become more common. Species that used to annually immigrate, may find temperatures to overwinter in Lower Saxony, while Mediterranean species may migrate to regions further north (Bale et al. 2002). For several pest species, data about their basal developmental temperature and their developmental time are available, but for most of them the upper developmental temperature is not known. Therefore this thesis reflected in the first part the appropriate literature and gathers the available data about the most important vegetable pests in Lower Saxony.

In the following paragraphs, pest species of currently important vegetable crops (sorted by vegetable species) are reviewed according to the predicted impact of the future climate on population development and relevance as a pest. Additional attention is given to the potential of invasive species in relation to the vegetable crop species.

2.5 Important field vegetable crops, pest species and predictions for Lower Saxony

2.5.1 Cabbage

Cabbage is the vegetable crop with most varieties and most pest species in Lower Saxony. More than 13 different varieties are grown on 3301 ha (16,037 ha total in Germany). The most important varieties in 2009 were white cabbage (235 ha, 232 635 dt), cauliflower and Kohlrabi (532 ha, 161600 dt). In general, more than 30 pest species of 10 different taxa (Nematoda; Arthropoda: Diptera, Hemiptera, Lepidoptera, Coleoptera, Heteroptera, Thysanoptera , Hymenoptera) are described for Lower Saxony, yet it is likely that climate change and globalization will increase this number even further. Nevertheless, only 6 are of major importance for growers at the moment:

2.5.1.1 The cabbage whitefly *Aleyrodes proletella*, (Fam. Aleyrodidae, Order Homoptera)

is a polyphagous phloem sucker with a general preference for Brassicaceae and Compositae. Since the 1970th the importance of *Aleyrodes proletella* as a cabbage pest has increased continuously in Central Europe. Especially during the last ten years, a rapid increase was observed (van Alebeek 2008). On the one hand, the reasons behind this can be attributed to climatic changes (better development due to a temperature increase of 1 °C in the last 100 years and more high temperature events), on the other hand to increased land use, i.e. cultivation of winter rape as energy plant, and therefore more favourable habitats for overwintering and mass outbreaks (Richter 2010). So far, the cabbage whitefly is not a pest in rape (Richter 2010). The cabbage whitefly has spread across Europe and is invasive in Taiwan, Australia and Brazil (DeBarro & Carver 1997).

Especially in warmer climates with low rainfall *A. proletella* is a serious cabbage pest (Leite et al. 2005). Among vegetables *A. proletella* shows distinct preferences and frequently is a serious pest on curly kale (Richter 2010). Whitefly feeding causes leaf yellowing and leaf drop, but more important are a sooty mould (growing on honeydew excretions) and virus transmission (i.e. BYNV, Broccoli necrotic yellow virus).

Adult *A. proletella* (Byrne & Bellows 1991) or L4 (Iheagwam 1978) overwinter on cabbage and other brassicae crops (winter rape) as well as wild plants (Richter 2010). Females undergo a reproductive diapause, but egg-laying is also possible during mild winters (Adams 1985). The main egg-laying period lasts from May to September and lifetime fecundity ranges from 40-400 eggs. Mostly, *A. proletella* is active in the morning and eggs are placed on the lower side of the leaf in ring formation. Eggs hatch approx. after 12d and the emerging first larval instars are mobile and select a suitable feeding site. The next three instars (L2-L4) are sessile and covered by wax (Byrne & Bellows 1991).

Development takes place in general above 8 °C, but depending on the larval stage is also possible at lower temperatures (Iheagwam 1978). Optimal developmental temperatures range between 28-33 °C (Alonso et al. 2009). In total, egg to adult development takes 420 °DD (Alonso et al. 2009).

High temperatures and rain are known factors to slow down development (Leite et al 2006). Currently 4-5 generations can develop in Germany within one year (Hill 1987). Mass outbreaks are normally in late summer, when egg to adult development only takes three weeks (Alonso 2009; Richter 2010).

Control of the cabbage whitefly is difficult, on the lower side of the leaves they are hardly reached by insecticide residuals. At present 73 insecticides are approved with 7 different active ingredients (rape oil, green soap, dimethoat, azadirachtin, thiacloprid, deltamethrin, pyrethrin, lambda-cyhalothrin). But most of these pesticides are only available for private gardening. For professional agriculture and horticulture only 7 other insecticides are allowed, with 3 different active ingredients being imidacloprid, gamma-cyhalothrin, lamda-cyhalothrin. It is likely that all neonicotionoids are going to be banished by the EU commission in the foreseeable future (Bundesamt für Verbraucherschutz und Lebensmittelsicherheit). The cabbage whitefly is attacked by several different natural enemy species. Among those, coccinellids (e.g. *Clitostethus arcuatus*, *Harmonia axyridis*), syrphids (*Episyrphus balteatus*, *Eupeodes corollae*, *Melanostona mellinum*) and parasitic wasps like *Encarsia tricolor* and *Encarsia formosa* (not on cabbage plants) are of major importance (Mound & Halsey 1978).

Since the cabbage whitefly is adapted to warmer climates and able to adapt quickly to new environmental conditions, it is likely, that in the future its pest status will not remain limited to field vegetables but also encompass agricultural crops like oilseed rape. Several analyses in fields found that the amount of whiteflies has increased rapidly in the last years (van Alebeek 2008; Richter 2010).

2.5.1.2 The cabbage aphid *Brevicoryne brassicae*, (Fam. Aphididae, Order Homoptera)

is a polyphagous phloem sucker and is found on most cabbage crops, but also on other Brassicaceae host plants. Originally from the Holarctic region, the cabbage aphid shows today an almost cosmopolitan distribution. Within the northern hemisphere and especially in warmer regions, the species is a serious pest (Capinera 2004).

Infested plants show deformations and are not marketable. Additionally, *B. brassicae* is a vector for more than 22 virus species including Cauliflower Mosaic Virus, while aphid honeydew favours growth of sooty moulds (Palacios et al. 2002; Moreno et al. 2005).

The cabbage aphid does not alternate between host plants. Overwintering takes place on cultivated or wild Brassicaceae in the larval stage, as adult aphid (mild winter conditions, anholocycle) as well as in the egg stage (holocycle). The lower developmental threshold is 4 °C for the first instar and development from egg to adult takes 142.9 °DD from a first instar to adult (Satar et al. 2005). Population development continues in April within the overwintering habitat but colonisation of new crop plants takes place with the development of winged adults in June. Winged aphids develop earlier if following a mild winter (Alford et al. 2000). Optimal developmental temperatures range between 20-25 °C (Satar et al. 2005). The number of generations ranges between 6-11 per year. A summer peak occurs from mid-July to mid-August, followed by a population crash. In autumn a population build-up with a second peak from mid-September to mid-December can be noticed. The cabbage aphid prefers warm climates. With dry and hot climatic conditions, population densities increase quickly. In contrast, low temperature and rain negatively influence population development (Leite et al. 2006).

Control of the cabbage aphid is predominantly done with synthetic insecticides. So far, resistance has not developed, although the number of approved insecticides and active ingredients declined over the last years. Today, 46 insecticides with 15 different active ingredients (e.g. thiacloprid, dimethoat, lamda-cyhalorin, thiamethoxam, imidacloprid) are allowed (Bundesministerium für Verbraucherschutz und Lebensmittelsicherheit). The management strategy includes frequent crop walks for monitoring. Early control is important since *B. brassicae* is difficult to control in autumn due to mass outbreaks and colonisation of new hosts in the case of crowding (Hughes 1963). Natural enemies include a range of aphidophagous predators like ladybeetles (e.g. *Coccinella septempunctata*, *Harmonia axyridis*), syrphids (*Episyrphus balteatus*) or green lacewings (*Chrysoperla carnea*). But most important is the aphid parasitoid *Diaeretiella rapae*, which is specialised on *B. brassicae* (but also parasitizes other aphid species).

Since the cabbage aphid has also adapted to warmer climatic conditions, it is likely that the relevance as cabbage pest increases in the future. The effect of mild rainy winters on aphid mortality is being discussed controversially. On the one hand warmer temperatures will allow the aphids to develop faster and build up big populations early in the year, but on the other hand rainy conditions could be disadvantageous, slowing down development and causing higher mortality.

2.5.1.3 The diamond back moth *Plutella xylostella*, (Fam. Plutellidae, Order Lepidoptera)

is a polyphagous lepidopteran pest on cabbage, rape, radish and other Brassicaceae. The origin is in the Mediterranean area but the distribution today is cosmopolitan. The species still expands its range northwards. Since the year 2000 the moth is also frequently found as far north as Spitsbergen, where yearly immigrations with southeast wind streams take place (Coulson et al. 2002). Worldwide, the diamond back moth is an important vegetable pest, especially in Europe, but also in South and North America and Asia (Kfir 1998; Shirai 2000). Damage is mainly caused by loss of leaf surface up to complete defoliation.

Overwintering takes place in the pupal stage, within a silky cocoon on plant debris. First adult moths occur in May, to lay their eggs singly or in small groups on the upper surface of the leaf. The lower developmental threshold is at 7 °C and the upper threshold at 39 °C. Optimal developmental conditions are between 15 and 30 °C (Shirai 2000). In total, development from egg to adult needs 268.2 °DD (egg 51.0, larva 143.2, adult 74.0). Up to 4 generations can develop per year in the UK (Golizadeh et al. 2007). Due to the fact that the average annual temperature in the UK is 9.7 °C while it is 8 °C in Germany, we assume that *Plutella xylostella* can complete 3-4 generations per year in Germany depending on the conditions of the individual year. In the tropics, i.e. lowland Malaysia, 15 generations can develop per year (Capinara 2004). Under optimal conditions the lifecycle is completed in 12-15 days (Hill 1987). Severe damage occurs mainly in warm, dry summers, when this pest can develop rapidly. Again in contrast, increased adult mortality can be caused by rain (Guilloux et al. 2003). Studies so far also indicate that increasing CO_2 levels have a negative impact on the growth rate of *Plutella xylostella* (Reddy et al. 2004), while increasing ozone levels lead to higher feeding activity (Pinto et al. 2008).

The diamond back moth is resistant to several insecticides and therefore difficult to control. Currently no appropriate agents are approved in Germany. Natural enemies of the diamond back moth are of minor relevance, although the parasitoid species *Cotesia plutella* and the egg parasitoid *Trichogramma pretiosum* are dominant. Control with *Bacillus thurgeniensis* toxin or *P. xylostella* granulovirus (PlxyGV) (Subramanian et al. 2010) is feasible. In the latter case, the optimum threshold for PlxyGV application is at 15 larvae per ten plants (Subramanian et al. 2010).

Under prospective climatic conditions it is likely that the relevance of this species will also increase in Lower Saxony.

2.5.1.4 The Cabbage Moth *Mamestra brassicae*, (Fam. Noctuidae, Order Lepidoptera)

is a polyphagous generalist lepidopteran pest found on several Brassicaceae species and other crops, but it prefers cruciferous pest, especially kale and cabbage (Cartea et al. 2010). The insect is native in the Palaearctic, especially Northern Scandinavia and Northern Russia (Harvey & Gols 2011). It is known to be one of the major pests in Europe and Asia (Finch & Thompson 1992) and is the most important cabbage pest in Spain, leading to damages of 80% in the area under cultivation (Cartea et al. 2009). It is also an important pest species in Germany (Forster & Hommes 1992) and the Netherlands (van Alebeek 2008).

The larvae perforate the leaves and this affects the value of the cabbage rendering it not marketable (Cartea et al. 2009). The second generation, which lives in August and September, is the most damaging. They also feed on paprika and lettuce.

The Cabbage moth overwinters in the pupal stages in the soil and develops at temperatures over 7 °C (Johansen 1997a). After a preovipostion period of four days, the females start to lay eggs for around 6 days (Rojas et al. 2001). The egg-laying period takes places only in the scotophase (Rojas et al. 2001). Peak times are in May- June and August-September and the females lay several eggs on the upper side of the leaves. The fifth instar is sensitive to light and hides in the cabbage (Johansen 1997 b). *Mamestra brassicae* has two generations per year with a summer diapause (Goto et al. 2001). The eggs develop in approximately 9 days (at 15.5 °C) to the first larval instar. The lower developmental threshold is 5.4 °C and the upper threshold is not known. In total, development from egg to adult takes 660 °DD (egg 75, larvae 496, and pre-pupae 100) (Johansen 1997b). But the developmental time also depends on the cabbage cultivar the larvae are feeding on (Gols et al. 2008).

The control with *Bacillus thuringiensis* toxin or Bt-plants has not been successful for this species, because the toxin is merely distributed into the alimentary canal and does not reach the hemolymph (Kim et al. 2008). Another possibility of biological control is the releasing of *Trichogramma evanescens* which decreased the attack of *M. brassicae* by 50% (Krnjajic et al. 1997b). Further approaches to fighting the cabbage moth are the fungi *Paecilomyces fumosoroseus* and *Nomuraea rileyi*. These fungi are more effective under temperatures of 25 °C instead of 20 °C against *M. brassicae* (Maniania & Fargues 1992). Thus, an increase in temperature can lead to a more successful protection against the cabbage moth and may reduce the impact of this species in the future.

2.5.1.5 The Cabbage White *Pieris rapae*, (Fam. Pieridae, Order Lepidoptera)

is the most common butterfly species in Europe. The species is native to the Palaearctic and is invasive in North America and Australia. Today it is distributed worldwide (Scott 1986; Capinera 2000). It feeds on several cruciferous plants, but also on other herbs. It is a pest species in many cabbage crops. It is one of the most important pests in Germany (Forster & Hommes 1992) and the most important invasive cabbage pest in North America (Capinera 2004). The larvae feed on the leaves and contaminate them with their droppings.

The species overwinters as pupae 1-3 m above soil level on plants and fences. The egg-laying takes place in May and the female lays single eggs on the upper side of the leaf.

The lower development threshold is 10 °C and the upper developmental threshold is not known. The development from egg to adult takes 184 °DD (Gilbert & Raworth 2000). The growths rates of the larvae are temperature-dependent and reach their peak at temperatures of 35 °C. Above 35°C the growth rates are declining. At temperatures over 40 °C the mortality is very high. The optimal temperature for the larvae is 30.5 °C (Kingsolver 2000).

The reaction of the Small White to temperature changes is ambivalent. The abundance of Small Whites is known to be highest when the previous and current growing session is relatively cool and winter precipitation has been high (Woods et al. 2008). In the case of global warming, it is predicted that mainly the cold extremes, the nights and the winters will warm. Under warmer nights the larvae of *Pieris rapae* develop faster (Whitney-Johnson et al. 2005). But in the same experiment Whitney-Johnson et al. (2005) found, that the pupal mass, which is an indicator for fecundity, is decreasing with increasing night temperatures. But this effect was overcompensated by the shorter developmental time.

For Cabbage Whites 15 different insecticides with 9 active ingredients (thiacloprid, beta-cyfluthrin, gamma-cyhalothrin, cypermethrin, deltamethrin, alpha-cypermethrin, lamba-cypermethrin, tau-fluvalinat, esfenvelerat) are accredited (Bundesamt für Verbraucherschutz und Lebensmittelsicherheit). But also biocontrol methods are effective in the reduction of the Small White. In most cases the parasitoids are not able to reduce the pest effectively (Parker & Pinnell 1972; Lundgren et al. 2002). Treatments with *Bacillus thuringiensis* can reduce the activity of the Small White significantly (Chen et al. 2008). But in combination with the parasitoids *Cotesia rubecola* (McDonald et al. 1990) or *Trichogramma evanescens*, the bacterium can reduce the caterpillars much more effectively (Krnjajic´ et al. 1997a).

2.5.1.6 The Cabbage Root Fly *Delia radicum*, (Fam. Anthomyiidae, Order Diptera)

is the most important pest on cabbage. It is native to Europe and was introduced to Northern America around 100 years ago (Turnock et al. 1998). The insects feed on cruciferous plants and cause high damage to cabbage crops. In Canada it is one of the main pests in canola and can lead to losses of 20% to 50% (Griffiths 1991). The insects prefer turnips and rutabagas (Dreves et al. 2006). The larvae of the species feed on the fine roots, which can lead to wilting or dying especially of young plants. It also opens the way for pathogens (Hemachandra et al. 2007) such as black leg (*Phoma lingam*), bacterial soft rot (*Erwinia carotovora*) and root rot (*Fusarium* and *Rhizoctoinia ssp.)* (Griffiths 1986; McDonald & Sears 1992). As pupae in the soil, the species hibernate from October until middle of April. From the middle of April to May, the first flies are hatching more or less at the same time (Johansen & Meadow 2006). Three days after the flight peak they are starting to lay eggs into the soil next to the stem or into the floret of Brussels sprouts. There are three generations a year with the flying peak in April-May, in July and in September. (Landesamt für Landwirtschaft Mecklenburg-Vorpommern). One female can lay up to 100 eggs. The eggs hatch within 3-9 days and the larvae will then start to feed on the roots. After 2-3 weeks of feeding the larvae pupate and after 1-2 weeks the new generation of flies hatch (Dreves et al. 2006).

The lower developmental threshold is 6 °C (Collier & Finch 1985) and the insects need 580-600 °DD to complete their life cycle (Aguiar et al. 2007; Dreves et al. 2006).

It is assumed, that with an average warming of 3 °C in the UK, *Delia radicum* would emerge one month earlier (Collier et al. 1991). In North America two different populations of *Delia radicum* occur, one which is early emerging and one late-emerging. In early summers the early emerging can complete three generations and the late emerging 2.5. The last of the year suffers high mortality. In late summers it is the other way round, with the first population completing 2.5 generations followed by 2 later the year (Hance et al. 2007). In face of climate change we expect more early summers which would lead to a dominance of the early emerging population. With a temperature increase of five or ten degrees the species would be able to complete four generations per year. Yet, average day temperatures over 25 °C inhibit the egg laying and under dry soil conditions, the eggs would die. At temperatures of over 21 °C pupal development stops and starts again when it’s getting cold (Collier & Finch 1985).

With climate change, also the conditions for control of *D. radicum* could change. One option of biological plant protection is the release of the entomopathogenic nematode *Steinernema felitae*. *S. felitae.* is not very effective at the low temperatures of springtime, but can reduce the amount of cabbage maggots considerably, when released in the summer (Chen et al. 2003). The nematodes efficiency could therefore increase with rising temperatures and shifts of the season.

2.5.1.7 The Cabbage flea beetle *Phyllotreta cruciferae*, (Fam. Chrysomelidae, Order Coleoptera)

is a species with increasing importance in the last years. The insects overwinter as adults in the soil or in leaf litter (Vig 1998). They become active in the spring when the daily temperature exceeds 15 °C (Mihailova et al. 1982), and migrate in May, when the soil temperature exceeds 15 °C (Ulmer 2006), from wild cruciferous plants and rape oil fields to young cabbage crops (Toshova et al. 2009). The females lay their eggs into the soil next to the fine roots and the larvae feed on the roots. In June, the young beetles which feed on the leaves hatch but only cause little damage. The adults migrate to their hibernation sites early in autumn. In Europe, the beetles normally have one generation per year (Vig 1998). In some years there is a second period of egg-laying in autumn, which is mainly observed in Canada and Massachusetts (Andersen et al. 2006).

The beetles damage the plants due to the adults feeding on the leaves while the larvae devour the roots. Especially young plants suffer from high mortality by this two-pronged assault. Yet, even the mere feeding of the adults alone can lead to large damages and wilting of the plants (Toshova et al. 2009). When plants are beyond the seedling stage they are less vulnerable to the damage (Gavloski & Lamb 2000). Especially under dry conditions the feeding of the beetles can be harmful to the plants. Flea beetles can also cause indirect damage by transmitting the Turnip yellow mosaic virus, the Radish mosaic virus and the fungus *Alternaria brassicicola* (Shelton & Hunter 1985; Dillard et al. 1998; Stobbs et al. 1998; Glits 2000).

The base developmental temperature for these insects lies around 11 °C and they need 455 °DD to complete their life cycle (Kinoshita et al. 1979). The upper developmental temperatures and the optimal temperatures are not investigated. But it is known, that low winter temperatures and high summer temperatures have a negative effect on the flea beetles (Howard 1920; Toshova et al. 2009), while very warm and dry weather has a positive effect (Hiiesaar et al. 2003). Due to fact that future scenarios predict warmer summers and winters it is likely that the importance of the flea beetles will decrease.

New pest species:

2.5.1.8 The Cabbage semi-looper *Trichoplusia ni*, (Fam. Noctuidae, Order Lepidoptera)

is a lepidopteran pest, which in Europe is mainly distributed in the South, migrating from subtropical regions. The species regularly reaches several regions in Germany, but it cannot survive the winter. The Cabbage Looper has spread globally except reaching Australia (Forster & Wohlfahrt 1971). In North America and in the Southern regions of Europe it is one of the most important pest species (Capinera 2004). It is a multivoltine generalist species (McCloud & Berenbaum 1999).

It overwinters in Southern regions as larvae and pupates in spring in a white cocoon. The adults of the first generation hatch in May and June, while the adults of the second generation fly from July till September (Forster & Wohlfahrt 1971).

The base developmental temperature lies around 10 °C (Toba et al. 1973) and the species needs around 350 °DD to complete its development (Butler et al. 1975).

With a warming of the climate it would become possible for this species to overwinter in northern European areas such as Germany and hence infest plants in earlier stages then today. This would increase its damage potential and change its status to an important pest species in the future.

2.5.2 Asparagus

Asparagus is the crop with the highest area under cultivation dedicated to it in Lower Saxony (3948 ha in Lower Saxony and 19,634 ha in Germany). Since asparagus is cultivated in monoculture on the same field and for several years on end, it is likely that especially pests related in their biology close to that crop will increase with time. There are three important pest species in asparagus (invasive species are not known), two coleopteran species and one dipteran species:

2.5.2.1 The Asparagus Fly *Platyparea poeciloptera*, (Fam. Tephritidae, Order Diptera)

is next to the asparagus beetles the most important pest species in asparagus (Crüger 1991). It causes damage in all European countries (Fischer et al. 1989). It is distributed in the whole of Europe except in the Mediterranean (Merz 1994).

The species overwinters as pupae in the soil on old asparagus plants and in spring the young adults start to hatch. The hatching can last up to several months (Eckstein 1934). Some days after hatching, the females lay eggs into the asparagus stems. The main flying period is from May to June (Otto 2002). One female can lay up to 80 eggs (Dingler 1934). The larvae feed on the plant tissue causing damage with the feeding holes. After one month they pupate in the dying asparagus stems (Otto 2002) and spend the rest of the year, around ten months, as pupae (Merz 1994). Their flight activity lasts from April until July or August (Otto 2002). The species is strictly univoltine (Otto 2002).

The asparagus fly is known to damage mainly young plantings (Crüger 1991; Otto 2002). Below temperatures of 15 °C the adults are in a cold rigor (Koch 2011). There are no data about the lower and upper developmental temperature available. The eggs develop after 3-10 days to larvae and the larvae need 17-35 days to develop to pupae (Nijvelt 1957). Field studies show that the larvae develop in three to four weeks with three ecdyses (Koch 2011). It is assumed that asparagus flies show a higher flying activity under temperatures over 25 °C (Dingler 1934).

In the last years, the importance of the asparagus fly increased due to the covering of fields with foils and earlier harvesting. The increased temperature under the foils leads to a faster development and earlier harvesting of the asparagus. Thereby, the harvesting time of the asparagus matches the peak of flight activity of the asparagus fly. The importance of the asparagus fly will increase the more growers start to harvest asparagus early in the year and as warmer springs will promote the development of *Platyparea poeciloptera*.

2.5.2.2 The Spotted Asparagus Beetle *Crioceris duodecimpunctata*, (Fam. Crysomelidae, Order Coleoptera)

is closely related to the Common Asparagus Beetle, but bears a lower damage potential. He is native to the Palaearctic region and was introduced to North America at the beginning of the last century (LeSage et al. 2008). It is the second most important pest species on asparagus. The species is monophagous on asparagus (Clark et al. 2004). The beetles hibernate as adults in the soil or under fallen leaves. The Spotted Asparagus Beetle occurs at the same time as the Common Asparagus Beetle, though its oviposition starts one month later than its latter cousin (Fink 1913). The eggs need 7 to 12 days to develop to larvae (LaSage 2008). The larvae then crawl to the berries of the asparagus plants and bore into it (Capinera 2001). After three to four weeks and four larval stages the larvae pupate in the soil (LaSage 2008). Pupation lasts 12-20 days (Fink 1913). There are two generations per year with a peak in July and September (Armand 1949). There may be no data about the temperature dependence of this species available, yet it appears likely that they are similar to the Common Asparagus Beetle (See 2.5.2.3.).

But the damage of the Spotted Asparagus beetle is in contrast to the Asparagus Beetle mainly important for plants which are already weakened by cold stress (LaSage 2008). The relevance of this species will decrease, since rising temperatures will reduce cold-stress and thereby the vulnerability of plants.

2.5.2.3 The Asparagus Beetle *Crioceris asparagi*, (Fam. Crysomelidae, Order Coleoptera)

is a specialist on asparagus and native to the Palaearctic having originated in the Mediterranean (Fara 2007; LeSage et al. 2008). The beetles are a common pest in Europe and North America, feeding exclusively on asparagus. The adults overwinter hidden under stones, sticks, litter or decomposing asparagus stems (Drake & Harris 1932). In April or May they start with the egg-laying and place the eggs under the plants’ leaves or stem. After three to eight days the larvae emerge and feed on the foliage for 10 to 14 days until reaching full growth (Watts 1912; Capinera 2001). The first generation appears in June. The individuals of the second generation that appears in July then go into diapause until the next spring. There are two to three generations of beetles per year, with flying peaks in June, early July and early August (Campbell et al. 1989). The damage is caused by the feeding of larvae and adults alike (Watts 1912).

The base developmental temperature is 8 °C and the upper developmental temperature is 34 °C (Taylor & Harcourt 1978). The optimal temperature is 32 °C for the first and the second larval instars and 30 °C for the third and fourth instars (Taylor & Harcourt 1978).

Due to the fact that the optimal development temperatures of the Asparagus Beetle are very high, it seems probable that the impact of this species increase in the future.

2.5.3 Salad

Salad is the second most important horticultural crop in Lower Saxony with an area under production of 3732 ha. The most important cultivars are iceberg lettuce (4700 ha in Germany), corn salad and mini romana (334 ha) (Monatsschrift Magazine für den Gartenbauprofi 2009). Salad is host to around 20 pest species, mainly aphids.

2.5.3.1 The Lettuce Aphid *Nasonovia ribis-nigri*, (Fam. Aphididae, Order Hemiptera)

is the most important aphid pest in lettuce (Sauer-Kesper et al. 2011). It is native to temperate zones of Europe (Nebreda et al. 2004) but has gained worldwide distribution at this point (Fagan et al. 2010). The aphids are holocyclic, their primary hosts being currants, but use a wide range of plants, including lettuce, as secondary hosts (Collier et al. 1999). In temperate regions they are anholocyclic (Lacasa et al. 2003) and use the secondary hosts during the whole year (Blackman & Eastop 1984).

The feeding of the aphids lead to leaf distortion and secondary head rots (Fletcher et al. 2009), and they are an important transmitter of several viruses such as Necrotiv Yellow Virus (NYV) or the Lettuce Mosaic Virus (LMV) (Vasicek et al. 2002). Normally, they hide in the lettuce head (Parker et al. 2002). The adult aphids overwinter on currant plants and migrate in spring to the lettuce plants. The females deposit the offspring next to the terminals of young leaves and they colonise the wrapping leafs in the lettuce head (Palumbo 2000). The lower developmental threshold is 3.6 °C for apterous aphids and 4.1 °C for alate aphids, while the developmental time is 125-129 °DD and 143-144 °DD respectively (Diaz et al. 2007). The upper temperature threshold is 35.9 °C for apterous and 33.6 °C for alate aphids (Diaz et al. 2007). The optimal temperature for population development is between 20 and 24 °C (Diaz & Fereres 2005). The temperature has also an important effect on the ratio between alate and apterous insects. At temperatures of 20-28 °C the proportion of alate is around 40-57%. At temperatures below 16 °C nearly all of the adults are apterous (Diaz & Fereres 2005). The temperature seems to be the only parameter that influences the proportion of alates (Liu 2004a). Up to the year 2007 the control of the aphids was without any problems, yet, in the last years a new resistant biotype (rb-type) has emerged (Meyhöfer & Poehling 2013).

Due to the fact, that the Lettuce Aphid faces a high mortality under air temperatures above 30 °C (Diaz et al. 2007) and no nymphs are produced under air temperatures above 28 °C (Diaz & Fereres 2005), it is likely that the importance of this aphid species will decrease in the future.

2.5.3.2 The Potato Aphid *Macrosiphum euphorbiae*, (Fam. Aphididae, Order Hemiptera)

is native to North America but has been introduced to Europe and Asia (Blackman & Eastop 1984). The females hibernate on lettuce in greenhouses or on weeds (Rothamstead Research). In May and June they migrate to the host plants. In Europe they are mainly anholocyclic and they reproduce parthenogenetically, so that they can build up big populations in a very short time (Blackman & Eastop 1984). In North America a sexual phase on *Rosa spec*. occurs. The species is highly polyphagous, but they prefer plants from the family Solanaceae.

The insects can spread several viruses, such as the lettuce mosaic virus, the potato leaf roll virus (PLRV) or beet yellows virus (BYV). The base developmental threshold is lower than 5 °C (Barlow 1962), and 144.9 °DD are needed to complete the development (De Conti et al. 2011). The optimal developmental temperature is around 20 °C and the upper developmental threshold ranges between 25-30 °C (Barlow 1962).

Since the upper developmental threshold is relatively low with 25 °C it is likely that the importance of this species will decrease in future.

2.5.3.3 The Foxglove Aphid *Aulacorthum solani*, (Fam. Aphididae, Order Homoptera)

is a cosmopolitan species which is native to Europe (Vasicek et al. 2002; Blackman & Eastop 1984). Its primary hosts are common foxglove (*Digitalis purpurea*) and common perennial hawkweed (*Hieracium* spp.) (Wave et al. 1965). The anholocyclic tribes of the species live the whole year on secondary hosts, which include several herbaceous plants (Jandricic et al. 2010). The salivary secretion of this aphid is toxic to several plants and produces decolouration and deformation of the leaves. In high concentration it can lead to complete defoliation (Sanchez et al. 2007). On top of this, the species is an important vector of viruses (Stoltz et al. 1997).

The basal development threshold is 3.7 °C and the upper developmental threshold 35 °C. 141 °DD are needed to complete the development from egg to adult of the aphid. The optimal temperature for development is at around 23 °C (Jandricic et al. 2010).

The impact of this aphid increased in recent years (Jandricic et al. 2010) and it is likely that its importance will increase in the next years.

2.5.3.4 The Green Peach Aphid *Myzus persicae*, (Fam. Aphididae, Order Homoptera)

is one of the most common aphids in Lower Saxony. The species is believed to be native to Europe, yet today features worldwide distribution. The aphid is highly polyphagous to their secondary hosts, but very specialized on the primary host. The species overwinters in eggs on *Prunus persica* trees and the adults emerge in spring to migrate to their secondary host plants. In the summer months, the species reproduce asexually, which means that females give birth to nymphs and can build up big populations. In autumn, when the temperatures are dropping, sexual morphs are formed and eggs are laid on the trees again (Blackman & Eastop 1984). In warmer regions they can also be anholocyclic (Blackman 1972). High population of aphids lead to wilting and curling of the leaves. They are very efficient in transmitting viruses (Blackman & Eastop 1984), and are known to transmit more than 100 types.

The base developmental temperature is lower than 5 °C (Barlow 1962) and it takes 130 °DD to complete development (Whalon & Smilowitz 1979). The optimal temperature for development is 25 °C (Barlow 1962), while the upper developmental threshold is 34.2 °C (Davis et al. 2006).

It is likely that this species will continue to be one of the most important aphids in Lower Saxony, because it is highly polyphagous and will be able to adapt to other crop species easily.

2.5.3.5 The Lettuce Root Aphid *Pemphigus bursarius*, (Fam. Pemphigidae, Order Homoptera)

is a gall forming aphid on poplars (*Populus nigra*) (Miller et al. 2005). The species features worldwide distribution (Pike et al. 2007). The aphids overwinter as eggs, which are laid on the bark of a poplar. Out of every egg a female is hatching which is building up a population in the galls (Miller et al. 2005). Around 60 aphids are living in one leave gall, which are open most of the time (Pike et al. 2007). The alate offspring abandons the galls from May to September, with peak emergence in June-July and colonise the roots of several plants, e.g. salad (Collier et al. 1994). On secondary hosts they reproduce with parthenogenesis (Miller et al. 2005). In autumn, another winged generation is produced which returns to the poplars and gives birth to the sexuparae (Braendle & Foster 2004). But anholocyclic tribes which overwinter on the host roots are also known (Phillips et al. 1999). The Lettuce Root aphid is one of the few social aphids with soldiers defending the galls. The soldiers are nymphs which are not morphological specialised and are moderately aggressive (Pike et al. 2007).

The base developmental threshold is at 4 °C. The aphids feed on the roots of the lettuce plants and weaken them by their sucking. At the moment *Pemphigus bursarius* is a minor pest and damages the plants only in cases of drought stress (Collier et al. 1994).

Although droughts will occur more often in future, the importance of this species will not increase, because farmers will irrigate their plants to avoid crop loss due to droughts.

2.5.4 Carrots

Carrots are the second most common horticultural crop in Germany (10,504 ha) after asparagus and also one of the most important in Lower Saxony (1733 ha).

2.5.4.1 The Carrot Rust Fly *Psila rosae*, (Fam. Psilidae, Order Diptera)

is the most important carrot pest in Northern Europe (Dirksmeyer et al. 2005). It is native to Europe but has been introduced to the Americas. The insects are mainly living on Apiaceae and damaging carrots and celery. The insects hibernate as pupae in the soil or as larvae in plant material (Collier et al. 1994). The adults fly in April and May and the females lay their eggs into the soil next to the roots at that time. The first larval stage feeds on the fine roots, where after the second and third larval stage inflict damage by boring into the carrot itself. Four to seven weeks after hatching they pupate. At temperatures above 22-25 °C the pupae fall into diapause to avoid drying-out. The lower developmental threshold is between 2-4 °C and the development requires around 1140 °DD (Finch & Collier 1996). Up into the 1980s, only two generations of carrot flies developed in Germany, but since the 1990s, nearly every year a third generation is completed. The second generation is the most dangerous one. Feeding on young plants, it makes them wilt and perish. On older plants the larvae harm the carrot body and the feeding destroys it, make it unmarketable. In dry areas, fewer flies are found (Schoneveld & Ester 1994) and at soil temperatures above 26 °C, high egg mortality is observed (Burn 1984). Thus, the relevance of the carrot rust fly is likely to decrease in the future.

2.5.4.2 The Turnip Moth *Agrotis segetum*, (Fam. Noctuidae, Order Lepidoptera)

is one of the most important pests in carrots in Central Europe (Dirksmeyer et al. 2005). It is distributed worldwide in temperate as well as in subtropic regions (Svensson et al. 1997). The larvae of this species overwinter 3-7 cm below the soil surface. In April, they ascend to 1-3 cm below the surface to pupate (Ogaard & Esbjerg 1993). The adults of this first generation fly from May to July and the females lay their eggs on leaves in small groups. The larvae feed on several plants including crops like potatoes, salad and carrots and on coniferous plants. The larvae pupate in the soil and the second generation is flying from August till September.

From the beginning of the century to the 70s the population of the turnip moth did rise steadily, yet in the last years it decreased (Esbjerg & Mogens 2005), perhaps due to the wet June in the last years.

The basal developmental temperature is around 11 °C (Bongers & Weismann 1971) and depending on the diet around 520 °DD are needed to complete the development (Görnitz 1951). They are a serious pest to several crops and can lead to high damages of up to 30% in carrots (Zethner 1980). It has been assumed that hot summers would advance the development of the species (Esbjerg & Mogens 2005), increasing its importance under climate change conditions.

2.5.4.3 The Carrot Psyllid *Trioza apicalis*, (Fam. Triozidae, Order Hemiptera)

is an important pest species on carrot plants. This Psyllid species is distributed over the whole of Europe, yet more damaging in Northern and Central Europe (Munyaneza et al. 2010). The species hibernate as adults on common spruce or on other coniferous plants (Kristoffersen & Anderbrant 2007). In May, the egg-laying on the carrot leaves starts. The eggs are laid on the edges of the leaves one by one (Nehlin et al. 1996). Within around 10 days the little yellow larvae develop (Valterova et al. 1997). The nymphs need around six weeks to develop to adults, which then migrate over the duration of two to three days after exclusion back to their hibernation sites (Valterova et al. 1997). There is only one generation of carrot psyllids per year (Laska & Rogl 2008). The species is specialised on carrot plants and depends on them for reproduction (Kristoffersen & Anderbrant 2007).

The larvae and especially the adults damage the plants due to their phloem sucking (Nissinen et al. 2007) and the excretion of their saliva, which leads to a rippling of the foliage and the transmission of viruses (Munyaneza et al. 2010).

We assume that the meaning of this species will not change in future.

2.5.5 Onions

Onions are grown on approximately 2000 ha in Lower Saxony (9691 ha in Germany) and face three important pest species.

2.5.5.1 The Onion Maggot *Delia antiqua*, (Fam. Anthomyiidae, Order Diptera)

is native to Europe, but today the species is also common in North America and Japan (Otto 2002), and it is the most important onion pest in Europe (Dirksmeyer et al. 2005). The species is a pest on all bulbous plants due to the feeding of the larvae. Damaged by the larvae, bacteria and fungi can infest the plants (Everts et al. 1985). The species overwinter with pupae in the soil. The pupae are diapausing until mid-January (Otto 2002) and then start to finish their development. After a feeding period on flowering plants, the females lay their eggs in groups of 5-20 eggs next to the bulbs (Otto 2002). The larvae feed on the roots leading to wilting and dying of the plants. They pupate next to the bulbs in the soil (Carruthers 1979). If summer temperatures are above 24 °C the pupae are in a summer diapause, regardless of the photoperiod (Ishikawa et al. 2000). The optimal temperature to complete diapause is 16 °C (Ishikawa et al. 2000).

The lower developmental threshold is 4 °C and 640 °DD are needed to complete the life-cycle (Lui & McEwan 1982). For the development of the eggs around 60 °DD are needed and for the larvae around 260 °DD. In Europe one to four generations per year have been observed (Otto 2002), with one generation in Norway (Rygg 1960) and up to four generations in Austria and Turkey (Keyder & Atak 1972).

Nomura & Ishikawa (2001) found that non-diapausing pupae cannot survive temperatures above 35 °C for more than 6 days. If the heat lasts shortly, only some hours, they can recover. To prevent young onion plants from feeding, seeds are incrustated (Otto 2002). Heat waves, which are harmful to the pupae will occur more often in the next decades (Hartmann et al. 2013). Therefore it is likely that the importance of this species will lose importance in the future.

2.5.5.2 The Leek Moth *Acrolepiopsis assectella*, (Fam. Yponomeutidae, Order Lepidoptera)

is native to Europe and Asia and is distributed as far east as Japan. The butterflies are being introduced to other parts of the world for example Canada right now (Handfield 1997). The insects feed on cultivated Allium plants, especially on leek and onions (Mason et al. 2011). The feeding of the larvae weakens the plants and due to feeding holes the plants are not marketable (Mason et al. 2011). They overwinter as adults under leaf debris and emerge in April when the temperature is above 9.5 °C (Garland 2002). In May, the females lay their eggs in the leaves' axils. The larvae feed on the young leaves, undergo five larval stages and then pupate in cocoons on the plant surface or in the soil. In Europe two to four (in Italy even six) generations of the leek moth can be observed per year (Asman 2001). Mainly in hot and dry summers, they can cause big damages on onion crops. The base developmental threshold is 7 °C and full development requires around 445 °DD. The developmental time differs regarding to region (450 °DD in France and 630 °DD in Sweden) (Mason et al. 2011). It appears likely, that the developmental time in Lower Saxony will be between the data of France and Sweden, with an average of around 520 °DD. This species poses a problem for Integrated Pest Management. Due to their hidden life in the onion leaves, they are hard to reach for pesticides as well as for natural enemies. In Europe, the leek moth leads to minor damage compared to the other two pest species (*Thrips tabaci*, *Delia antiqua*). But due to the fact that it causes major damage under dry and hot conditions, this species can become more important in the future.

2.5.5.3 The Onion Thrips *Thrips tabaci*, (Fam. Thripidae, Order Thysanoptera)

is an important pest species in onion crops. Thrips are polyphagous sucking insects and distributed worldwide. Their origin is believed to be in the eastern Mediterranean (Mound 1997). Damage is inflicted on several cultivated crops, especially on onions and cabbage. Due to the sucking on the host plants' cell tissue, the plants cannot photosynthesize adequately. Thrips can also transmit viruses like TSWV (Morsello et al. 2008) or the much more dangerous Iris yellow spot virus (IYSV).

The adults of the species hibernate in the soil in onion fields or next to them (Larentzaki et al. 2007). They start to become active from March/April until October/November, with an activity peak in June-July (Bergant et al. 2005). One female can lay up to 260 eggs (Murai

2000). *Thrips sp*. can reproduce sexually and asexually. Mated females lay eggs which develop to males and females while unmated females lay eggs that develop to females (van Rijn et al. 1995). Due to this, one female alone can build up big populations (Diaz-Montano et al. 2011).

The lower developmental threshold is 6 °C and the species needs 260 °DD to complete their life cycle (Stacey & Fellows 2002; Bergant et al. 2006). Other authors investigate a basal threshold of 10 °C and a developmental time of 232 °DD (Murai 2000). The optimal temperature for development lies at around 25 °C (Murai 2000). Temperatures above 30 °C can cause high egg mortality (Murai & Toda 2002).

Under a changing climate, *Thrips tabaci* could become more important. Hotter summers are already followed by a bigger population of *T. tabaci* and warmer winters would lead to an early emerging of the species in spring (Bergant et al. 2005). Heavy rain (daily above 1.8 cm or more (Liu 2004b)) can inhibit the development of thrips (Leite et al. 2006) and it can wash the insects off the plants (North & Shelton 1986), but the positive effects of the temperature will predominate the effects of the rain.

Tab. 1: Cardinal values of important field vegetable pest species.

Crop	**Pest species**	**Order**	**Lower develop-mental threshold (°C)**	**Upper develop-mental threshold (°C)**	**Develop-ment time (degree days)**	**References**
Cabbage	*Aleyrodes proletella*	Hom.	6.88/ 10.4	>33	420	Alonso et al. 2009
	Brevicoryne brassicae	Hom.	4	?	142.9	Satar et al. 2005
	Plutella xylostella	Lep.	7.4	39	268.2	Liu et al. 2002
	Mamestra brassicae	Lep.	7		660	Johansen et al. 1997 b
	Pieris rapae	Lep.	10	?	184	Gilbert & Raworth 2000
	Delia radicum	Dipt.	6.1	?	580-600	Aguiar et al. 2007; Dreves et al. 2006
	Phyllotreta spp.		11	?	455	Kinoshita et al. 1979

	Trichoplusia ni	Lep.	10.9	?	342.7	Toba et al. 1973; Butler et al. 1975
Asparagus	*Platyparea poeciloptera*	Dipt.	?	?	?	
	Crioceri duodecimpunctata	Col.	?	?	?	
	Crioceris asparagi	Col.	8	34	317	Taylor & Harcourt 1978
Salad	*Nasonovia ribis-nigri*	Hom.	3.6/4	35.9/33.6	129/143-144	Diaz et al. 2007
	Macrosiphon euphorbiae	Hom.	5	>30	144.9	Barlow 1962
	Aulacorthum solani	Hom.	3.7	35	141	Jandricic et al. 2010
	Myzus persicae	Hom.	5	34.2	130	Barlow 1962, Whalon & Smilowitz 1979
	Pemphigus bursarius	Hom.	4.4	?	?	Collier et al. 1994
Carrot	*Psila rosae*	Dipt.	2-4	?	1140	Finch & Collier 1996
	Agrotis segetum	Lep.	11	?	520	Görnitz 1951; Bongers & Weismann 1971
	Trioza apicalis	Hem.	?	?	?	
Onion	*Delia antiqua*	Dipt.	4.4	?	643	Lui & McEwan 1982
	Acrolepiopsis assectella	Lep.	7	?	445	Mason et al. 2010
	Thrips tabaci	Thys.	10	?	232	Murai 2000

2.5.6 Natural enemies

2.5.6.1 Ladybeetles (Fam. Coccinellidae, Order Coleoptera)

are distributed worldwide. Most species of the ladybeetles feed on aphids and mealy bugs. The number of consumed aphids varies. The larvae of a *Harmonia axyridis* can consume around 300 per day (Hukusima & Kamei 1970), whereas the adults of *Hippodamia convergens* consumes 25-170 aphids per day (Dreistadt & Flint 1996). Most of these beneficial species are distributed throughout the subtropic and tropic regions, while in the temperate regions only few lady beetle species are found (Klausnitzer & Klausnitzer 1997).

The species overwinter as adults in big groups and from the end of April to the beginning of May, the females start to lay (up to 1600) eggs (Stathas et al. 2001). After five to eight days, the larvae hatch and then need another 30 to 60 days and four instars to pupate (Obrycki & Tauber 1981). Normally two generations are formed in Lower Saxony per year.

For most of the species in the region, the base developmental temperature is around 10 °C and 250 °DD are needed to complete the development (Honek & Kocourek 1988; Xia et al. 1999). It has been observed, that coccinellids are more successful in hot summers (Skirvin et al. 1997) so that it is likely that their efficiency will increase in the future.

2.5.6.2 Hoverflies (Fam. Syrphidae, Order Diptera)

are a family with 6000 species from which 1800 are found in the Palaearctic. They are important natural enemies to herbivores since the larvae can devour up to 100 aphids a day. The overwintering is species-specific. Some species overwinter as larvae while others like *Episyrphus balteatus* do so as adult females. For winter survival, the species *E. balteatus* shows two strategies: Some females overwinter in diapause while adults also immigrate in spring from warmer regions to Lower Saxony (Hondelmann & Poehling 2007). The females lay their eggs next to the food resource for the hatching larvae. After 8-14 days the larvae pupate and after a further 8-10 days they develop to adults.

One of the most important natural enemies of the Syrphid family in Lower Saxony is *Episyrphus balteatus* (Hondelmann & Poehling 2007). This species is distributed in Europe, Asia and Australia (Hondelmann & Poehling 2007). The base temperature for the development of this species is around 4 °C (Dixon 2003) and 260 °DD are needed to complete the development (Hart et al. 1997). Syrphid larvae, in contrast to cocconellids, are not very resistant to drought and depend on moist environments for development. Therefore, today's abundance of syrphids might wane in the future, since warmer summers with more drought periods are to be expected (Hartmann et al. 2013).

2.5.6.3 Parasitoids (Fam. Chalcidoidea, Order Hymenoptera)

designate several species. Some parasitize several hosts while others are specialised on a single host species. In Europe, around 2000 species of this superfamily are to be found. Of these parasitic wasps, two groups with different parasitation strategies are known: Ectoparasitoids, lay their eggs next to their hosts, while endoparasitoids lay their eggs into the host itself. Most endoparasitoids are koinoboints, which means that their host develops further after parasitation and thereby allows it to reach a distinct size to guarantee enough host biomass for the parasitoid. Many of the ectoparasitoids are idiobionts which normally paralyze their hosts and stop the hosts' development (Quicke 1997), often the size of the victims is much bigger than the parasitoid. Most of the commercially used parasitoids are endoparasitoids. They overwinter inside the mummified host and in late spring the adults hatch. The females are laying their eggs into suitable hosts and the larvae develop and pupate there. Normally, they kill their host before pupation. The basal developmental temperatures and the developmental time are depending on the species (e.g. *Encarsia formosa* 12.7 °C and 189 °DD or *Diaeretiella rapae* 3.56 °C and 292 °DD). The developmental time also depends on the size of the hosts, with a faster development in larger hosts (Rice & Allen 2009) and the host species (Sengonca et al. 2001).

2.6 Adaptation strategies in plant protection/ Are adaptation strategies necessary and how can they look like?

It is necessary for agricultural and horticultural production systems to adjust to the expected climate change. This can be achieved by:

- forecast models which not only focus on first appearances of pests

- a better understanding of source-sink relationships in the field, the ratio of natural areas and cultivated land
- advanced decision support models
- further selection of resistant crops/varieties
- advanced crop rotation schemes
- forceful use of integrated plant protection strategies
- a reliable integration of conservation biological control strategies
- automated monitoring tools
- on farm land-use management
- development of new advanced strategies
- reliable but sustainable intervention

Climate change will proceed slowly and development of new insecticides will keep pace. Yet, in the case of an "explosion" of pest species, the intensity of the application of pesticides might become important. To avoid resistances of pest species, damage of the environment and residues of insecticides in food, the use of insecticides should be minimized while alternative strategies will have to be intensified and improved. Molecular and biotechnological developments may be available to close some of the gaps in the future. Experiments are being made with the release of male insects, as for example *Episimus unguiculus*, which are sterilised with gamma radiation to then replace fertile individuals in nature and thereby reduce the population (Moeri et al. 2009).

It is expected that winters will warm, which will effectively prolong the vegetation periods, but since also insects can arrive early in the year, the plants may be harmed in a much more vulnerable stadium, if plants are seeded at the same time as today. The prolonged vegetation period will change the cultivation cycle and provide longer food availability for pests. This will allow them to produce more generations and build up bigger populations. Therefore, it is necessary to control the plants early in the year, to then use plant protection and if necessary to prepone sowing to avoid heightened plant vulnerability. Due to the higher probability of summer droughts more irrigation is needed (Döll 2002; Olesen & Bindi 2002). To avoid water stress is to avoid raised vulnerability to pests. Hence it is important to develop new water-saving irrigation systems and to try to breed plants which can handle the new climate (Karpenstein-Machan & von Buttlar 2012). It is also necessary to breed plants which grow better under warmer temperatures and which can handle a changed pest spectrum.

For the plant protection it is necessary to try to find new ways of integrated pest management. Pests may become resistant against pesticides due to the short generation time and their increased rate of mutations and the fact that by the application of pesticides, the resistant individuals of the population survive. In this context, the increasing interest of consumers to acquire foodstuffs produced without pesticides has to be taken into account. It is therefore necessary to combine natural enemies with conventional strategies, for example releasing *Encarsia tricolor* under foil tubes to defeat the cabbage whitefly (Schultz et al. 2010). Another important factor might become the promotion of natural enemies via flower strips or landscape items such as hedges (Ludwig & Meyhöfer 2012).

2.7 Is the available information sufficient to make predictions for pest outbreaks in future a propose adaptation strategies? (Need for research)

It is not known, how most of the pest species react to extremes like short-time heat waves and heavy rain. In most experiments only the influence of high temperatures, still in the range of developmental thresholds or singular heat events where tested. But the influence of slowly increasing repeated heat events hasn't been tested so far. Also the research on the impact of rain generally leaves a lot to be desired, especially the influence of heavy rains. Therefore, it is necessary, to study the influence of rain on the mortality and the development of selected pest species. Another predicted change is the increase of droughts in summer and autumn. It is not clear how pests and their natural enemies will react under these conditions and it is necessary to study this. Experiments were conducted to study the influence of repeated heat waves, heavy rain, drought stress and mild winters on the mortality and population development of *Aleyrodes proletella*.

3 Influence of repeated short-time heat waves on *Aleyrodes proletella*

3.1 Abstract

The climate changes which have become apparent in the last hundred years are likely to continue into the new century. Worldwide temperatures will increase as the precipitation regime changes. Very likely, extreme events such as heavy rains and dry spells will increase in occurrence and intensity. Temperature in particular has an enormous effect on insects: It will boost development if meeting the species' optimal requirements, but can also stunt development and cause high mortality if critical temperatures are reached. Up to know mainly regimes with sudden exposure to peak temperatures have been tested, but under this heat shocks, the temperature is increasing very fast and it is not clear, if the mortality is a result of the detrimental effect of lethal heat or the fast temperature change and missing adaptation time. Furthermore, only one heat event had been tested. In nature however slow temperature increases and decreases over daytime and multiple stress events can be expected. Therefore, the experiment features a model with slightly increasing and decreasing temperatures and additional high peak temperatures. Under these conditions, the mortality and the development of whiteflies, both in Petri dishes and on plants, were studied. Moreover, repeated heat cycles simulated daily heat waves, which might occur in Lower Saxony, to evaluate whether the animals could adapt to the repeated heat. Our results with whiteflies in Petri dishes show that they are extremely robust to one heat wave of even 8 hours and 42 °C, but that with an increasing number of heat cycles the mortality is increasing. Ninety percent of the adult females died after three heat cycles with peak temperatures of 38 °C and warmer temperatures and after four cycles all females were dead. The males were even more vulnerable to heat and suffered a mortality of over 90% after just two cycles. Even after one heat cycle of 38 °C the egg-laying decreased dramatically, while temperatures of 30 and 34 °C had no negative effect on egg-laying. When repeated on leaves, the results were quite different. The heat waves, even five cycles with peak temperatures of 38 °C, had no influence on the mortality of both females and males. There was also no measurable negative effect on egg-laying or the mortality of eggs and the development of larvae. The developmental time of eggs even

decreased with increasing temperature. It can be concluded, that the whitefly population will not suffer from short time heat waves whereas warm temperatures will even accelerate population development.

3.2 Introduction

At the rate climate has changed in the last century, it is likely that the climate will continue to evolve in the coming decades. Due to human impact, CO_2 levels have risen, followed by an increase in temperature (Hartmann et al. 2013). In Germany, temperatures increased about 0.9 °C in the last hundred years. It has been predicted that the temperature will further rise in the next years, that precipitation will change and that extreme weather events such as heavy rains, droughts and heat periods will occur more frequently. This temperature increase will likely manifest in cold weather extremes, leading to warmer winters and warmer nights, therefore decreasing temperature differences of day and night and finally influence insects (Stamp & Osier 1997). Temperatures are likely to rise around 2 °C (0.3-4.8 °C) until the year 2100. And it has been assumed, that heat waves will occur more frequent and with higher peak temperatures (Hartmann et al. 2013). As an example, 2003 had a summer with extremely high temperatures of up to 40.2 °C in Karlsruhe, Freiburg and other German cities. In Lower Saxony, the temperatures reached 38 °C in Hanover (German Weather Service). Swiss scientists assume that at the end of the century every second summer will be as hot as the summer of 2003 (ProClim 2005). The number of days with temperatures over 30 °C will increase by 5-10 days in Northern Germany in the years 2021-2050 and by 10-15 days from 2071- 2100. In Southern Germany they will even increase by 30-35 days per year (Becker et al. 2012).

Therefore, the effects of high temperatures on the mortality and the development of the cabbage whitefly as a model species was studied. In former studies, mainly the effects of constant temperatures or of singular high temperatures were investigated, while the effect of short-time high temperatures had only been tested in very few studies. In those experiments it was not clear, if the mortality had been caused by the high peak temperature or by the sudden temperature increase. Therefore climate data of Lower Saxony were analysed studying the occurrence of high temperatures in Lower Saxony and experiments were investigated testing the influence of repeated, slowly increasing, short-time heat waves on the development of *Aleyrodes proletella*.

The life cycle of most insects is regulated by temperature (Yurk & Powell 2009). Normally insects respond to increased temperatures with accelerated development, because their physiological processes are strictly temperature regulated. Under increasing temperatures the developmental time will decrease and insects with short generation periods such as whiteflies or aphids will be able to have more generations per season and build up bigger populations (Williams et al. 2000; Tobin et al. 2008). For example, Harrington et al. (2007) assumed that aphids in the UK would be able to have five more generations at an average warming of 1 °C. Beside the direct influence on mortality and development, an increase in temperature can also have indirect effects due to changes in host plant physiology, such as an altered C/N ratio could naturally influence the nutritional situation of herbivorous insects. Aphids for example produce more apterous offspring under high temperatures, is the latter being more fecund and able to build up high populations (Bale et al. 2002). Furthermore, higher temperatures lead to an earlier dispersal of alate aphids, so that they can reach host plants in a more vulnerable stage (Harrington et al. 2007). As a consequence they can build up earlier in the year colonies on the summer hosts leading to bigger populations. Some insects like the cricket *Gryllus texensis* reproduce better under high temperatures (Adamo & Lovett 2011). While herbivores would profit as indicated, so would beneficials. The Lady beetle *Coccinella septempunctata* is more successful controlling wheat aphids (*Sitobion avenae*) under warm temperatures (Cannon 1998). Also the parasitism rate of *Brevicoryne brassicae* (Belder et al. 2007) and the parasitoid rate of *Pieres rapae* and *Mamestra brassicae* caterpillars by *Microplitis mediator*, *Cotesia rubecula* and *Diadegma semiclausum* is higher (Pfiffner et al. 2006).

Yet, very high temperatures can also have negative effects on insects (Rosenzweig et al. 2001). At temperatures above 40 °C, the mortality of insects will increase (Tobin et al. 2008) and the egg stages especially will suffer from a higher mortality (Murai 2000). Under those extreme temperatures, the fecundity is reduced, too (Murai 2000). An increase in the night temperatures has also negative effects on several insects. Stamp & Osier (1997) found the developmental rate and biomass of the generalist caterpillar *Spodoptera exigua* to decrease at elevated night temperatures.

Our model organism *Aleyrodes proletella* has spread extensively in the last ten years and has become one of the most important cabbage pests in Lower Saxony (van Alebeek 2008). The population increase seems to correlate with the temperature increase. Therefore, this species' reaction to temperature extremes, both sudden heat shocks and slowly increasing temperatures will be examined. The upper temperature threshold for this species is not known and we wanted to evaluate the mortality and population development to evolve forecast models for the grower. For this reason the influence of sudden heat events on the parasitoid *Encarsia tricolor* will be studied as well. *E. tricolor* is a parasitic wasp which occurs naturally in Central Europe and its population might also be influenced by the climate change. Up to now the thermal development thresholds for this species are not known. Apparently, the parasitoid is not able to control the whiteflies in Lower Saxony successfully over the whole year. While it is most successful in September and October, it might become relevant for year-round integrated plant protection under a changed climate.

3.2.1 The cabbage whitefly *Aleyrodes proletella* (Fam. Aleyrodidae, Order Homoptera)

is a serious pest in cabbage and has spread extensively in the last 30-40 years. In the 1970ies the cabbage whitefly was merely observed in some household gardens. Since this time the population has increased and, especially in the last ten years, has spread throughout Europe (van Alebeek 2008). Reasons for this increase might be global warming and also the cultivation of rape oil which, as a habitat for overwintering, might intensify the problem (Richter 2010).

Especially in warmer climates with low rainfall *A. proletella* is a serious cabbage pest (Leite et al. 2005). The lower developmental threshold is 8 °C, but depending on the larval stage, development is also possible under lower temperatures. The development from egg to adult requires 420 °DD and the optimal temperatures for the development rank between 28-33 °C. But very high temperatures can slow down the development and cause a high mortality (Leite et al 2006). (See also chapter 2.5.1.1)

3.2.2 The parasitoid *Encarsia tricolor* (Fam. Aphelinidae, Order Hymenoptera)

Encarsia tricolor Foerster (1878) is an autoparasitoid that occurs on 10 different whitefly species over Europe and Russia. Their host species include *Aleyrodes proletella* (Butler 1936, Gomez-Menor, 1943), *Aleurotrachelus jelinekii* (Laudonia & Viggiani 1984), and *Trialeurodes vaporariorum* (Albajes et al. 1980; Arzone 1976). The females primarily develop as endoparasitoids, the males as hyperparasitoids of several species (Williams 1995) e.g. *E. formosa* (Arzone 1976, Huang et al. 2009) or *E. inaron* (Williams 1989), including their own. The longevity of the females is higher than the males', due to the bigger body size of the females (19.9 ± 0.62 days for females and 13.8 ± 0.66 for males) and faster development of the males (Williams 1995). Imagos of *Encarsia tricolor* ingest water, honey dew and body fluid of the hosts (Stüben 1949). They can consume hemolymph of a particular host, by piercing it with the ovipositor without laying eggs. This host-feeding is increasing the mortality of the host (Williams 1995). The females lay about 7.3 (±0.27) eggs per day summing up to a lifetime fecundity of 85.4 (±13.85) eggs per female (Williams 1995). The number of eggs laid per day depends on the temperature, with a peak at 28 °C allowing a life time fecundity of 123 eggs per female (Artigues et al. 1992). At higher temperatures it decreased considerably (Artigues et al. 1992). During egg-laying, the host is paralyzed by a toxin which is inserted along with the egg (Stüben 1949). When acting as hyperparasitoids the females can distinguish between hosts parasitized by their own species and by a foreign species and will prefer foreign species as hosts for hyperparasitism and the development of males. (Williams 1989; Avilla et al. 1991). If the hosts are abundant the females will lay their eggs on primary hosts and avoid hyperparasitism that would lead to a female-biased population (Avilla et al. 1991). The larvae overwinter in their hosts and hatch in late spring as adults. The females are laying their eggs into suitable hosts and the larvae develop in the host larvae and pupate there, killing the host during development. The developmental temperature range, as well as the developmental time are not known for *Encarsia tricolor.* Other parasitoids, like the close relative *Encarsia formosa* have a basal developmental temperature of 12.7 °C and a developmental time of 189 °DD, while *Diaeretiella rapae,* which exists in the same region needs 3.56 °C and 292 °DD. The developmental time also depends on the host species (Sengonca et al. 2001), as well as on the size of the hosts, since they develop faster in larger specimen (Rice & Allen 2009). *Encarsia formosa*, a close relative to *Encarsia tricolor,* prefers the third and the fourth larval instar as host (Fransen & Montfort 1987). Due to this, we will assume that *Encarsia tricolor* also prefers the later larval instars, although males and females can develop in all larval instars (Williams 1995). Older host have several advantages: They reduce the danger of hyperparasitism and serve as better source of forage due to their bigger size. Even more important is the fact that the developmental time decreases with later host larval instars. On larvae of the first instar the wasps need 22.3 days to complete their development, while they need just 18 days on L3-larvae (Avilla & Copland 1987). The females that emerge from L1-larvae and L3-larvae are bigger than females hatching from L4-larvae or pupae (Avilla & Copland 1987). The temperatures for development of females range between 14-32 °C and between 16-28 °C for males (Avilla & Copland 1988). Next to the host size, the developmental time depends on temperature. At temperatures of 14 °C the insects need 51.1 days to complete their development and 14.3 days at 28 °C (Avilla & Copland 1988). Males develop faster with a developing time of 11.8 days at 28 °C (Avilla & Copland 1988). The lethal temperature for pupae is 34 °C (Avilla & Copland 1988). The optimal development temperature is 20-22 °C (Katz, unpublished).

3.3 Material and Methods

3.3.1 Frequency of heat waves in Lower Saxony

To evaluate how often heat waves occur in Lower Saxony and how long they last, climate data from the DWD (German Weather Service) was analyzed and the results were used to model the heat cycles in the climate chambers.

Temperatures above 30 °C occurred about forty times in the years from 1996- 2010 and lasted up to twelve days. Temperatures above 32 °C lasted up to nine, temperatures above 34 °C up to five days and temperatures above 36 °C up to four days. But the events with high temperatures above 36 °C lasting for several days occurred only once in ten years (Data from 1996-2010 (**Fig. 2**)

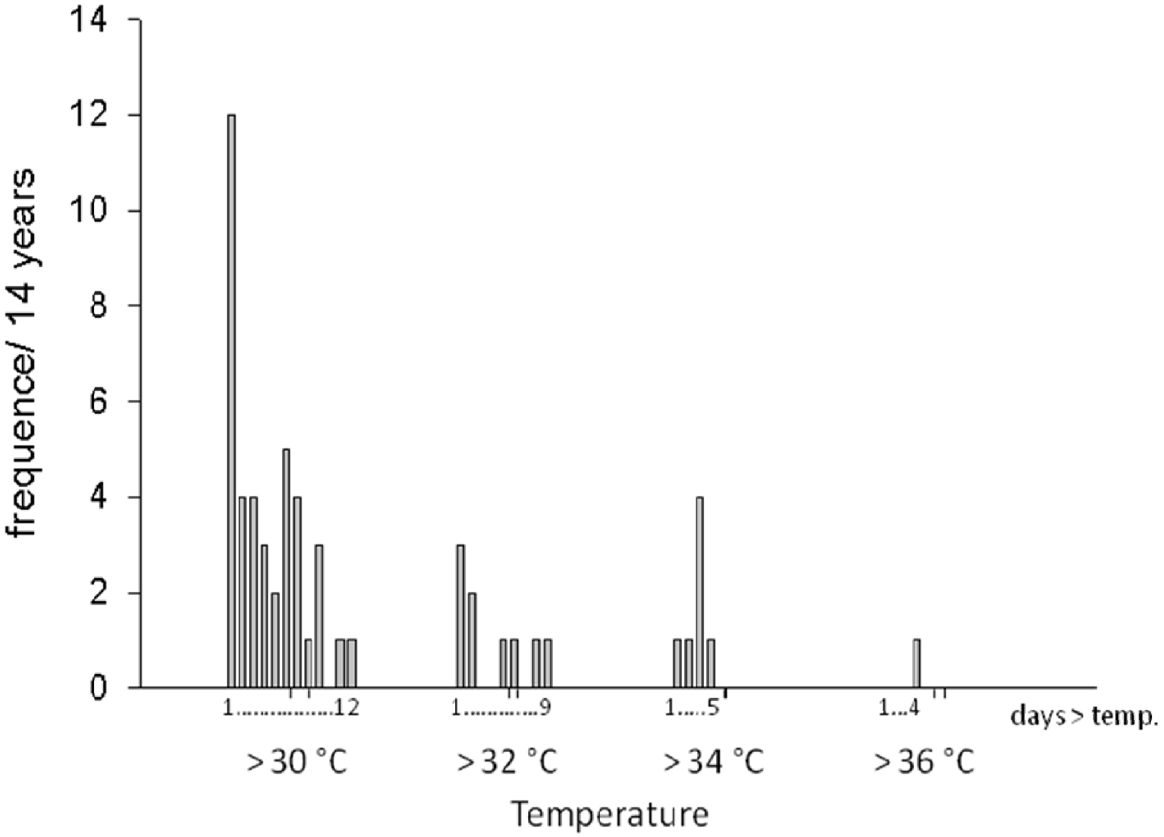

Fig. 2: Frequency of heat waves from 1996-2010 in Lower Saxony. Different weather stations in Lower Saxony were analyzed for the occurrence of temperatures above 30 °C.

3.3.2 Experiment

The results from the weather stations created a profile of heat waves that the actual experiment on insects shall be modelled to. Thus, the experimental simulation will be consistent with environmental conditions.

The cabbage whiteflies for the experiments were taken from the rearing of the Institute of Plant Disease and Plant Protection in Hanover (Institut für Gartenbauliche Produktionssystme Abt. Phytomedizin, früher Institut für Pflanzenkrankheiten und Pflanzenschutz). The insects were reared on Brussels sprouts at temperatures of 21 °C and light conditions of 18/6 (light/darkness). The stock culture was maintained isolated for five years, but approximately every six months individuals from the fields close to the institute were introduced to avoid inbreeding effects.

The *Encarsia tricolor* for this experiment were taken from the rearing of the Institute of Plant Disease and Plant Protection as well. The parasitoids were reared on whiteflies on Brussels sprout under temperatures of 24 °C and light conditions of 18/6 (light/ darkness). The culture was held isolated since one year and the start population was provided by Katz Biotech AG.

The first experiments (Experiment No. 1) shall investigate the upper developmental temperature and the influence of very high temperatures. Therefore, five 3 days old, synchronised whiteflies (males and females were separated with a brush after visual checking with a binocular microscope) on well-watered Brussels sprout leaves in Petri dishes were exposed for either four, six or eight hours to three different temperatures (36, 39 and 42 °C). 12 replicates per treatment were run. Immediately after the heat exposure the dead individuals were counted and the survivors were observed for five days to study delayed mortality and the fecundity after the heat shock. All experiments took place in control environments of climate cabinets (Vötsch - BioLine Prüfschrank, Modell VB 1100 Vario).

In the second experiment (Experiment No. 2) specific temperature profiles with a base temperature of 20 °C were used. The temperature increased over a time period of 7.5 hours to the peak temperature (30, 34, 38, 40, 42 °C). The peak temperature lasted for three hours. After this time the temperature decreased 7.5 hours back to the base temperature. The increase of the temperature started with the onset of the light period. We used long-day conditions (18L/6D) and a humidity of 60%. One run of this program was one heat cycle (**Fig. 3**).

In the first part of this second experiment (Experiment No. 2.1) we exposed the adults, separated as males (n = 5) and females (n = 5) on well-watered leaves in air conditioned Petri dishes to the heat and checked the mortality immediately after the exposure. Then the egg-laying per female was determined three days after the exposure. The impact on the insects was checked after one, two, three and four days of heat-cycles. Nine replicates per treatment were used.

In the second part of this experiment (Experiment No. 2.2) five adults (divided by males and females separated as in the first experiment) in clip-cages on plants were exposed to the heat (30, 34, 38 °C). After every cycle, the mortality and rate of egg-laying were checked. In this part of the experiment, also eggs and larvae were exposed to the heat and their mortality and developmental time were measured. Ten different plants with clip-cages were used as replicates. The impact on the insects was checked after one, three and five days of heat-cycles.

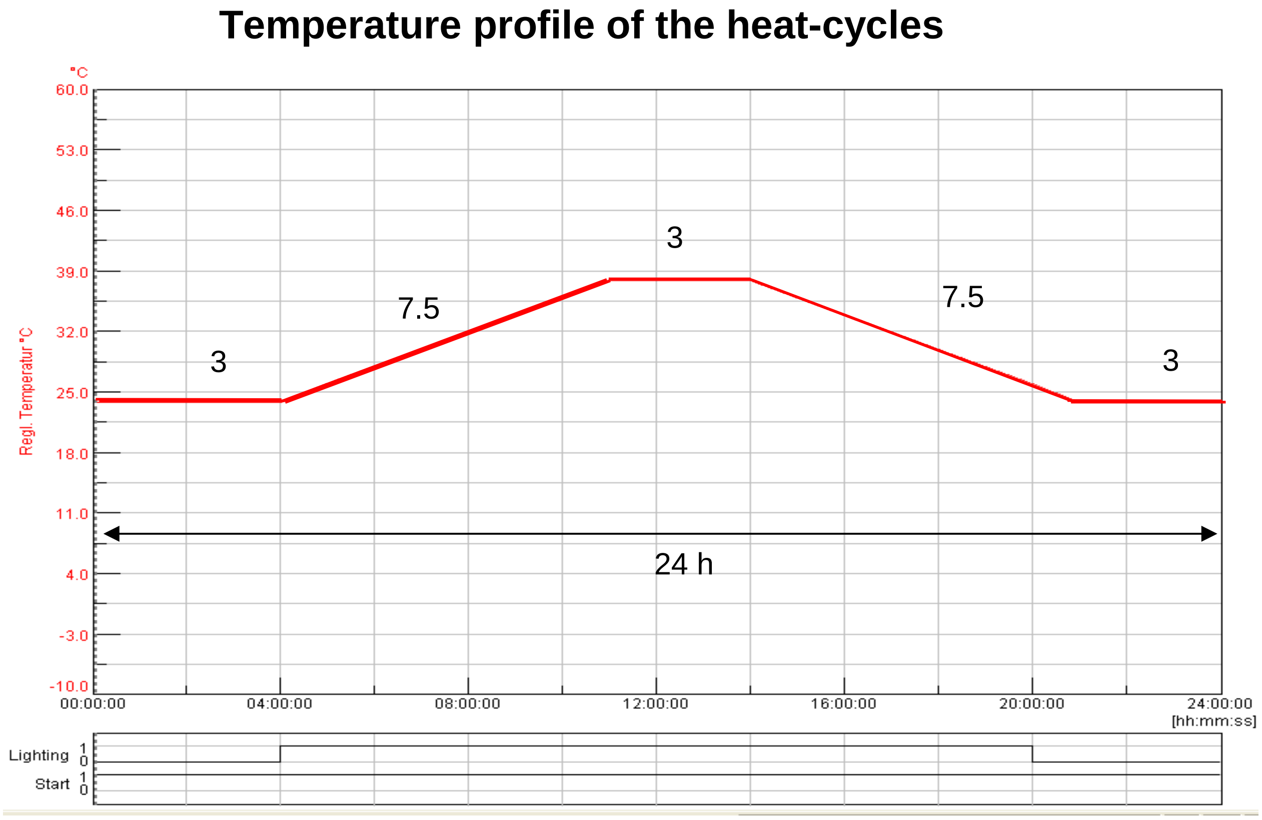

Fig. 3: Example of daily temperature profile of the heat cycles. The temperature increased slowly over a time period for 7.5 hours, then a peak temperature lasted for three hours and afterwards the temperature decreased for 7.5 hours. These cycles were repeated one, three or five times.

3.3.3 Statistical analysis

The data was visually checked for normality of residuals, creating histograms and box plots, and if necessary transformed and pooled for the replicates. The percentage data for the mortality of the males, females and larvae underwent arc sine square root transformation, the counting data for eggs square root transformation respectively.

Main emphasis of the experiment was put on the relationships between mortality and temperature and number of heat cycles. To that end, the effects of the heat cycles and the temperature on the insects were tested with an ANOVA. The influence of sex was also tested to see if there would be important differences. ANOVAs that yielded significant results were followed by a post-hoc-test (Tukey's Test). IMB SPSS 19 was used for all statistical analyses.

3.4 Results

3.4.1 Mortality of adults in the Petri dishes with single heat shocks (Experiment No. 1)

The temperature had a highly significant effect on the direct mortality ($F_{2,220} = 174.28$; $p < 0.001$, **Fig. 4**). and the delayed mortality after one ($F_{2,220} = 283.922$; $p < 0.001$) and two days ($F_{2,220} = 54.30$; $p < 0.001$). With increasing temperature the direct and the delayed mortality increased. It also had a significant effect on the egg-laying ($F_{2,220} = 4.35$; $p = 0.017$). With increasing temperature the amount of eggs decreased. And it had a significant influence on the development of the eggs ($F_{2,220} = 3.79$; $p = 0.027$; **Fig. 5**).

The duration of applied heat had also a significant effect. As expected the direct ($F_{3,220} = 42.91$; $p < 0.001$; **Fig. 4**) and the delayed mortality after one day ($F_{3,220} = 86.70$; $p < 0.001$) increased with increasing number of heat hours. Under all heat exposure times, the delayed mortality after two days ($F_{3,220} = 64.28$; $p < 0.001$) was significantly high, yet in this regard, the different exposure times bore no significant difference. The number of eggs decreased with an increasing time of heat exposure ($F_{3,220} = 13.95$; $p < 0.001$), while the development changed marginal significantly with the number of heat hours ($F_{3,220} = 2.46$; $p = 0.069$; **Fig. 5**). With increasing exposure time the number of hatched larvae decreased.

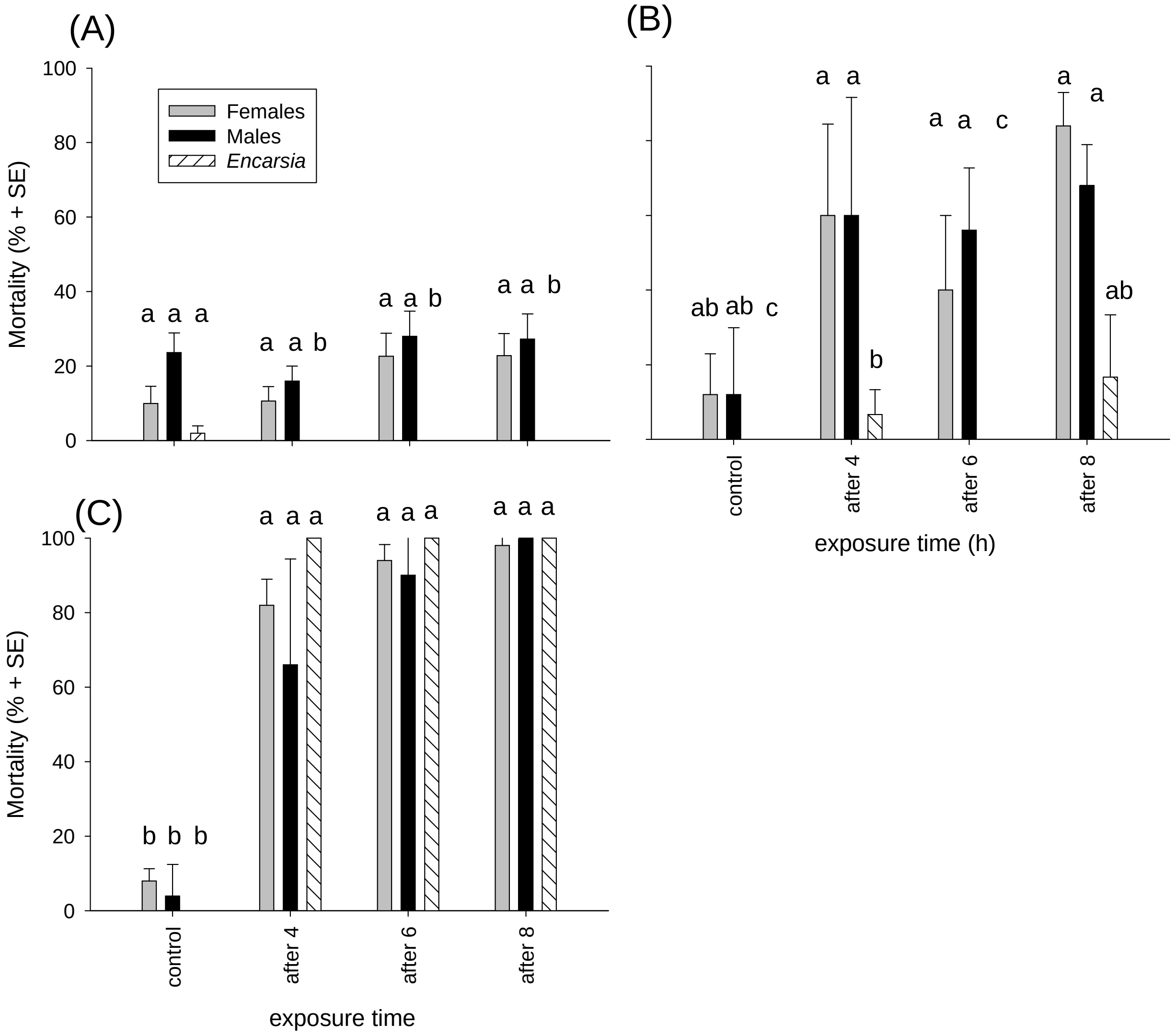

Fig. 4: Mortality at different temperatures and exposure times, comparing male and female whiteflies (*Aleyrodes proletella*) and the parasitoid *Encarsia tricolor* (A) mortality at 36 °C (B) mortality at 39 °C (C) mortality at 42 °C. n = 12 for each experiment and treatment. Different characters representing significanes ($\alpha \leq 0.05$).

The sex had a marginal significant effect on the delayed mortality after one day ($F_{1,220} = 2.91$; $p = 0.089$). Though there was also a big difference on the direct mortality of males and females but this difference was not significant ($F_{1,220} = 2.11$; $p = 0.15$). Overall, males were more vulnerable to heat and suffered a higher mortality (**Fig. 4**).

The interaction between the factors temperature and number of heat hours had a significant effect on the direct ($F_{6,220} = 26.810$ $p < 0.001$) as well as on the delayed mortality ($F_{6,220} = 29.07$; $p < 0.001$; $F_{6,220} = 9.27$; $p < 0.001$; one day delayed, two days delayed, respectively). Furthermore, it bore a marginal significant effect on the development of the eggs ($F_{6,220} = 2.08$; $p = 0.069$). Yet, this interaction had no impact on the egg-laying ($F_{6,220} = 1.06$; $p = 0.39$).

The interaction between temperature and sex on the other hand had no significant effects, merely displaying a marginal significant impact on direct mortality ($F_{2,220} = 2.66$; $p = 0.073$) and delayed mortality after two days ($F_{2,220} = 2.63$; $p = 0.074$).

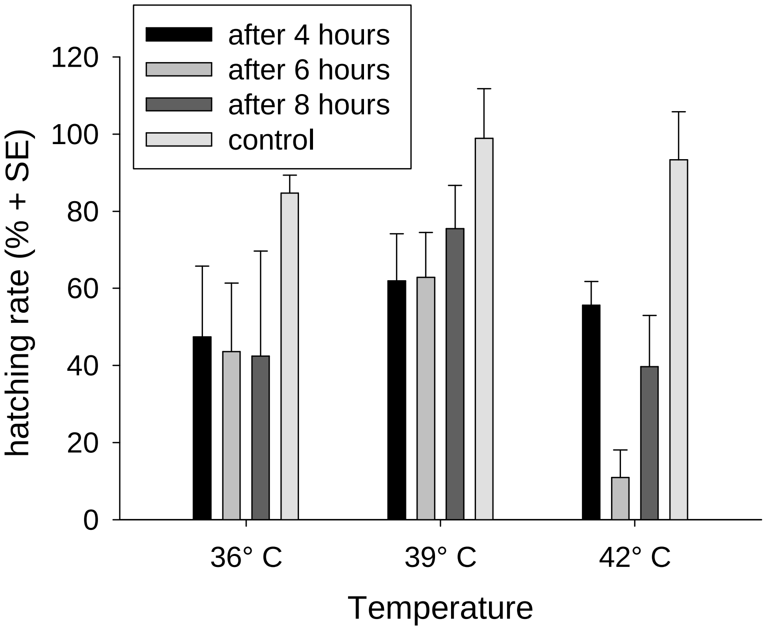

Fig. 5: Impact of exposure time on the hatching rate of cabbage whitefly (*Aleyrodes proletella*) eggs. Eggs were exposed to the different heat treatments in climate chambers and successful hatching evaluated in the following five days. n = 12 for each experiment and treatment.

The interaction between number of heat hours and sex had a significant effect on direct mortality ($F_{3,220} = 4.48$; $p = 0.005$). It had no significant effect on delayed mortality.

The combination of all three factors (temperature, exposure time and sex) had a significant effect on direct mortality ($F_{6,220} = 2.38$; $p = 0.031$). It had no significant effects on delayed mortality and egg-laying.

Tab. 2: Influence of temperature, exposure time and sex on mortality and development.

	Direct mortality	**Mortality after 1 day**	**Mortality after 2 days**	**Egg laying**	**Egg development**
Temperature	$F_{2,220}$ = 174.28 **$p < 0.001$**	$F_{2,220}$ = 283.92 **$p < 0.001$**	$F_{2,220}$ = 54.30 **$p < 0.001$**	$F_{2,220}$ = 4.35 **$p = 0.017$**	$F_{2,220}$ = 3.79 **$p = 0.027$**
Exposure time	$F_{3,220}$ = 42.91 **$p < 0.001$**	$F_{3,220}$ = 86.70 **$p < 0.001$**	$F_{3,220}$ = 64.28 **$p < 0.001$**	$F_{3,220}$ = 13.95 **$p < 0.001$**	$F_{3,220}$ = 2.46 $p = 0.069$
Sex	$F_{1,220}$ = 2.11 $p = 0.15$	$F_{1,220}$ = 2.91 $p = 0.089$	$F_{1,220}$ = 1.047 $p = 0.307$		
Temperature* exposure time	$F_{6,220}$ = 26.81 **$p < 0.001$**	$F_{1,220}$ = 29.07 **$p < 0.001$**	$F_{1,220}$ = 9.27 **$p < 0.001$**	$F_{1,220}$ = 1.06 $p = 0.39$	$F_{1,220}$ = 2.08 $p = 0.069$
Temperature* sex	$F_{2,220}$ = 2.66 $p = 0.073$	$F_{2,220}$ = 0.57 $p = 0.57$	$F_{2,220}$ = 2.63 $p = 0.074$	$F_{2,220}$ = 8.95 **$p < 0.001$**	
Exposure time* sex	$F_{3,220}$ = 4.48 **$p = 0.005$**	$F_{3,220}$ = 0.083 $p = 0.97$	$F_{3,220}$ = 0.743 $p = 0.53$	$F_{3,220}$ = 13.95 **$p < 0.001$**	
Temperature* exposure time* sex	$F_{1,220}$ = 2.38 **$p = 0.031$**	$F_{1,220}$ = 0.695 $p = 0.65$	$F_{1,220}$ = 0.55 $p = 0.77$	$F_{1,220}$ = 1.046 $p = 0.40$	

For the parasitic wasp *Encarsia tricolor* nearly no mortality could be found at temperatures of 36 °C and 39 °C. Only after eight hours at 39 °C mortality of 20% was registered. Opposite to this, at temperatures of 42 °C mortality of *Encarsia tricolor* was at 100% (**Fig. 4**). Temperature and exposure time had a highly significant effect on the mortality of the parasitoid ($F_{3,120}$ = 5000.67, $p < 0.001$; $F_{2,120}$ = 14.71, $p < 0.001$; respectively). Also, the combination of the factors temperature and exposure time had a significant effect ($F_{6,120}$ = 16.13 $p < 0.001$).

3.4.2 Mortality of adults in Petri dishes with repeated heat waves (Experiment No. 2.1)

In this part of the experiment the Petri dishes were used again, while now applying the heat waves with different exposure times.

The temperature had a merely significant effect on the delayed mortality three days after the heat exposure ($F_{1,35} = 4.21$; $p = 0.05$). With increasing temperature, mortality increased as well. It had no significant effect on neither direct nor delayed mortality after one or two days. But these mortalities also increased with increasing temperature. However, it had a highly significant effect on the egg-laying ($F_{1,35} = 4.69$; $p < 0.001$). With an increasing temperature the number of laid eggs decreased (**Fig. 6 (C)**).

The number of heat cycles had a significant effect on the delayed mortality not before two days after heat exposure ($F_{1,35} = 4.57$; $p = 0.041$). It had no effect on direct mortality or other delayed mortalities. With an increasing number of heat cycles the mortality increased. On the egg-laying it had only a marginal significant effect ($F_{1,35} = 2.21$; $p = 0.075$), as a consequence of the longer time span the insects had available to lay eggs. Below temperatures stages of 30 °C and 34 °C the number of laid eggs increased with increasing number of heat cycles, but this was not significant. However, after a single heat cycle at 38 °C or higher temperatures there was no egg-laying at all (**Fig. 6 (C)**).

The sex of the animals had a significant effect on direct mortality ($F_{1,35} = 4.54$; $p = 0.042$) and delayed mortality after four days ($F_{1,35} = 6.13$; $p = 0.02$). The delayed mortalities after two and three days were not influenced. The mortality of males was higher, being more vulnerable to the heat (**Fig. 6 (B)**). Four days after the heat exposure all males were dead, whereas the females' mortality was just at 80% (**Fig. 6 (A)**). The mortality of females constantly increased at temperatures above 38 °C. At the lower temperatures there was nearly no mortality for the first three or four heat cycles (at 34 °C and 30 °C, respectively). After this time, the mortality increased rapidly. The males already suffered a mortality of 100% after two cycles of 38 °C or higher temperatures. For the lower temperatures (30, 34 °C) the mortality increased constantly and reached a mortality of 100% after four cycles.

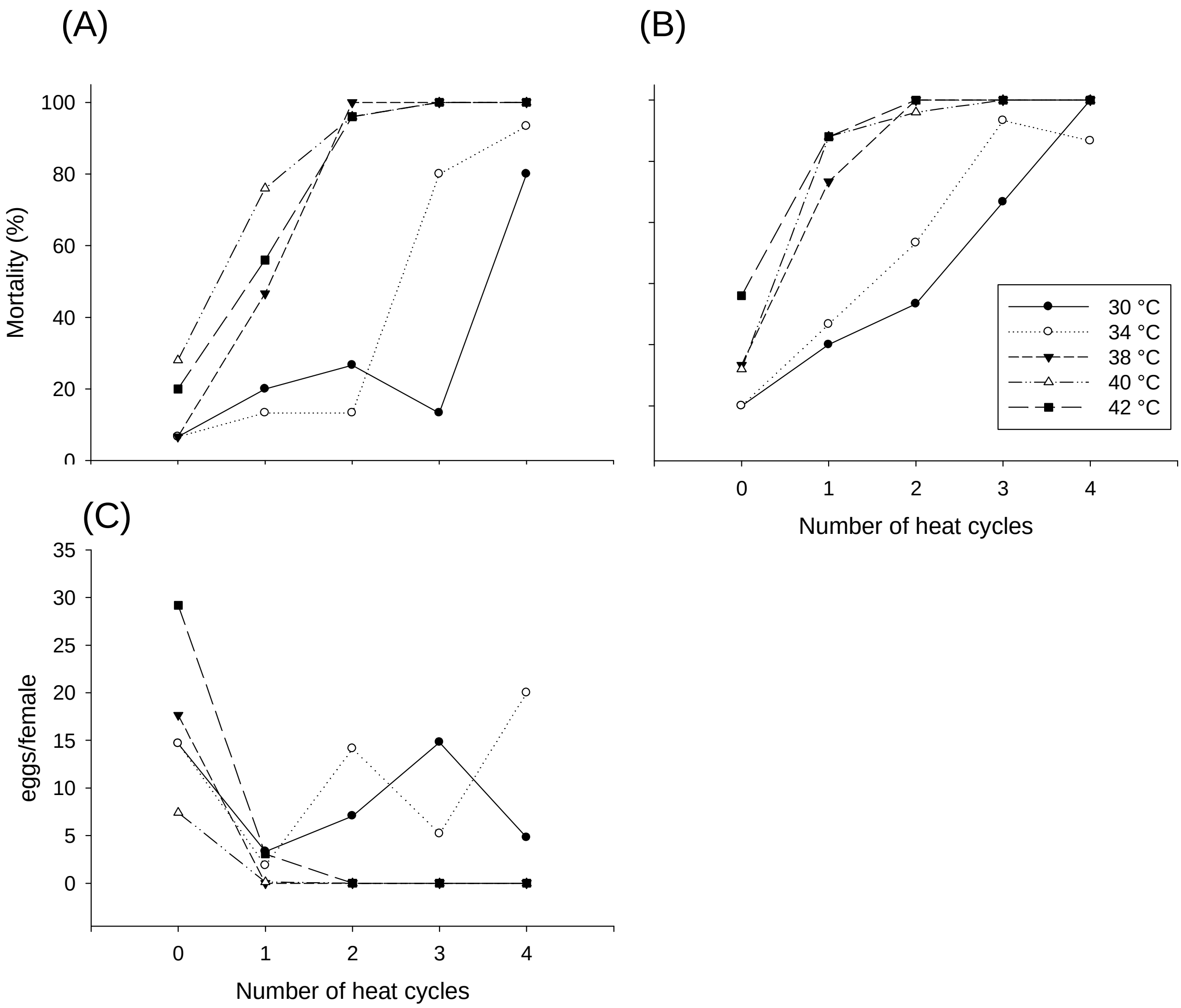

Fig. 6: Influence of different temperatures and different numbers of heat cycles in a climate chamber on the mortality of *Aleyrodes proletella*. (A) Influence on the mortality of females (B) influence on the mortality of males (C) influence on the egg-laying during the heat exposure. Error bars were left out for better visual clearness. n = 9 for each experiment and treatment.

The ANOVA with the combination of the factors temperature and heat cycle yielded no significant results.

The combination of the factors temperature and sex had a significant effect on the delayed mortality after two ($F_{1,35} = 4.57$; $p = 0.041$) and after three days ($F_{1,35} = 9.47$; $p = 0.005$).

The combination of the number of heat cycles and sex had no significant effect, as well as the combination of all three factors.

Tab. 3: Influence of temperature, number and sex on the mortality and egg laying.

	Direct mortality	**Mortality after 2 days**	**Mortality after 3 days**	**Mortality after 4 days**	**Egg laying**
Temperature	$F_{1,36}$ = 1.135 p = 0.30	$F_{1,36}$ = 0.840 p = 0.37	$F_{1,36}$ = 4.21 **p = 0.05**	$F_{1,36}$ = 0.182 p = 0.67	$F_{1,36}$ = 4.69 p < 0.001
Number of heat cycles	$F_{1,36}$ = 2.018 p = 0.17	$F_{1,36}$ = 4.57 **p = 0.041**	$F_{1,36}$ = 0.066 p = 0.80	$F_{1,36}$ = 0.007 p = 0.93	$F_{1,36}$ = 2.21 p = 0.075
Sex	$F_{1,36}$ = 4.54 **p = 0.042**	$F_{1,36}$ = 0.84 p = 0.37	$F_{1,36}$ = 0.592 p = 0.49	$F_{1,36}$ = 6.113 **p = 0.02**	
Temperature* heat cycle	$F_{1,36}$ = 1.135 p = 0.30	$F_{1,36}$ = 0.093 p = 0.76	$F_{1,36}$ = 0.263 p = 0.61	$F_{1,36}$ = 0.007 p = 0.99	$F_{1,36}$ = 0.742 p = 0.70
Temperature* Sex	$F_{1,36}$ = 1.135 p = 0.30	$F_{1,36}$ = 4.573 **p = 0.041**	$F_{1,36}$ = 9.465 **p = 0.005**	$F_{1,36}$ = 0.065 p = 0.80	
Heat cycle* sex	$F_{1,36}$ = 0.505 p = 0.48	$F_{1,36}$ = 0.093 p = 0.76	$F_{1,36}$ = 0.066 p = 0.80	$F_{1,36}$ = 0.007 p = 0.93	
Temperature* heat cycle* sex	$F_{1,36}$ = 1.135 p = 0.30	$F_{1,36}$ = 2.333 p = 0.14	$F_{1,36}$ = 0.263 p = 0.61	$F_{1,36}$ = 0.007 p = 0.93	

3.4.3 Mortality of adults on plants with repeated heat waves (Experiment No. 2.2)

When testing the influence of heat waves on insects on plants, no influence of the temperature on either the mortality of males ($F_{2,27} = 0.34$; $p = 0.72$) or the mortality of females ($F_{2,27} = 0.29$; $p = 0.76$) could be registered. The temperature had as well no effect on the egg-laying during the heat wave and no impact on life time fecundity. Furthermore, no effect on the longevity of the females could be assessed.

The number of the heat cycles had no influence on the mortality of neither males (**Fig. 9 (A)**) nor females (**Fig. 9 (B)**), but it had a significant effect on the number of eggs a female laid during the heat period ($F_{2,27} = 6.66$; $p = 0.007$; Fig. **8 (A)).** It had no effect on the lifetime fecundity of the females (**Fig. 8 (B))** or on their longevity. The number of heat cycles had a significant effect on the developmental time of the eggs ($F_{2,33} = 8.17$; $p = 0.002$; **Fig. 7 (A**)), yet all eggs survived the heat wave without impairment of the development of the larvae (**Fig. 7 (B)**).

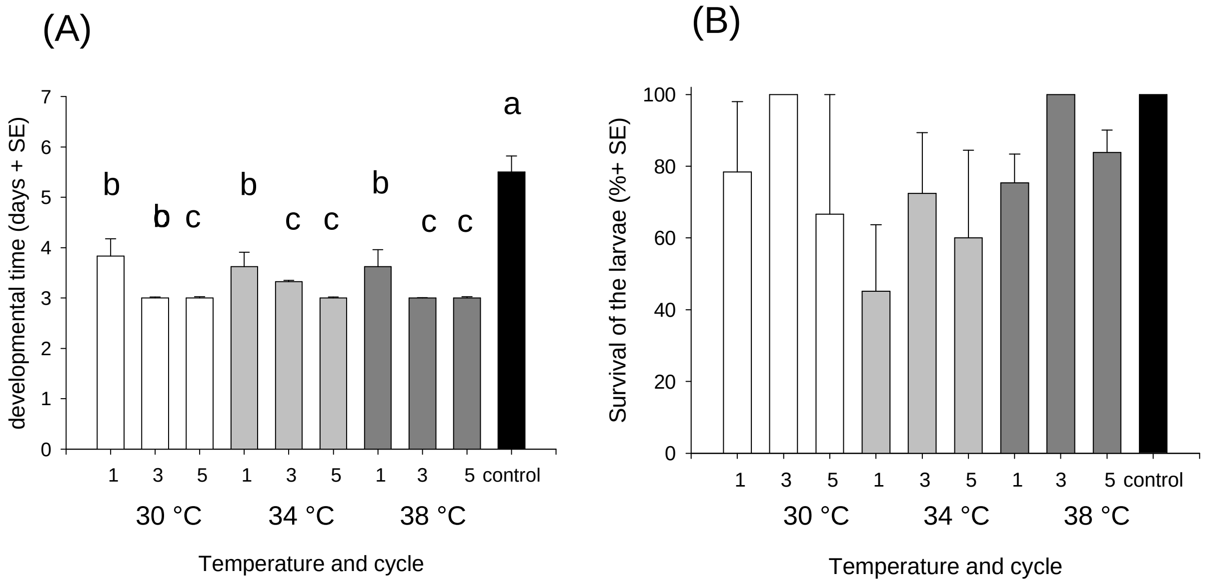

Fig. 7: Impact of different temperatures and different number of heat cycles on eggs and larvae (A) the developmental time from egg to larvae of *Aleyrodes proletella* and (B) the survival rate of the larvae of *Aleyrodes proletella*. n = 9 for each experiment and treatment. Different characters representing significanes (α ≤ 0.05), graphs without characters show no significances.

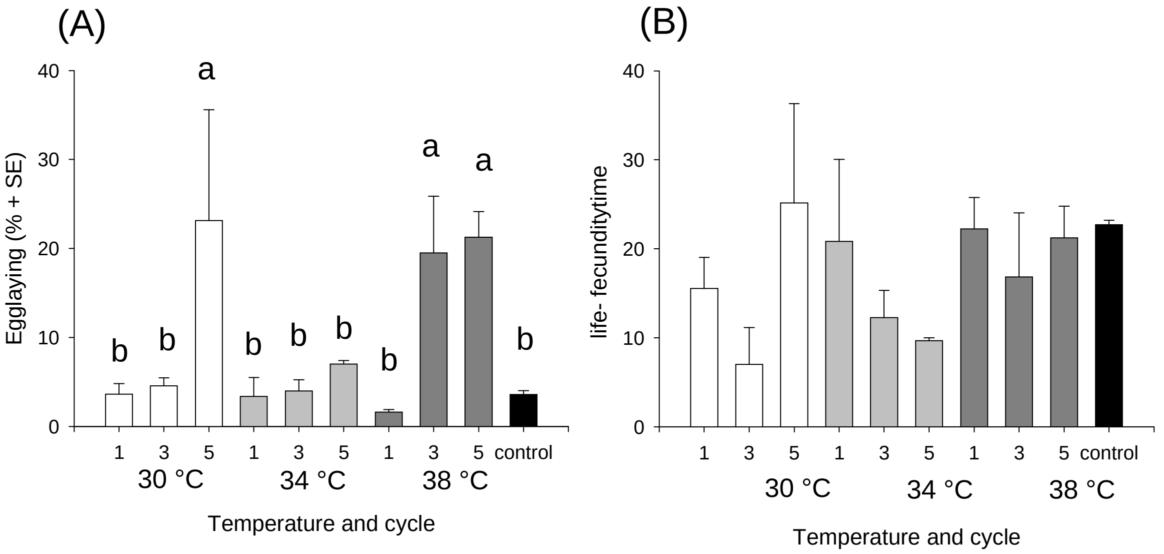

Fig. 8: Impact of the different temperatures and number of heat cycles on egglaying and life-time fecundity(A) egg-laying per female of *Aleyrodes proletella* and (B) and the life-time fecundity of female *Aleyrodes proletella*. The treatments were repeated 10 times. n = 9 for each experiment and treatment. Different characters representing significanes (α ≤ 0.05), graphs without characters show no significances.

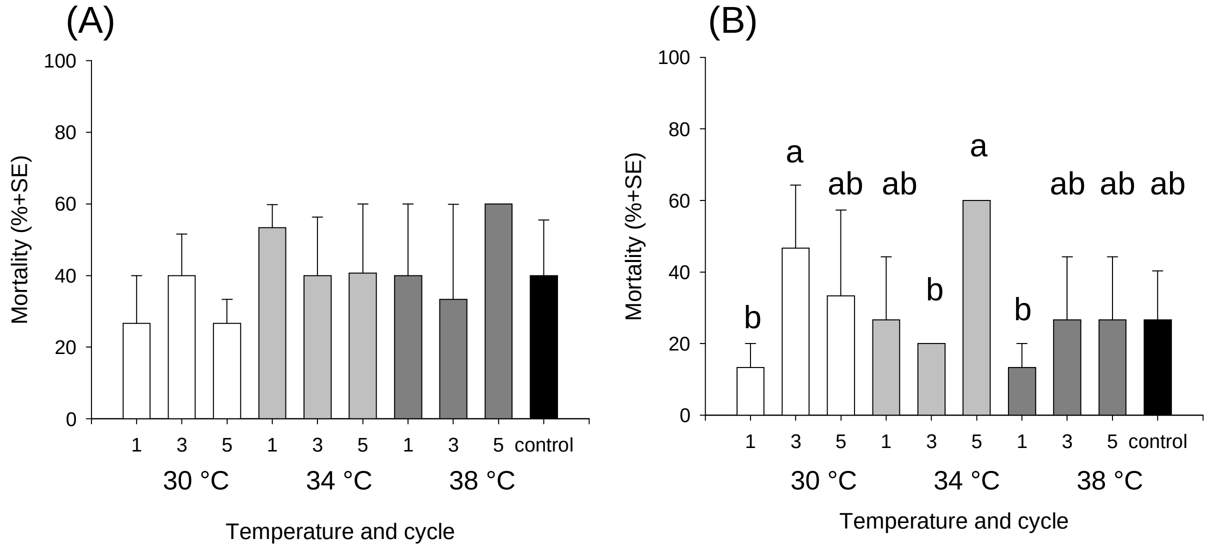

Fig. 9: Mortality after different heat cycles with different peak temperatures on *Aleyrodes proletella* (A) males (B) females. 5 individuals were used per treatment and the treatments were repeated 10 times. n = 9 for each experiment and treatment. Different characters representing significanes (α ≤ 0.05), graphs without characters show no significances.

The combination of the factors temperature and heat cycle had no effects at all. Also, sex had no influence on mortality ($F_{1,54}$ = 1.47; p = 0.23).

Tab. 4: Impact of temperature, number and sex on mortality, egg development, lifetime fecundity and longevity of *Aleyrodes proletella*.

	Mortality of males	**Mortality of females**	**Egg laying**	**Egg develop-ment**	**Lifetime fecundity**	**Longe-vity**
Temperature	$F_{2,27}$ = 0.34 p = 0.72	$F_{2,27}$ = 0.29 p = 0.76	$F_{2,27}$ = 1.858 p = 0.19	$F_{2,33}$ = 0.306 p = 0.74	$F_{2,27}$ = 1.008 p = 0.38	$F_{2,27}$ = 0.707 p = 0.51
Number of heat cycles	$F_{2,27}$ = 0.009 p = 0.99	$F_{2,27}$ = 0.857 p = 0.44	$F_{2,27}$ = 6.66 **p = 0.007**	$F_{2,33}$ = 8.17 **p = 0.002**	$F_{2,27}$ = 2.063 p = 0.16	$F_{2,27}$ = 1.593 p = 0.23
Sex	$F_{1,54}$ = 1.47 p = 0.23	$F_{1,54}$ = 1.47 p = 0.23				Not tested
Temperature* heat cycle	$F_{4,27}$ = 0.303 p = 0.87	$F_{4,27}$ = 0.465 p = 0.76	$F_{4,27}$ = 1.88 p = 0.16	$F_{4,33}$ = 0.093 p = 0.98	$F_{4,27}$ = 1.051 p = 0.41	$F_{4,27}$ = 0.974 p = 0.45
Temperature* Sex	$F_{2,54}$ = 0.565 p = 0.57	$F_{2,54}$ = 0.565 p = 0.57				Not tested
Heat cycle* sex	$F_{2,54}$ = 0.413 p = 0.67	$F_{2,54}$ = 0.413 p = 0.67				Not tested
Temperature* heat cycle* sex	$F_{4,54}$ = 0.028 p = 0.99	$F_{4,54}$ = 0.028 p = 0.99				

3.5 Discussion

It is likely that temperatures above 30 °C on two or more consecutive days will occur much more often in the future (Hartmann et al. 2013). Even in the last fourteen years they occurred several times (**Fig. 2**). The analysis of temperatures in Lower Saxony could show that temperatures above 30 °C already occurred about five times annually for several days in this region and due to the climate prognoses the frequency of such warm days will increase. Even days with temperatures above 40 °C could be measured twice in Germany in the last decade (Karlsruhe, DWD).

In the first experiment (Experiment No. 1) above temperatures of 36 °C no increase in mortality could be found independent of the duration of exposure. But at temperatures above 39 °C and 42 °C the mortality increased rapidly; the different temperatures had a significant effect on mortality. The increase in the mortality was to be expected, because higher temperatures normally lead to a higher mortality due to the denaturation of proteins such as enzymes and membrane proteins in the insects by the cracking of the polypeptide chain (Nguyen et al. 1989; Campell 2000; Neven 2000). Surprisingly, even after eight hours at 42 °C some animals still survived, indicating this species to be robust to high temperatures. In a similar experiment with *Bemisia tabaci* Chen et al. (2011) found that survival was at 49% at temperatures of 41 °C. Most whitefly species are distributed in lower latitudes up to the equator and most of these species can cope with very high temperatures (Byrne & Bellows 1991). Even the species *Trialeurodes vaporariorum* and *Bemisia tabaci* biotype B which are common in Lower Saxony in greenhouses can survive temperatures of up to 45 °C, although the survival and the development are significantly influenced by these temperatures. Up to 40 °C the mortality of these two species is not influenced by the heat, but under higher temperatures the mortality increases and at temperatures above 45 °C all males die when exposed to a one-hour heat-shock (Cui et al. 2008). The insects have several adaptation strategies to the heat. Under high temperatures heat-shock-proteins are formed and the metabolism changes. Salvucci et al. (1999) could show that the whitefly *Bemisia tabaci* accumulates polyhydric alcohol and sorbitol under temperatures of above 30 °C. Sorbitol is enriched in the bodies of whiteflies serving as heat protection (Hendrix & Salvucci 1998). They could also show that the insects incorporate more sucrose in their bodies under high temperatures compared to the control. The activation of enzymes changes under high temperatures, too (Salvucci et al. 1999). It has also been found, that heat tolerant whiteflies have several secondary endosymbionts; mainly the endosymbiont *Rickettsia* seems to be responsible for an adaption to heat (Brumin et al. 2011). Another adaption to heat seems to be that even virgin females of *T. vaporariorum* which normally produce male offspring can produce females under high temperatures (Mittler 1946).

The mortality of the males was higher than the mortality of the females. Adams (1985) could show that male whiteflies are more vulnerable to cold temperatures, because only females can survive the winter. And Cui et al. (2008) found in their experiments that males are also more vulnerable to high temperatures. Due to this, we assume males generally to be more vulnerable to extreme changes in temperature, leading to a higher mortality. Moreover, the females have to be more robust, because they are responsible for the egg-laying and the offspring (Darwin 1871). Cui et al. (2008) could show that females whiteflies of *Bemisia tabaci* biotype B are more resistant to heat due to differently expressed genes followed by a higher expression of Expression Sequence Tags, which seem to increase the heat-resistance. Females of the leaf beetle *Chrysomela aeneicollis* produce more of the heat shock protein HSP70 than males and thus are more robust to heat (Rank & Dalhoff 2002). Secondary endosymbionts cannot be responsible for the different mortality rates of males and females, because they occur in both sexes (van Opijnen & Breeuwer 1999).

It could also be observed that the amount of eggs laid by females during heat exposure decreased with temperature and exposure time and that the number of eggs that developed to larvae decreased. The same is true for the whitefly species *Bemisia tabaci* (Chen et al. 2011). The decreased egg-laying could be caused by stress of the females or the conscious avoiding of unfavourable conditions. The preference-performance hypothesis predicts that the females of offspring with limited mobilisation should choose the best host plant for oviposition. Wennström et al. (2010) could show that females of the phytophagous beetle *Gonioctena linnaeana* prefer hosts that maximise offspring. The plants under heat treatment are not an optimal host plant for the offspring and so females avoid egg-laying and wait for better conditions. The females might also be in a less favourable condition to lay eggs, because Lee & Hou (1987) could show that the brown plant hopper *Nilaparvata lugens* transfers less secondary symbionts to its eggs under heat and that thereby the eggs were not viable.

The reduced egg development could be caused by dehydration of the eggs. Ingrisch (1986) could show that a lack of water supply can stop or prolonged the embryonic development. The age of the eggs is also important for the impact of the heat. In the early developmental stage, including the disc stage, a heat shock causes high mortality rates of eggs. In later developmental stages the heat causes segmentation problems, which lead to abnormalities that can prohibit hatching (Mee & French 1986). During the embryonic development, the vulnerability to heat is particularly high, since no heat shock proteins are induced (Lindquist 1986). Zwick (2003) could show that the eggs of the stonefly *Dinocras cephalotes* do not develop under high temperatures, but that they are in a parapause and not dead. We classified the eggs which did not hatch as dead without waiting for further development.

In the same experiment (Experiment No. 1) the mortality of the whitefly`s natural enemy *Encarsia tricolor* was studied and no mortality at temperatures above 36 and 39 °C were found. However, at temperatures above 42 °C *Encarsia tricolor* faced a mortality of 100%. Due to this data it can be speculated, that under an increase of the average temperature, *Encarsia tricolor* might be able to control the population of the whitefly in the field. Yet, the parasitation success of *Encarsia tricolor* is depending on several factors beside the temperature. This study did not incorporate the parasitation rate under high temperatures, but we can assume that an increase in temperature would positively affect the population development of the parasitoid. Recent experiments with whiteflies and the parasitoids under foil show that the parasitoid is able to control the whitefly population compared to experiments in the wild (Schultz et al. 2010). Therefore it seems probable that *Encarsia tricolor* is able to control the whiteflies under warmer conditions even in the field.

The repeated heat experiments (Experiment No. 2.1) showed that even at temperatures of 30 and 34 °C the mortality of the females increased rapidly after four heat cycles. At higher temperatures mortality increased as soon as after two days. The males showed to be even more vulnerable to high temperatures. The high mortality due to repeated heat waves is surprising in face of the results of our previous experiment (Experiment No. 1) where the specimens survived very high temperatures. Egg-laying dropped after one day at temperatures of 38, 40 and 42 °C but the lower temperatures (30, 34 °C) had no significant effect on the egg-laying.

In experiment No. 2.2 the same procedure was conducted with whiteflies on Brussels sprout plants to test if there are differences between the experiments in the Petri dishes and in nature. These experiments showed that the different heat waves had no effect on the mortality of both males and females. It seems to be normal that the longevity of the females like in our experiment, is not influenced by heat (Chen et al. 2011). The different temperatures also had no significant effect on the egg laying. Cui et al. (2008) found similar results in his experiments. The number of eggs oviposited by *B. tabaci* or *T. vaporariorum* did not differ in the different treatments. The females of these species stopped egg-laying at 43 °C and 45 °C, respectively. Development from eggs to larvae and the hatching success was also not influenced. All eggs hatched and nearly all larvae developed to the next larval stage. In contrast to this, the developmental time of the *A. proletella* eggs was indeed influenced by the temperature. As expected, the eggs developed faster under higher temperatures. Compared to placing them in Petri dishes, the whiteflies boasted a better rate of survival when on leaves and under more natural circumstances. Although the temperatures next to the leaves were nearly the same as the temperature in the climate room, air humidity was approximately 20% higher (Paz, unpublished). This different microclimate on the leaves seems to protect the animals and decreases the mortality. The higher humidity next to the leave decreases the mortality of adults (Oida et al. 2009) and is known to promote the hatching success for mites (Ferrero et al. 2010).

3.6 Conclusions

Due to the fact that the animals can survive hot temperatures for a long time and that they survive high temperatures for several consecutive days, we assume that the cabbage whitefly will become more relevant in the future. This phenomenon has been registered with several species and, if found to be true for the cabbage whitefly, will lead to an even bigger increase in the population density. Under extreme heat events, especially those whiteflies which are protected by secondary endosymbionts will survive. And based on the fact that endosymbionts are transmitted from the female to the offspring, it is likely that the proportion of whiteflies which are well-adapted to high temperatures will increase. It is also likely that *A. proletella* will adapted to higher average temperatures within some generations, but it is not clear if it is able to handle extreme events like heat waves. Therefore, we propose that future experiments should consider several consecutive generations. It is likely that the whitefly *Aleyrodes proletella* will become the most important pest species in cabbage. With increasing temperature it might be possible that the employment of the parasitoid *Encarsia tricolor* can become one major option to efficiently control *Aleyrodes proletella* in the field.

4 Influence of repeated heat waves on glucosinolates in the leaves

4.1 Abstract

The increase in the temperature as a consequence of climate change, will have direct and indirect effects on the insects. An important indirect effect could be a change in nutritional quality for instance the C/N ratio or the availability of important primary nutritional plant compounds such as amino acids or proteins or changes in the composition of plant secondary compounds often related to plant defence against herbivores. One group of important secondary plant compounds are the glucosinolates, which are produced mainly by Brassicaceae as a defence mechanism against herbivory. We tested if these plant compounds changed under repeated heat waves and may influence the development of the insect population in the short term. Therefore temperature profiles with slightly increasing and decreasing temperatures and a peak temperature of 30 (34, 38 °C) in controlled environments (climate cabinets) were used to simulate heat waves which might occur in future Lower Saxony. These heat waves were repeated one or five times and secondary compounds were analysed by GC-MS. Our results show that the total amount of glucosinolate is increasing under high temperatures, but only the increase of the glucosinolate 4-Methoxy-Glucobrassicin was significant. The glucosinolates also increased more intensively after one heat wave compared to five heat waves. The most significant effect on the amount of glucosinolates had the feeding of the pest *Aleyrodes proletella*. The feeding activity caused threefold increase of the total amount of glucosinolates.

4.2 Introduction

Due to human impact the CO_2–level has risen, which was followed by an increase in temperature in the last century. It has been predicted that the temperature will increase in the next years (Hartmann et al. 2013).

Normally insects respond positively to increased temperatures, with decreased developmental time, higher reproduction (Adamo & Lovett 2011) and more generations per year (Bergant et al. 2006; Tobin et al. 2008), but very high temperatures can also have negative effects like an increased mortality and a decreased fecundity (Skirvin et al. 1997). High temperatures may also affect the insects indirectly via the plant nutrients or secondary plant compounds. An important group of plant compounds are the glucosinolates which are released with herbivory and repel herbivores, whereas they can attract natural enemies of the pests. Glucosinolates are a group of secondary compounds common in Brassicaceae which repel generalist herbivores and attract specialists (Louda & Mole 1991; Braven et al. 1996). They are also associated with abiotic stress like heat or humidity (Khan et al. 2011a; Ramakrishna & Ravishankar 2011). (See also chapter 4.3.2.)

In former studies mainly the effect of constant temperatures or of singular high temperatures was investigated and the effect of short-time high temperatures has only been tested in few studies. That’s why we tested the influence of repeated, slowly increasing, short-time heat waves on the production of glucosinolates in Brussels sprout plants to study if a change in this secondary compounds may cause the changes in the mortality and development of *Aleyrodes proletella*.

4.2.1 The cabbage whitefly *Aleyrodes proletella*, (Fam. Aleyrodidae, Order Homoptera)

is a serious pest in cabbage plants. The species is common in Lower Saxony and especially in the last ten years a rapid range expansion has been observed (van Alebeek 2008). The species is a polyphagous phloem sucker with a general preference for Brassicaceae. The reasons behind the higher population development might be the climate warming on the one hand and the increased cultivation of rape oil on the other (Richter 2010). Development takes place in general above 8 °C, but depending on the larval stage is also possible at lower temperatures. Optimal developmental temperatures range between 28-33 °C. In total egg to adult development takes 420 °DD. But very high temperatures slow down the insects development. (See also chapter 2.5.1.1)

4.2.2 Glucosinolates

Glucosinolates are plant secondary compounds and part of the plant defence system against bacteria, fungi and herbivores (Zhao et al. 1994). They are common mainly in Brassica plants, but also in Rasedaceae and Capparidaceae (Fenwick et al. 1983b; Ludwig-Müller et al. 1996). Glucosinolates are sulphur and nitrogen based compounds which are cleaved by myrosinase into small toxic molecules (Himanen et al. 2008). According to their side chain and precursor amino acid they are divided in aliphatic, aromatic and indolic glucosinolates (Fahey et al. 2001; Himanan et al. 2008). The glucosinolates can be found in the plant vacuole separated from the enzyme myrosinase, which exist in special myrosinase cells. (Bones & Rossiter 1996). The myrosinase is only released after destruction of the different cell compartments due to, for example, the chewing of herbivores (Vaughn & Boydston 1997). Depending on the pH-value the products of the reduction change. Under a neutral pH-value volatile isothiocyanates are hydrolyzed from aliphatic glucosinolates (Lambrix et al. 2001). Indolglucosinolates are also hydrolyzed to nitrils and instable isothiocyanates which degrade quickly to non-volatile compounds (Mithen 1992; **Fig. 10**). The feeding of insects can also lead to a higher content of glucosinolates, especially indolic ones (Bidart-Bouzat et al. 2005). Although glucosinolates play an important role in plant defence, specialist and generalist herbivores react different to these plant compounds. Generalist insects are in most cases repelled by the agent, whereas specialists are often attracted by glucosinolates. For several specialists, for example *Brevicoryne brassicae*, *Plutella xylostella* or *Delia radicum* (Braven et al. 1996) glucosinolates serve as oviposition stimuli or they use them as part of their own defence system (Louda & Mole 1991).

It is likely that the contents of glucosinolates will change with climate change and Reddy et al. (2004) showed that they decreased under an increase of CO_2 due to a change of the defence from nitrogen-based to carbon-based defence compounds (Bidart-Bouzat & Imeh-Nathaniel 2008). Also a higher amount of O_3 leads to a decrease of glucosinolates (Gielen et al. 2006). But there’s also evidence that they will increase under higher temperatures due to the fact that the plants will be stressed by the temperatures and abiotic stress is followed by an increase of glucosinolates (Bidart-Bouzat & Imeh-Nathaniel 2008; Zhao et al. 1994). But to our knowledge there are no studies to show how they may react to repeated high temperatures.

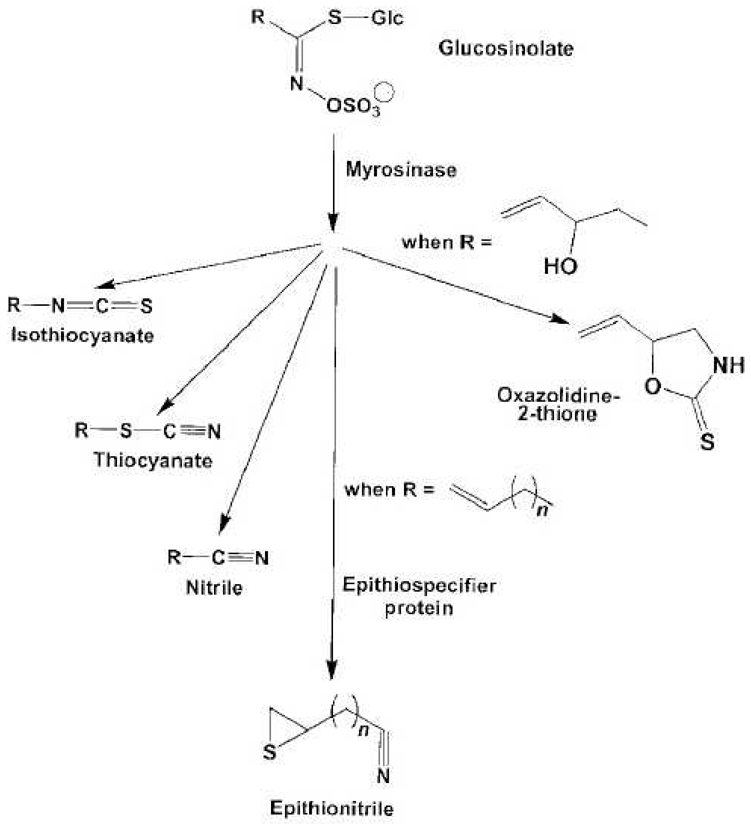

Fig. 10: Degradation products of glucosinolates after hydrolysis by myrosinase (Lambrix et al. 2001).

4.3 Material and Methods

4.3.1 Experiment

The cabbage whiteflies for the experiment were taken from the rearing of the Institute of Plant Disease and Plant Protection in Hanover. The insects were reared on Brussels Sprout under temperatures of 21 °C and light conditions of 18/6 (light/darkness).

All experiments took place in controlled environments of climate cabinets (Vötsch - BioLine Prüfschrank, Modell VB 1100 Vario). Specific temperature profiles with a base temperature of 20 °C were used. The temperature increased over a time period of 7.5 hours to the peak temperature (30, 34, 38 °C). The peak temperature lasted for three hours. After this time the temperature decreased 7.5 hours back to the basal temperature. The increase of the temperature started with the onset of light. We used long-day conditions (18L/6D) and a humidity of 60%. One run of this program was one heat cycle (**Fig. 11**). Leaf samples were taken after one and five cycles.

The plants were exposed either with *Aleyrodes proletella* or without any insects in the climate chamber and three samples per treatment were taken. After the experiment one leaf of the plants was cut, and immediately frozen with liquid nitrogen. Then the leaves were freeze-dried and send to Prof. Dr. Monika Schreiner at the Leibniz-Institute of Vegetable and Ornamental Crops to analyse the glucosinolates in the leaves via the HPLC method reported by Krumbein et al. (2005). Therefore 0.5 g of the leaf material was heated and incubated at 75 °C for 1 min, then 4 min extracted with a mixture of methanol and water (v/v = 7:3, T = 70 °C) then 1 ml barium acetate was added and the extract centrifuged for 10 min at 4000 rpm. This process was repeated three times with 3 ml of the water/methanol mixture (v/v = 7:3, T = 70 °C). The supernatants were combined and mixed with 10 ml of the water/methanol mixture (v/v = 7:3, T = 70 °C). 5 ml of this extract was applied to a 250 µl DEAE-Sephadex A-25 ion-exchanger (acetic acid-activated, Sigma-Aldrich Chemie GmbH, Taufkirchen, Germany), rinsed with 10 ml of bi-distilled water before applying 250 µl of a purified aryl sulphatase solution (Boehringer-Mannheim GmbH, Mannheim, Germany) and leaving it for 12 h. Then the desulpho-compounds were flushed with 5 ml of bi-distilled water. The analysis of the glucosinolates was conducted using a Merck-Hitachi HPLC system (Merck-Hitachi, Darmstadt, Germany) with a Spherisorb ODS2 column (Bischoff, Leonberg, Germany, 5 µm, 250 x 4 mm). A gradient of 0-20% acetonitrile in water was used from 2 to 34 min, followed by 20% acetonitrile in water until 40 min, and then 100% acetonitrile for 10 until 50 min. They conducted the determination at a flow of 1.3 ml/min and a wavelength of 229 nm. To calculate the glucosinolate concentration 2-propenyl glucosinolate was used as a external standard (Sigma-Aldrich Chemie GmbH, Taufkirchen, Germany) and the response factor of each compound relative to 2-propenyl glucosinolate (European Union 1990) was used. According to previous work (Zimmermann et al. 2007) the glucosinolates were identified from the protonated molecular ions [M + H]+ and the fragment ions corresponding to [M + H - glucose]+ by HPLC-ESI/MS2 using Agilent 1100 series (Agilent Technologies, Waldbronn, Germany) in the positive ionisation mode (Schreiner et al. 2006).

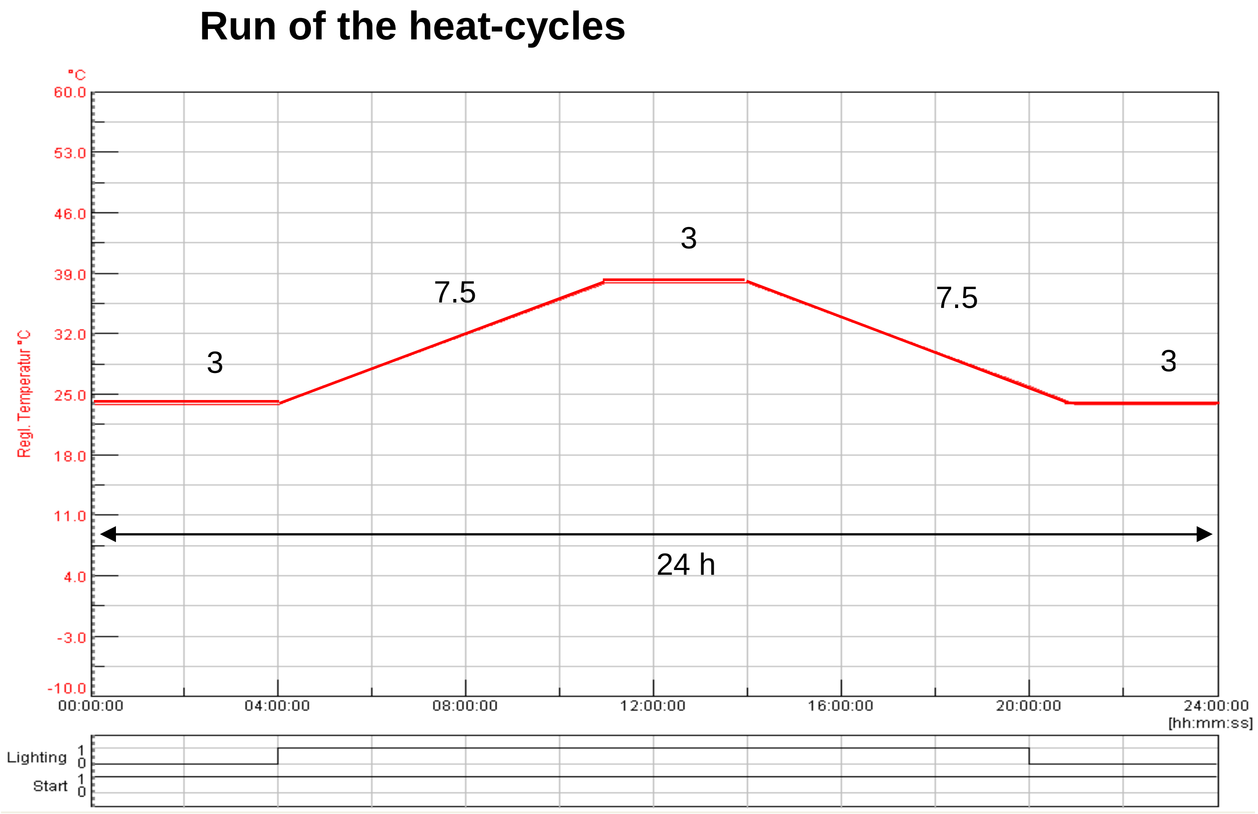

Fig. 11: Example of daily temperature profile of the heat cycles. The temperature increased slowly over a time period for 7.5 hours, then a peak temperature lasted for three hours and afterwards the temperature decreased for 7.5 hours. These cycles were repeated one, three or five times.

4.3.2 Statistical analysis

Data were visually checked for normality of residuals, creating histograms and box plots and if necessary transformed and pooled for the replicates. The percentage data for the different glucosinolates were arc sine square root transformed.

Main emphasize of the experiment was on the relationships between amount of glucosinolates and temperature, number of heat cycles and presence of a pest species. We tested the effects of the heat cycles and the temperature on the glucosinolates with an ANOVA. Also the influence of the pest species was tested to see if there were important differences. Every ANOVA which yielded significant results was followed by a post-hoc-test (Tukey's Test). IMB SPSS 19 was used for all statistical analyses.

4.4 Results

We studied the influence of different heat cycles on the glucosinolates in the leaves to see if the heat reduces or increases them. The most common glucosinolate in all samples was glucobrassicin (2.08 ± 0.31 µmol/g TG; mean ± standard error), followed by glucoraphanin (1.05 ± 0.17 µmol/g TG; M ± SE) and sinigrin (0.82 ± 0.13 µmol/g TG; M ± SE). Less common was glucoiberin (0.63 ± 0.09 µmol/g TG; M ± SE) and progroitin (0.36 ± 0.07 µmol/g TG; M ± SE). We found only small amounts of glucobrassicanapin (0.19 ± 0.015 µmol/g TG; M ± SE), gluconapin (0.16 ± 0.02 µmol/g TG; M ± SE), 4-Methoxy-glucobrassicin (0.06 ± 0.004 µmol/g TG; M ± SE) and neoglucobrassicin (0.03 ± 0.004 µmol/g TG; M ± SE; **Fig. 12**). Total amount of glucosinolates differed in the different treatments.

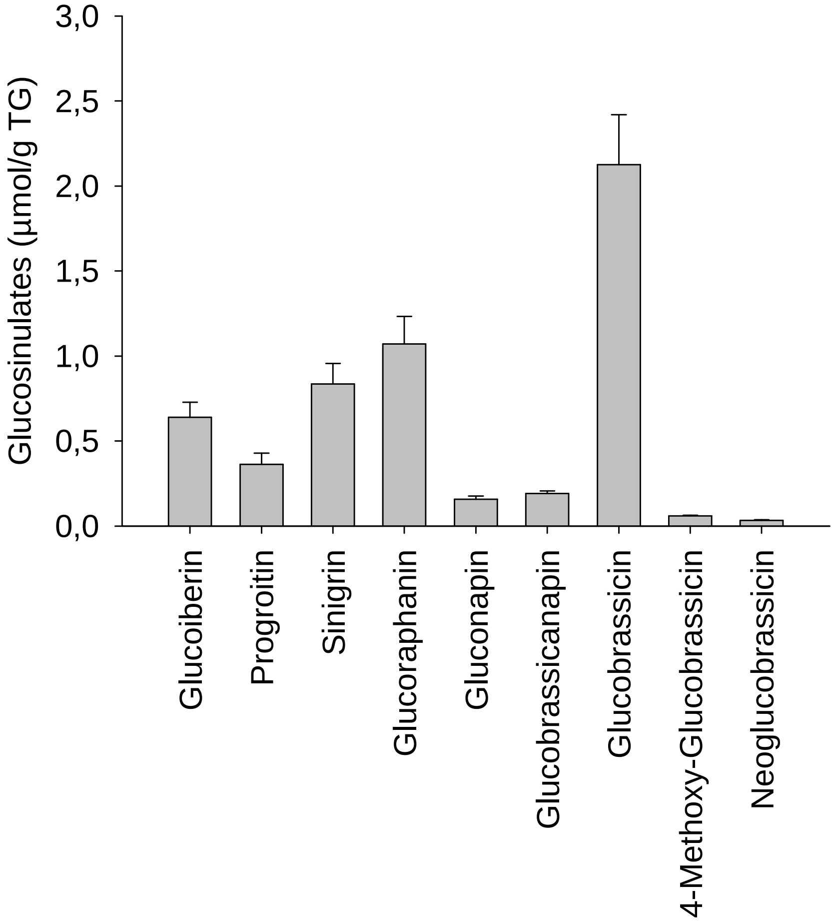

Fig. 12: Average amount of the different glucosinolates in the Brussels sprout leaves independent of treatment. n = 9 for each treatment.

There was a big difference in the amount of glucosinolates in plants with and without the cabbage whitefly *Aleyrodes proletella*. Plants infested with the cabbage whitefly contained double or even three times higher amounts of glucosinolates than plants free of whiteflies (**Fig. 13**). Mainly the amount of progroitin and sinigrin increased considerably, but not significantly.

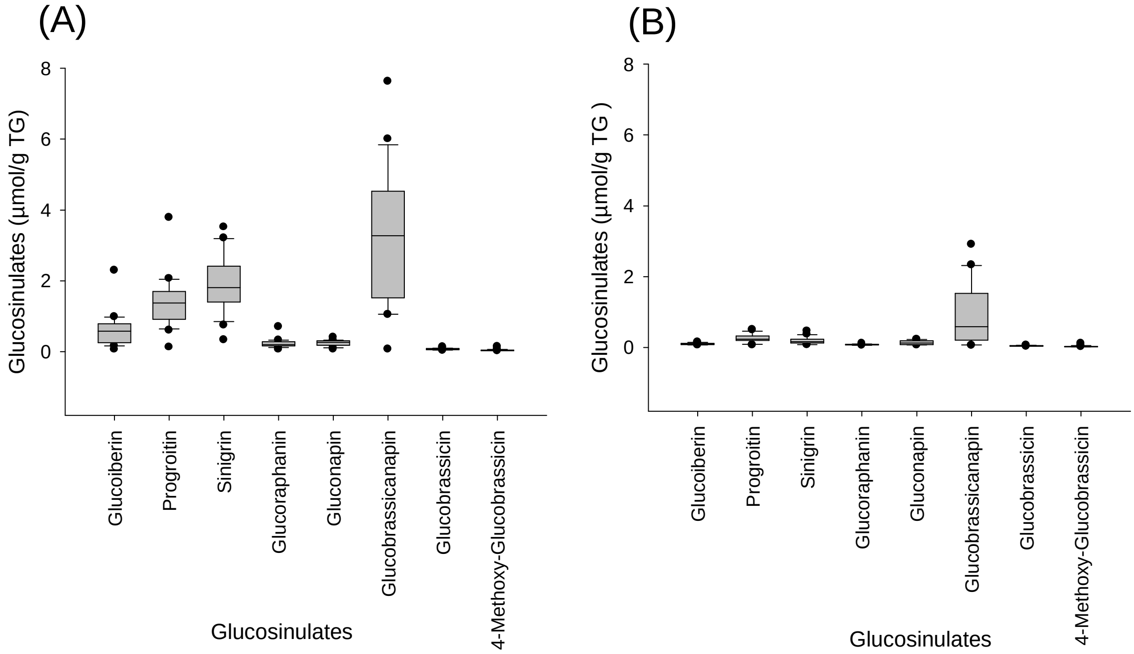

Fig. 13: Amount of different glucosinolates of plants with and without insects. (A) shows the amount of the glucosinolates of plants with *Aleyrodes proletella* (B) shows the amount of glucosinolates on plants without whiteflies. n = 9 for each experiment and treatment.

The sucking of *Aleyrodes proletella* had a highly significant effect ($p < 0.001$) on the amount of all glucosinolates (**Fig. 14 (B)**), besides neoglucobrassicin ($F_{1,41} = 1.24$; $p = 0.27$; **Fig. 14 (A)**). Plants without whiteflies did not react to high temperatures with changes in the amount of total glucosinolates or individual glucosinolates, not even to temperatures of 38 °C for five days, but on plants with *A. proletella* the amount on glucosinolates increased **(Fig. 14).**

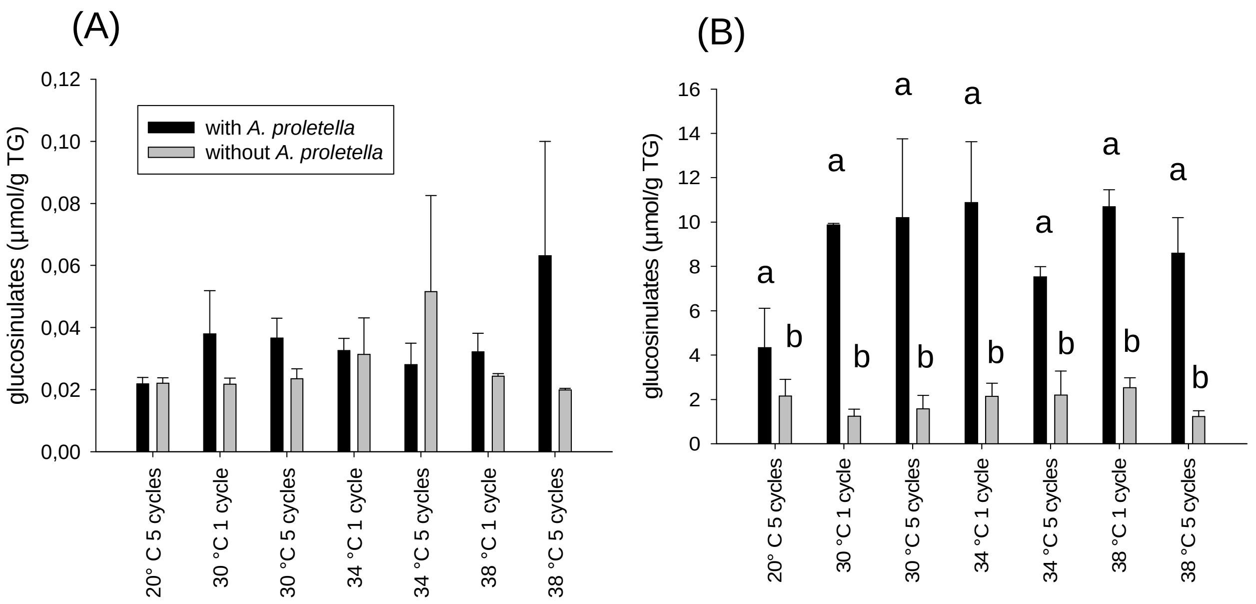

Fig. 14: Influence of the sucking of the whitefly in the different treatments (A) amount of Neoglucobrassicin (B) total glucosinolate amount. n = 9 for each experiment and treatment. Different characters representing significanes (α ≤ 0.05), graphs without characters show no significances.

High temperatures strengthen the inducing effect of the whitefly sucking. One exposition with 30 °C was enough to increase the amount of glucosinolates (**Fig. 15**). Higher temperatures had no additional effect to the further increase effect. The glucosinolates increased with increasing temperature compared to the control, but there was no significant difference between the different heat cycles or temperatures. The difference to the control was also not significant (**Fig. 15**).

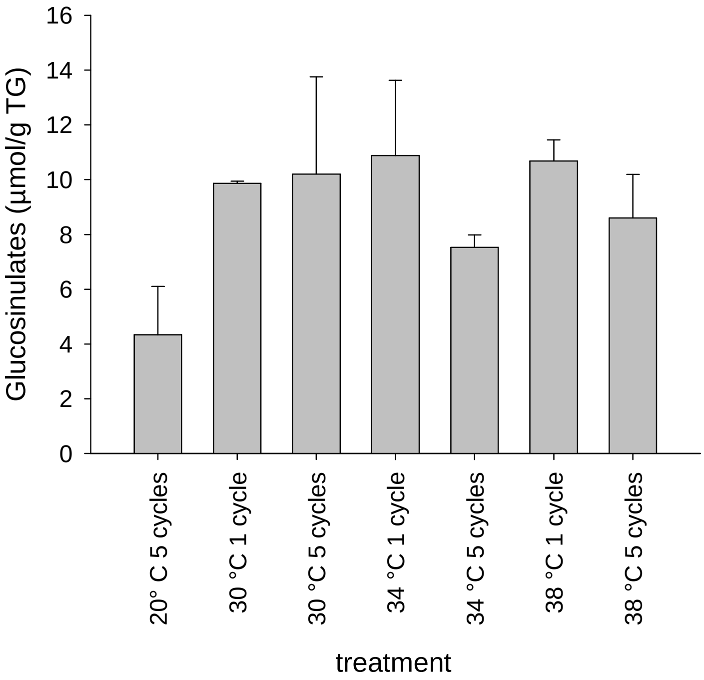

Fig. 15: Total amount of glucosinolates in different treatments on plants with *Aleyrodes proletella* under different temperatures and different numbers of heat cycles. n = 9 for each treatment.

To analyse the influence of the temperature and the number of cycles the influence of the whiteflies was excluded from our analysis by using "insect" as a covariate. After this we found no significant differences of the temperature on the different glucosinolates. Altogether the amount of glucosinolates increased under higher temperatures, but there was no significant difference between the different temperatures (**Fig. 16 (B)**). We could just find a marginal significant effect of the temperature on the amount of 4-Methoxy-Glucobrassicin ($F_{3,41} = 2.79$; $p = 0.058$; **(Fig. 16 (A)).** The amount of this glucosinolate was significantly higher under the higher temperatures compared to the control.

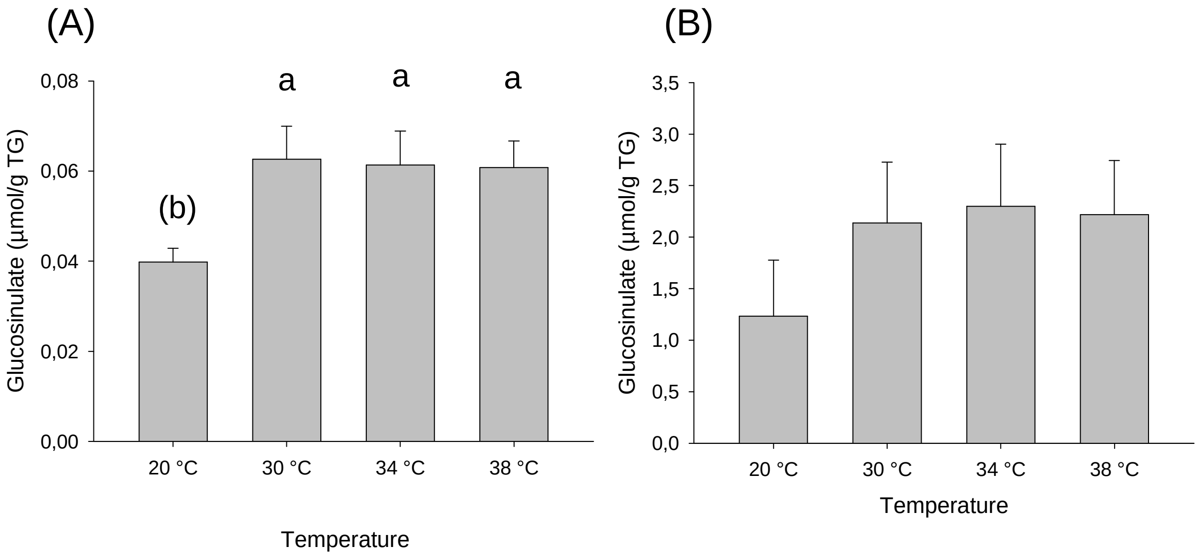

Fig. 16: Influence of temperature independent of heat cycles on different glucosinolates on plants with *A. proletella.* (A) Influence of the different temperatures on the amount of the glucosinolates 4-Methoxy-Glucobrassicin (B) Influence of the different temperatures on the amount of glucobrassicin. n = 9 for each experiment and treatment. Different characters in braces representing significanes ($\alpha \leq 0.1$), graphs without characters show no significances.

The number of different heat cycles had only a significant effect on the amount of glucoiberin ($F_{1,41} = 6.30$; p = 0.017; **Fig. 17 (A)**) and Glucoraphanin ($F_{3,41} = 4.46$; p = 0.042; **Fig. 17 (B)**). We could also find a marginal significant effect on the amount of 4-Methoxy-Glucobrassicin ($F_{3,4} = 2.75$; p = 0.058). The other glucosinolates showed no significances (**Fig. 17 (C)**). But altogether the amount of glucosinolates was higher after one heat cycle compared to five heat cycles. This indicates that one heat cycle is enough to increase the amount of glucosinolates and support the effect of the sucking of the insects. More heat cycles had no additional effect.

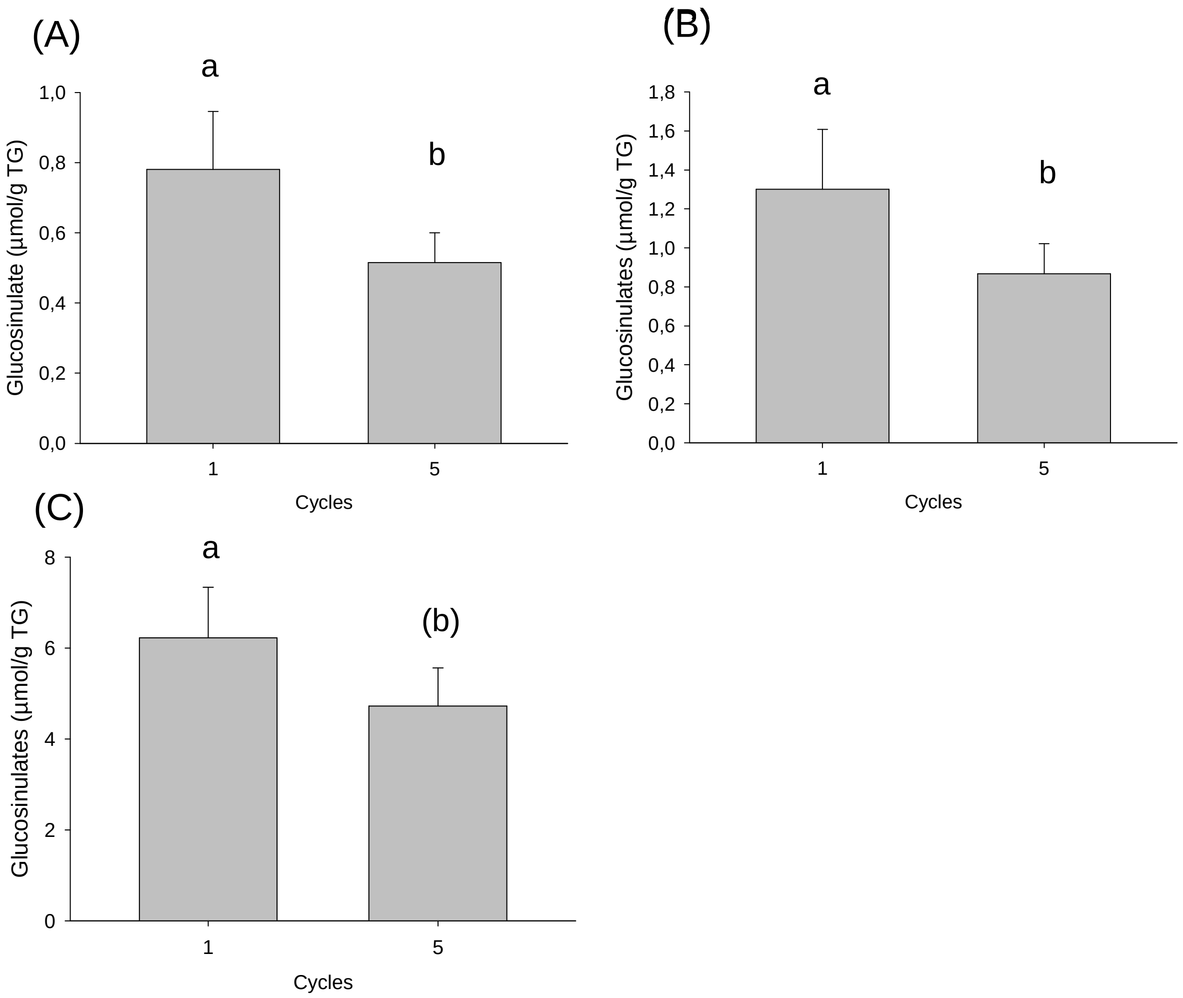

Fig. 17: Amount of total glucosinolates on the different heat cycle treatments on plants with *A. proletella* independent of temperature, comparing plants after one heat cycle with plants after five heat cycles. (A) amount of Glucoiberin (B) amount of Glucoraphenin (C) total amount of glucosinolates. n = 9 for each experiment and treatment. Different characters representing significanes ($\alpha \leq 0.05$), charateres in braches represtenting significanes ($\alpha \leq 0.1$), graphs without characters show no significances.

There was no significant effect on the interaction of temperature and cycle and also no interaction between temperature, cycle and insect.

4.5 Discussion

The total amount of glucosinolates in Brussels sprout control plants infested with whiteflies, but without a treating in the climate chamber was 4.3 µmol/g TG, whereas the highest amount of glucosinolates was found in the 34 °C treatment after one cycle with whitefly infestation. The amount of glucosinolates was 10.8 µmol/g TG. In the control without insects the amount of glucosinolates ranged between 1.2 µmol/g TG and 2.5 µmol/g TG. This data were compared to contents of glucosinolates found in other studies. Kushad et al. (1999) found contents of 25 µmol/g TG and Tiedink et al. (1988) found even 34 µmol/g TG in Brussels sprout plants without insect infestation. Sarikamis et al. (2009) and Kushad et al. (1999) showed that beside the influence of the variety the climate and high temperatures have an important effect on the amount of glucosinolates. Due to the fact that their experiments as well as our experiments were realised under high temperatures, temperature impacts cannot be an explanation for the differences in the results. But other climatic factors might influence the amount of glucosinolates. Furthermore the quality of the soil and the fertilisation might have an impact on the content of glucosinolates. Most experiments were done under outdoor conditions with supplementary fertilisation whereas our experiments were done in the lab without fertilisation. Josefsson (1970) found that the quality of the soil has an important effect on the glucosinolates and that especially under loamy soil more glucosinolates are produced. The fertilisation is another factor that can influence the content of glucosinolates. Zhao et al. (1994) pointed out that the fertilisation especially with sulphur and nitrogen has an influence and Böhlendorf (2010) showed that the amount of glucosinolates increased with increasing fertilisation. In other studies (Herbst, unpublished) conducted in Hanover in greenhouses with the same soil (Fruhstorfer Erde®) the amount of glucosinolates in Brussels sprout was on average 2.1 µmol/g TG. In the study the contents of glucosinolates were determined on plants without whiteflies or other herbivores. The amount in this experiment was even less than the amount in our study, but the differences were small compared to the other studies. Due to this we can assume that the cause for the differences lay on the one hand on the variety of the Brussels sprout and on the other hand on the different soil.

The most common glucosinolate in the Brussels sprout plants in our experiment were glucobrassicin (2.08 µmol/g TG) and glucoaphanin (1.05 µmol/g TG). In our study sinigrin (0.82 µmol/g TG) was the third most glucosinolate in the plants. Normally sinigrin and glucobrassicin are the most common glucosinolates in Brussels sprouts followed by progroitin and gluconapin (Heaney & Fenwick 1980; Kushad et al. 1999) with sinigrin contents of 8.9 µmol/g TG and 3.2 µmol/g TG glucobrassicin (Kushad et al. 1999). Heaney and Fenwick (1980) found that the amount of glucosinolates is differing due to the planting site, but that the percentages of the different glucosinolates are quite similar. The amount and the composition of the glucosinolates depend on several factors (Rosa 1997). Due to the fact that total amount and the side chains are under genetic control (Kliebenstein et al. 2001) variety is the most important one (Böhlendorf 2010). But also other factors like climate, stress, plant age, date of harvest and many more factors are important (Ludwig-Müller et al. 1996; Ciska et al. 2000;).

With increasing temperature the amount of glucosinolates was increasing in our experiment as well, but this increase was not significant beside a marginal significant effect in the amount of 4-Methoxy-Glucobrassicin. It has been found that stress (cold, heat) increases the amount of glucosinolates (Schreiner & Huyskens-Keil 2006). High temperatures can increase the glucose- and amino acid synthesis, the primary stage of the glucosinolate synthesis, leading to a higher content of glucosinolates (Cartea et al. 2008). The amount of glucosinolates was highest in the 30 °C treatment.

The increase of the number of heat cycles effected only the amount of glucoiberin and glucoaphanin. The amount of glucosinolates was higher after one cycle compared to five cycles. We assume that the stress of the warming leads to an increase in the glucosinolates, but that the plants after five cycles are either accustomed to the heat or that the energy expenditure is too high to hold it for such a long time.

The infestation with whiteflies increased the amount of glucosinolates up to the threefold compared to the control. The concentration of glucosinolates in the plant tissue is increasing after feeding of a herbivore (Martin & Müller 2007; Poelman et al. 2008). Especially the accumulation of indolic glucosinolates is increased by herbivore attack, whereas the amounts of aliphatic and aromatic glucosinolates may decrease (Textor & Gershenzon 2009). Mainly the feeding of specialists are followed by an increase in glucosinolates, whereas feeding of the generalist aphid *Myzus persicae* causes a decrease in glucosinolates (Kim & Jander 2007). According to expectations the concentration of glucosinolates should increase only slightly after feeding of a specialist, Rohr et al. (2012) could also show that feeding of the specialist *Pieris brassicae* lead to an increase in glucosinolates. Glucosinolates are commonly used by the plant as a defence mechanism against fungi, nematodes and insects (Rosa 1997). The effect of glucosinolates on insects depends on the specialisation of the insect. Normally generalist herbivores are repelled by glucosinolates and specialist can handle them or they are even attracted by them (Rojas 1999;

Miles et al. 2005; Halkier & Gershenzon 2006; Lankau 2007). Gols et al. (2008) for example could show that the caterpillar of *Pieres rapae* was not influenced by an increasing level of glucosinolates, while the larvae of the generalist *Mamestra brassicae* suffered high mortality under high concentrations of glucosinolates. High amounts of glucosinolates stimulate for example the specialist *Pieres rapae* (Stoner 1990; Müller et al. 2010) or *Hellula undalis* (Mewis et al. 2002) to oviposit and other specialist also use them to find oviposition places (Agerbirk et al. 2009). Glucosinolates also promote the larval feeding of *Pieres rapae* and *Plutella xylostella* (Müller et al. 2010). Specialised insects have developed several strategies to handle these compounds; the cabbage aphid *Brevicoryne brassicae* for example uses the glucosinolates for its own defence (Bridges et al. 2002) and is avoiding its toxicity by storage of the myrosinase in crystalline micro bodies (Bridges et al. 2002). The generalist aphid *Myzus persicae* in contrast is also sucking on cabbage plants and it excretes the toxic components with its honeydew (Hopkins et al. 2009). The sawfly *Athalia rosae,* a specialist on turnip roots however, store glucosinolates in the hemolymph for several hours and then excreted them into yet unidentified metabolites (Müller & Wittstock 2005). Similar for all herbivores feeding on plants rich in glucosinolates is the avoiding of the breakdown to toxic isothiocyanates by e.g. rapid metabolising of glucosinolates to harmless compounds or avoiding cell disruption (Winde & Wittstock 2011). Other generalists like snails (Newton et al. 2010) or *Thrips tabaci* (Bukovinszky et al. 2010) are repelled by glucosinolates. Overall herbivores seem to avoid plants with high concentrations of short side chain alkenyl glucosinolates, whereas they prefer plants with elongated side chains (Poelman et al. 2009). Beside herbivory abiotic stress factors can change the composition and amount of glucosinolates. Drought reduced the concentration of glucosinolate in the leaves of Broccoli plants (Khan et al. 2010). Whereas it increased the amount of aliphatic glucosinolates in the study of Mewis et al. (2012) and the total amount of glucosinolates in the study of Tariq et al. (2013). Khan et al. (2011b) could show that the amount of glucosinolates is increasing under water stress after the feeding of the generalist *Myzus persicae,* whereas the feeding of the specialist *Brevicoryne brassicae* leads to an increase independent of water-stress. CO_2 is another abiotic factor influencing the concentration of glucosinolates. Under CO_2-concentrations as expected in the future the total amount of glucosinolates increased, while the amount of indole glucosinolates decreased (Schonhof et al. 2007). Also UV-B is an abiotic factor leading to an increase in glucosinolates in plant tissue (Schreiner et al. 2009).

These plant compounds does not only influence the herbivore but also higher trophic levels like predators and parasitoids. The turnip sawfly *Athalia rosae* elicits a bleeding behavior releasing hemolymph at predator contact. The hemolymph contains sinalbin and the larvae is protected by this release (Müller & Brakefield 2003). In other studies Müller et al. (2001) could show that the glucosinolate released in the "reflex bleeding" depends on the glucosinolate composition of the host plant. Moreover parasitoids, which feed on herbivores that do not sequester the glucosinolates but store them in their body, face a higher mortality and worse growth rate (Gols & Harvey 2009).

In our study especially progroitin and sinigrin increased with the sucking of the whitefly. Sinigrin and progroitin are the compounds which are responsible for the bitter taste of cabbage plants (Fenwick et al. 1983a; van Doorn et al. 1998). Newton et al. (2010) showed that an increasing amount of sinigrin is correlated with an increasing population of *Aleyrodes proletella*. Whereas sinigrin had a negative effect on the whiteflies in the study of Ibanez et al. (2012). But Kuhlmann & Müller (2009) could show that whiteflies are more influenced by radiation or other abiotic factors than the plant chemical composition.

4.6 Conclusion

Due to our results that the glucosinolates are just slightly increasing under short periods of high temperatures and the increase even lasts only for one heat cycle, we assume that more frequent heat waves with even higher peak temperatures will have no indirect effect on the population of the whitefly versus changes in the amount of glucosinolates. Furthermore the whiteflies are not negatively affected by the high contents of glucosinolates, so that even an increase in the glucosinolates won’t have a negative effect on the population of *Aleyrodes proletella*.

5 Influence of heavy rain on the development of the cabbage whitefly *Aleyrodes proletella*

5.1 Abstract

Precipitation is next to temperature another important climatic factor for insects. Like all other climatic factors also the precipitation regime has changed with the climate change and will continue to change. It has been assumed, that the precipitation will shift into winter and that the summers in Lower Saxony will face more heavy rain storms intermitted by dry periods. Concrete studies to the influences of heavy rain on insects are rare. To test the influence of heavy rains on *Aleyrodes proletella* we developed an arena, in which different levels of heavy rain were tested. We used three rain levels, medium (0.6 l/min), heavy (2 l/min) and torrential (6 l/min) rain and exposed all life stages of the whitefly to them. The medium and heavy rain had no influence on the mortality of the whiteflies, just under the torrential rain treatment the mortality of the adults increased about 50% due to washing off effects from the leaves. The number of eggs laid after a torrential rain of 20 minutes also decreased about 50% and the hatching success of the eggs declined under all rain treatments. In opposite to this the rain had no effect on the development of all larval and the pupal stage. Repetitions with medium rain in the field had no effect on *Aleyrodes proletella*.

5.2 Introduction

The precipitation regime will change in the future with more rain in the winter and lesser rain in the summer. In winter the precipitation will more often fall as rain instead of snow and in the summer it will rain less, but more heavy rain events intermediated with dry periods are expected (Hartmann et al. 2013).

The German Weather Service defines heavy rain as a precipitation of 5 mm in 5 minutes. The highest precipitation ever measured in Germany was measured in Füssen on 25th of May, 1920 and was 126 mm in 8 minutes (Häuser 1922). And in other countries especially in the tropics precipitation can be even higher. In Barot, Guadeloupe in 1970 a precipitation of 38 mm in 1 minute or 401 mm in one hour in Shangdi, China was measured (WMO 1995).

High rain can cause high direct mortality to herbivorous insects, in particular small, soft bodied species or indirectly affect insects by cooler temperatures (Bale et al 2002; Harrington et al. 2007). Heavy rains can increase the mortality especially of soil dwelling species (Fuhrer 2003), such as *Thrips tabaci* pupating in the soil (Bergant et al. 2005) or also aphids moving on the soil when switching host plants after artificially dislodged (Leite et al. 2006; Harrington et al. 2007). But in the tropics it could be observed that the population of the whitefly *Bemisia tabaci* increased in the months with high rainfall (Dengel 1981) and populations are higher in regions with higher annual rainfall (Robertson 1985). This increase in the population is likely due to the increase in fresh leaves of the host plant and better plant growth due to higher soil moisture (Legg 1994). Higher precipitation in summer can lead to denser vegetation which is followed by more pest species, due to the higher food availability (Fuhrer 2003). But besides the direct and indirect effects on the mortality, rain can also influence other life history parameters. For example a delayed begin of the flight activity of aphids (Harrington et al. 2007) leading to an asynchrony between pest and host plant. Rain can also slow down the development or prohibit it as shown for the diamond back moth (*Plutella xylostella*) (Guilloux et al. 2003). Morsello et al. (2008) found that heavy rain can kill the larvae of *Thrips tabaci* and prevent the development. Other species like the cabbage fly *Delia radicum* (Esbjerg & Mogens 2005) are not influenced by rain.

We used the cabbage whitefly as a model organism in our experiments, because the populations of this species increased rapidly in the last ten years and the species has become one of the most important pest species in cabbage in Lower Saxony. Besides temperatures rain may have a crucial effect on the population development and the influence of the precipitation is necessary for prognosis models. Due to the fact that the whiteflies are most common in dry regions (Leite et al. 2005) and that, no studies, to our knowledge, about the population development of the cabbage whitefly under weather conditions like heavy rain, exist, we designed an experiment to test the adult behaviour and the development of the pest under heavy rain conditions.

5.2.1 The cabbage whitefly *Aleyrodes proletella*, (Fam. Aleyrodidae, Order Homoptera)

is a common in pest of Brassicaceae in Europe. The species is spreading heavily since the last ten years (van Alebeek 2008) and is assumed to become one of the main pest species in cabbage in the future. High temperatures and rain are known factors that slow down development (Leite et al 2006). Currently 4-5 generations can develop within one year in Germany. Mass occurrence is normally in late summer when egg to adult development only takes three weeks. (See also chapter 2.5.1.1)

5.3 Material and Methods

5.3.1 Experiment

Before starting the experiments the occurrence of heavy rain events in Germany and especially in Lower Saxony were evaluated. Therefore the rain data of the years 1996-2010 on four randomly chosen weather stations were analysed. The results of this analysis were used to calculate the rain intensity in our rain arena to use rain intensities that already occur in Lower Saxony and may occur in the future.

The cabbage whiteflies for the experiment were taken from the rearing of the Institute of Plant Disease and Plant Protection in Hanover. The insects were reared on Brussels Sprout under temperatures of 20 °C and light conditions of 18/6 (light/darkness). The insects were under artificial rearing for about five years and the initial specimen were obtained from the JKI in Braunschweig. Every six month new insects from the wild were added to the rearing.

To test the influence of heavy rain, a rain arena with shower heads was constructed to simulate different rain intensities. The size of the rain droplets was measured using liquid nitrogen. The size of the droplets fluctuated between 2-4 mm, which is similar to the droplet size in nature. Then three different rain levels of medium (droplet size: 2-4 mm; amount of rain: 0.6 l/min*m²), heavy (droplet size: 2-4 mm; amount of rain: 2 l/min*m²) and extraordinary heavy/torrential (droplet size: 2-4 mm; amount of rain: 6 l/min*m²) rain were used. Nine Brussels sprout plants with three-day-old, synchronised whiteflies in clip-cages (five individuals per cage) were exposed under shower heads, the clip-cages were removed and rain delivered for twenty minutes. During this time the behaviour of whiteflies was observed to study if they are staying on the plants or flying away and after the twenty minutes the cages were clipped over the remaining flies. Those were counted and the missing assessed as dead. Then we visually observed the flies for the following five days in the greenhouse chamber, in which the experiments were conducted, to study the fecundity and delayed mortality. The experiments were repeated with eggs, larvae and pupae. For the experiments with the eggs five 2-day-old females were put on Brussels sprout plants and given two days for egg-laying. After the removing of the females the eggs were counted. For the experiment with the larvae and pupae, plants were infested with female whiteflies and after two days of egg-laying the females were removed and after the development of the eggs to larvae or pupae the plants were used for the experiments.

In the second part of the experiment five adults were clipped on ten different plants, but these plants were exposed to rain in the field. The exposition took place in June and July 2011 under a rain density of 0.5 l/min*m² and a droplet size of 2-4 mm The experiments were repeated with previously prepared plants with eggs, larvae and pupae. While it was raining the clip-cages were removed and after twenty minutes clipped again and the plants were brought inside. Again direct actual mortality was determined, the delayed mortality and the fecundity.

5.3.2 Statistical analysis

Data was visually checked for normality of residuals, creating histograms and box plots and if necessary transformed and pooled for the replicates. The percentage data for the mortality of the males, females and larvae was arc sine square root transformed. The counting data for the eggs was square transformed.

Main emphasize of the experiment was on the relationships between mortality and the different rain intensities. We tested the effects of the rain intensities on the insects with an ANOVA. Every ANOVA which yielded significant results were followed by a post-hoc-test (Tukey's Test). IMB SPSS 19 was used for all statistical analyses.

5.4 Results

The analyses of the rain data showed that rain events with more than 5 l/h*m² appeared 214 (±23) times, events with more than 10 l/h*m² 15 (±7.6) times and events with more than 25 l/h*m² 3.5 (±0,6) times (demonstrating medium and heavy rain, respectively in accordance with the German Weather Service; **Fig. 18**). The rain data on the weather stations were checked hourly, making it impossible to know how long the rain shower really lasted. Furthermore it must be taken in account the heavy rain events are often small-scaled and therefore might not be detected by weather stations.

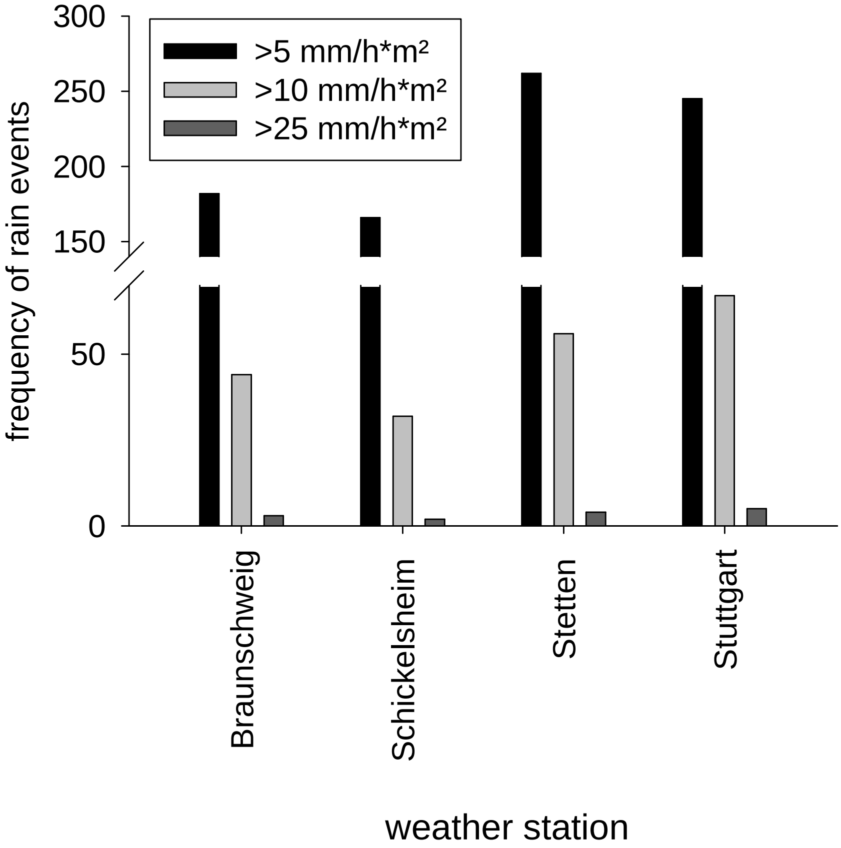

Fig. 18: Frequency of heavy rain events in Germany on four randomly chosen weather stations over the years 1996-2010.

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5.4.1 Simulated rain

The different rain intensities of the simulated rain had a significant effect on the survival of the adults. Under the normal and the heavy rain the survival was about 80% compared to 100% in the control, which was no significant difference. But under the third rain level, the torrential rain we found a mortality about 50%, which was significantly higher than the mortalities of the other rain intensities ($F_{3,44} = 6.260$; $p < 0.001$; **Fig. 19**). While it was raining the adults were hiding under the leaves and we couldn’t observe any flight activity. Due to this we assume that all missing insects were washed off the leaves and hence were dead. There was no delayed mortality due to the rain. All insects that survived the rain shower lived as long as the animals in the control.

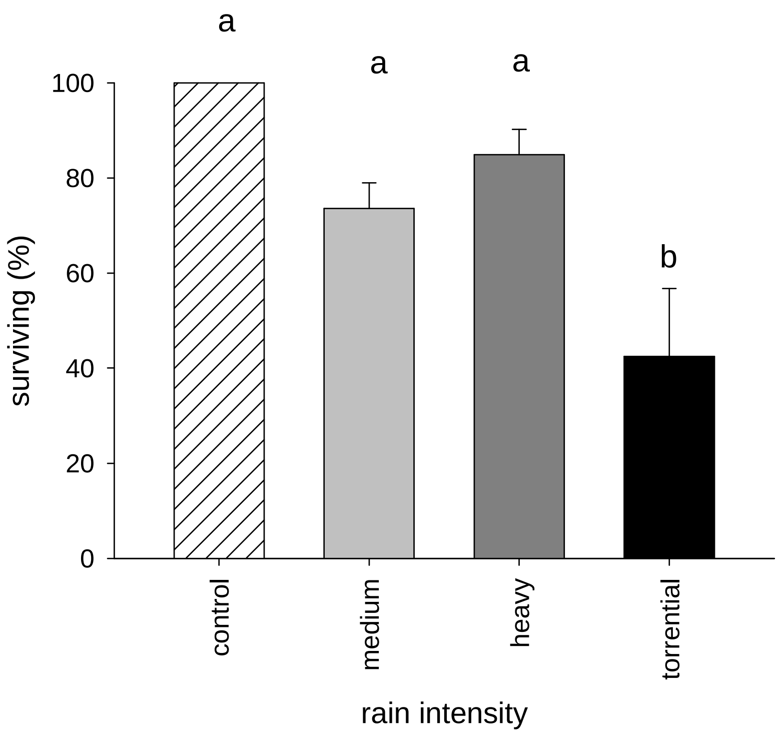

Fig. 19: Influence of different rain intensities on the immediate survival of adult *Aleyrodes proletella* directly after the rain. The rain lasted for 20 minutes. n = 9 for each treatment. Different characters representing significanes ($\alpha \leq 0.05$).

Egg-laying during a 3-d period subsequent to rain exposure was reduced slightly but non-significantly for the treatment with torrential rain. ($F_{3,30} = 1.511$; $p = 0.23$; **Fig. 20**). For the other rain intensities no difference in the egg-laying could be found.

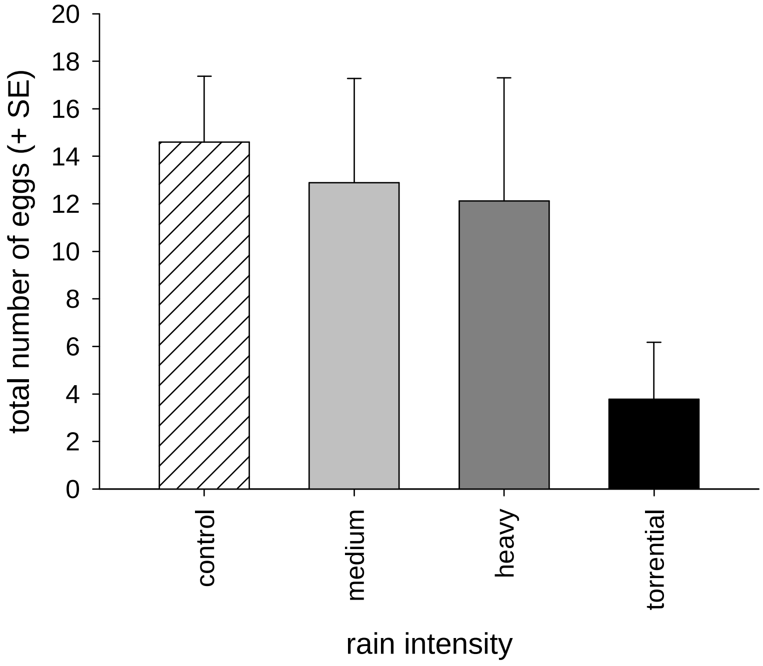

Fig. 20: Egg-laying of *Aleyrodes proletella* in three consecutive days after the females have faced a 20 minute rain shower. n = 9 for each treatment.

After the short-time rain the egg development decreased to less than half of the control data ($F_{3,30}$ = 4.664; p = 0.009; **Fig. 21**), but there was no difference between the different rain intensities. Several egg clutches were destroyed by the rain, but there was no difference in the amount of destroyed clutches.

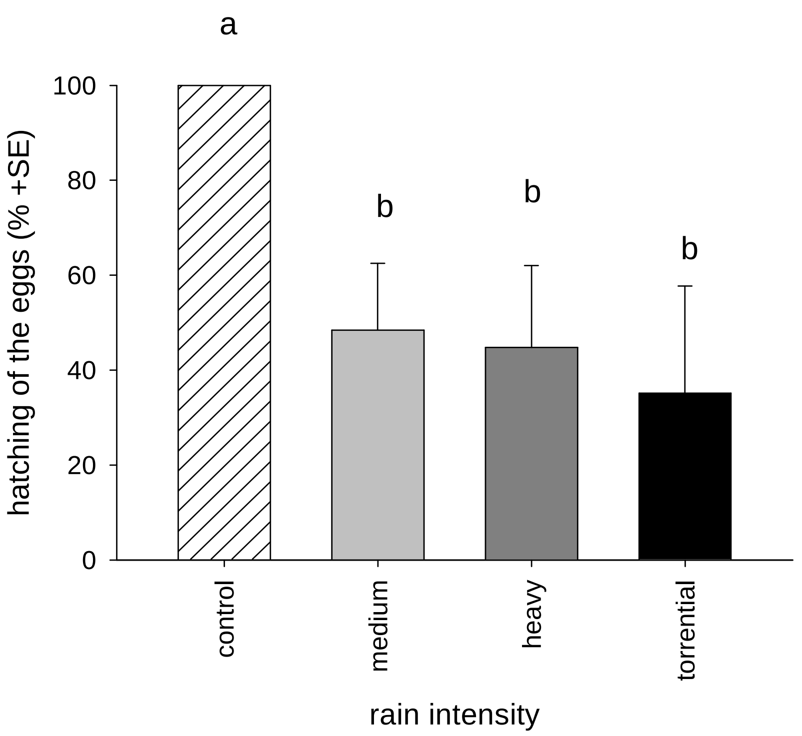

Fig. 21: The influence of different rain intensities on the development of *Aleyrodes proletella* eggs. The eggs faced a 20 minute rain shower and developed then under greenhouse conditions. n = 9 for each treatment. Different characters representing significances (α ≤ 0.05).

The different rain intensities didn’t influence the development of the L1-larvae ($F_{3,15} = 0.775$; p = 0.53, **Fig. 22 (A)**) and it had also no influence on the development of the L3-larvae ($F_{3,10} = 1.172$; p = 0.39; **Fig. 22 (B)**).

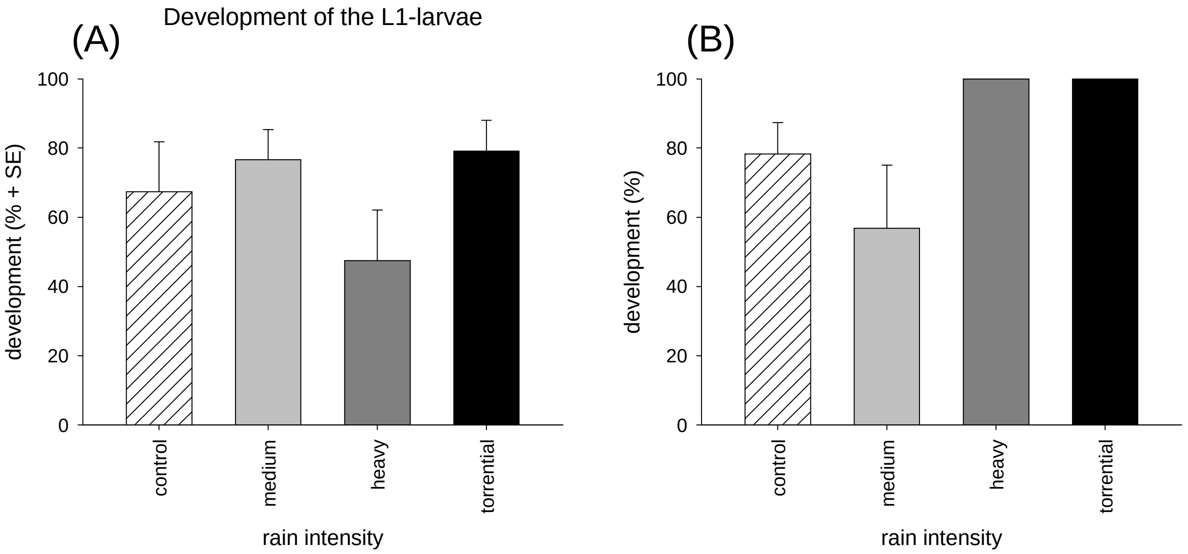

Fig. 22: The influence of different rain intensities on the development of the larvae (A) the L1-larvae of *A. proletella* and (B) the L3-larvae. The larvae faced a 20 minute rain shower and developed then under greenhouse conditions. n = 9 for each treatment.

The simulated rain shower had also no effect on the development of the pupae ($F_{3,10}$ = 3.128; p = 0.097; **Fig. 23**). In the control and under the medium rain nearly 100% of the pupae developed to adults. Under the heavy rain and the torrential rain around 80% developed to adults, but the difference was not significant.

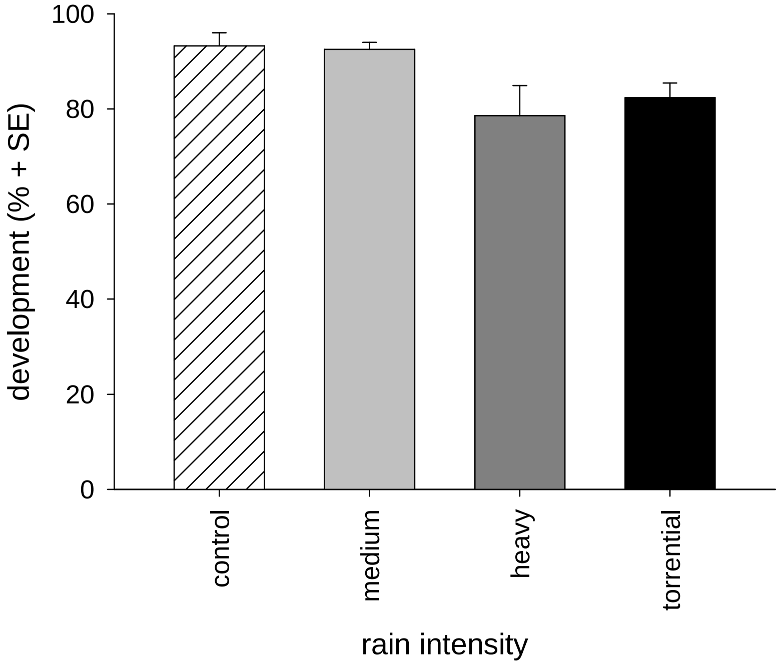

Fig. 23: Development of the L4-larvae after a rain shower. The larvae faced a 20 minute rain shower and developed then under greenhouse conditions. n = 9 for each treatment.

5.4.2 Real rain

No differences in the mortality of the adults exposed to real rain and the adults in the control could be found ($F_{1,19}$ = 0.72; p = 0.41; **Fig. 24**). In the experiment the mortality was a little bit higher but this was not significant.

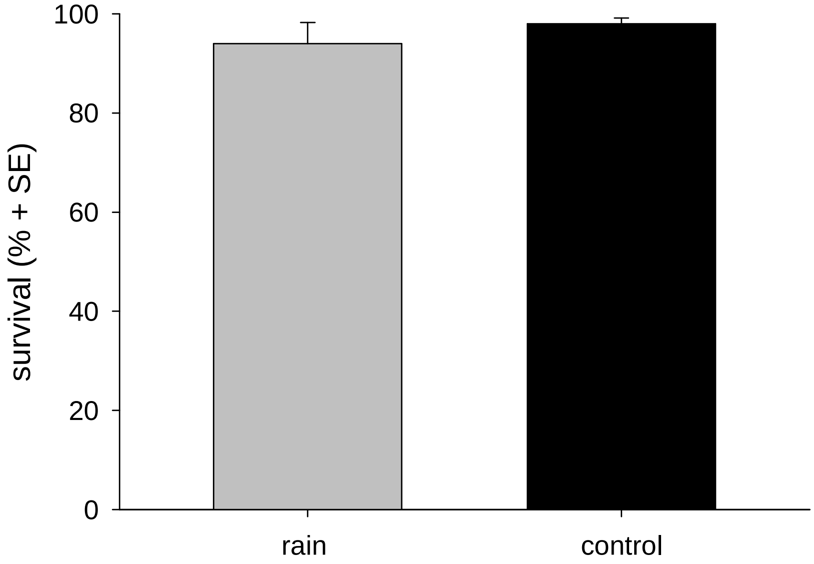

Fig. 24: Survival of the adults after a twenty minute rain shower in the field with an intensity of 0.5 l/min*m² and a droplet size of 2-4 mm with five adults per plant and ten replications. n = 9 for each treatment.

There was also no difference in the mortality of the L1- or L3-larvae ($F_{1,19} = 0.415$; $p = 0.53$; $F_{1,19} = 0.44$; $p = 0.52$, respectively). The mortality in the control as well as in the treatment was around 85% (**Fig. 25**).

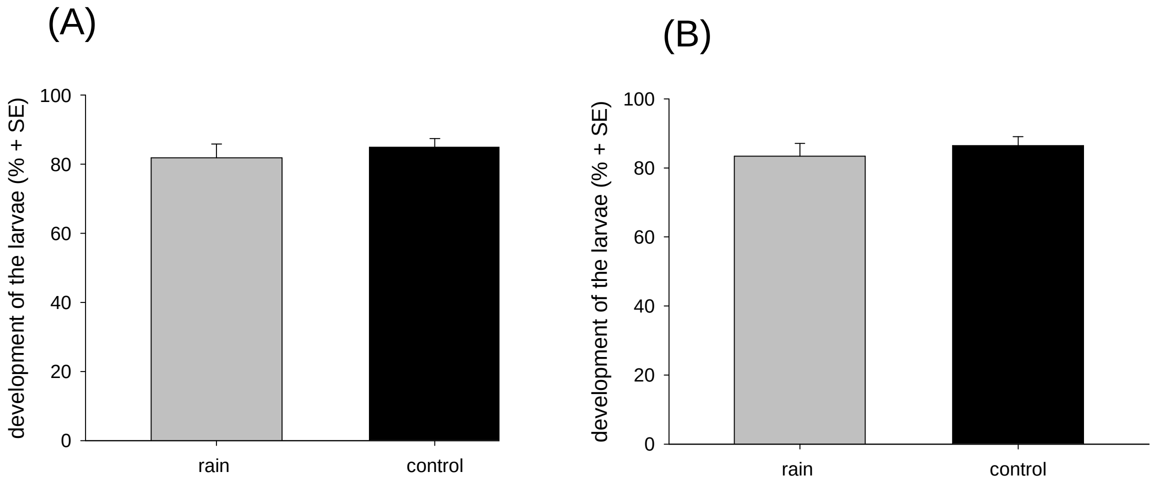

Fig. 25: Mortality of the larvae after a twenty minute rain shower in the field with an intensity of 0.5 l/min*m² and a droplet size of 2-4 mm compared to the control (A) L1-larvae (B) L3-larvae. With ten replicates per treatment. n = 9 for each treatment.

The egg-laying was slightly influenced by the rain ($F_{1,19}$ = 0.74; p = 0.4; **Fig 26 (B)**). Females which faced the rain laid fewer eggs than the females in the control. The development of the eggs was not significantly influenced by the rain ($F_{1,19}$ = 0.14; p = 0.7; **Fig 26 (A)**). Under rain a few less eggs developed.

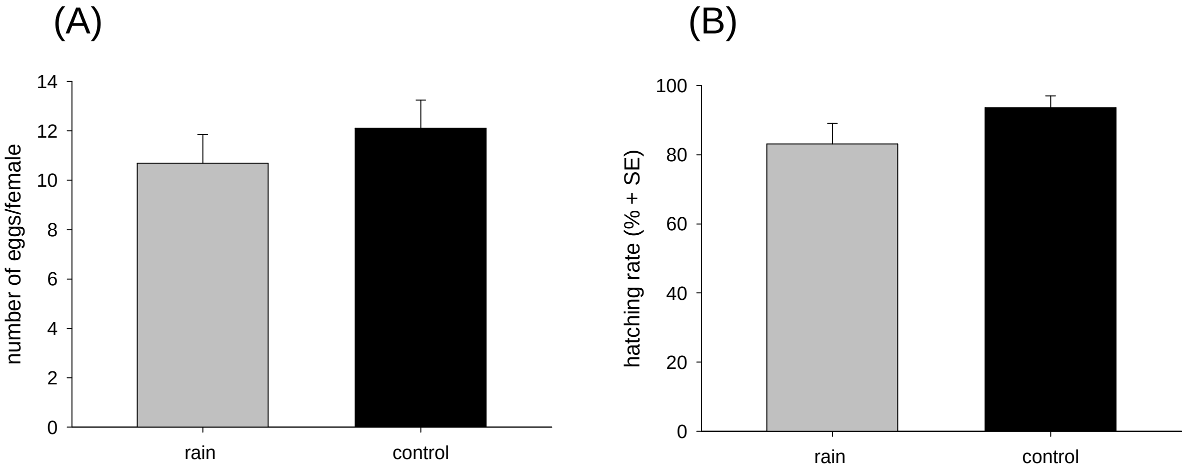

Fig. 26: Egg-laying and hatching aftere a rain shower in the field (A) Egg-laying after the females have faced a rain shower with an intensity of 0.5 l/min*m² and a droplet size of 2-4 mm (B) hatching out of eggs which have faced a rain shower with an intensity of 0.5 l/min*m² and a droplet size of 2-4 mm. n = 9 for each treatment.

The development of the pupae was not influenced by the rain. In both the treatment and the control the survival was around 95% ($F_{1,19}$ = 0.29; p = 0.6; **Fig. 27**).

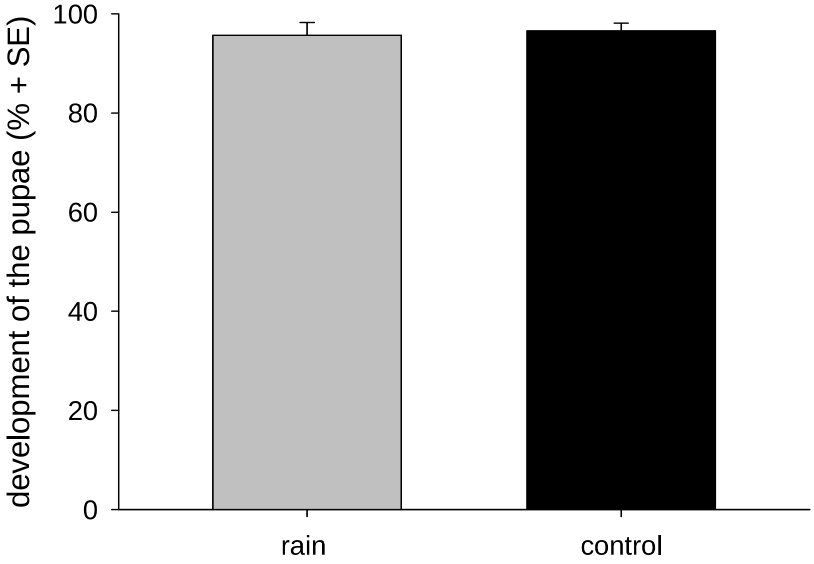

Fig. 27: Development of the L4-larvae in the field after a twenty minute rain shower with an intensity of 0.5 l/min*m² and a droplet size of 2-4 mm with ten larvae per plant and ten replications. n = 9 for each treatment.

5.5 Discussion

5.5.1 Simulated rain

In the simulated experiments nearly all adults died under the torrential rain due to washing off of the leaves. Under the other rain levels almost no mortality could be observed. Studies on *Bemisia tabaci* showed that rain seem to have nearly no influence on this whitefly species (Asiimwe et al. 2007). Although studies in tropical regions show that after heavy rain showers or the raining season the populations of both *Bemisia tabaci* and the spiralling whitefly (*Aleurodicus dispersus*) rapidly decline due to washing off all stages of the whiteflies of the leaves (Banjo 2010), Golding (1936) assumes that the decline of the population is due to mechanically destruction of the whiteflies. Whiteflies are normally found on the lower side of the leaves and are thereby protected from rain. Under the torrential rain they were dislocated and killed by the rain drops or washed away. The movement of the plants due to rain drops is important for the dislodging of small insects e.g. *Sitobion avenae* both due to active movement or washing off (Mann et al. 1995). The potato aphid *Macrosiphum euphorbiae* shows an increased movement under rain events, perhaps to find shelter (Narayandas & Alyokhin 2006). In the experiment of von Berg et al. (2008) rain decreased the population of an aphid species by 27% and about 57% of the aphids were dislodged. On the soil they often became prey for ground-dwelling predators (von Berg et al. 2008). Other aphids like the Yellow Sugarcane Aphid (*Sipha flava*) also suffers high mortality after rain storms due to mechanical destruction by rain drops (Miskimen 1970). Not only pest but also their parasitoids are influenced by rain showers. The wasp *Aphidius rosae* stops searching for oviposition places and egg-laying under rain events (Fink & Völkl 1995). But moderate rainfall might even provide conditions that promote development or lead to higher movement between or within habitats (Pellegrino et al. 2013). But insects have adaption strategies to avoid the danger of rain storms. Some insects seem to be able to detect a coming rain storm via the change in the atmospheric pressure and Pellegrino et al. (2013) could show that mating behaviour of the cucurbit beetle (*Diabrotica speciosa*), the true armyworm moth (*Pseudaletia unipuncta*) and the potato aphid (*Macrosiphum euphorbiae*) decreased under decreasing atmospheric pressure, indicating that the insects change their behavior to avoid death or injury due to unfavorable conditions. Other insects like the parasitoids *Trichogramma evanescens* and *Trichogramma pretiosum* also react with a decreased flight activity to a rapid change in atmospheric pressure (Fournier et al. 2005). It is likely that several flying insects species are able to detect changes in barometric pressure and change their behaviour accordingly. Mosquitoes in contrast survive rains due to their small bodies and their strong exoskeletons. In contact with the mosquito the rain drop losses a little momentum and therefore its impact on the mosquito (Dickerson et al. 2012). Therefore we assume that the whitefly is adapted to rain events and reacts with a decreased flight activity and searching of shelter. But torrential rain leads to a mechanical destruction of the plants and consequently also of the whiteflies.

The eggs development and the egg-laying were influenced, whereas only the influence in the egg development was significant. Only half of the eggs under all rain treatments hatched compared to the control due to the damage of the egg clutches. The destruction of the egg clutches was visible directly after the rain shower and the eggs were washed off of the leaves. The egg-laying of the females which were opposed to the rain dropped to one third under the torrential rain treatment compared to the control, but this result was not significant. Is this reduced egg-laying due to the direct impact of the rain or is the impact of the high air humidity which follows the rain? It is known for spider mites that they lay more eggs under a dry climate than under high air humidity (Boudreaux 1958). Also clover mites *Bryobia praetiosa* are negatively affect by additional irrigation (Kramer & Cranshaw 2009). The decreased egg-laying might also be a consequence of the change in the behaviour. It is likely that the females spend some time after the rain with drying and cleaning (Fink & Völkl 1995).

In opposite to this the larvae, regardless of larval stages, and the L4-larvae were not influenced by the rain. The larvae and the L4-larvae are sessile and they are enclosed by a wax layer. This wax layer is a very effective protection for the larvae and even torrential rain cannot harm them. In opposite of this Fishpool et al. (1995) reported that the population decrease is a consequence of the reduced oviposition activity. This is in consensus with our observation.

5.5.2 Real rain

In nature precipitation has several impacts on insects, either direct or indirect. They can change the conditions of the host plant via water supply or they can have effects on the natural enemies (Beirne 1970). Directly they can impinge the insects and kill them or dislodge them. In our experiment we only tested the direct effect on the whiteflies.

The real rain in nature had no significant influence on the insects at all. The rain intensity (0.5 l/min*m²) was comparable to the medium rain in our experiment (0.6 l/min*m²). Under simulated circumstances this rain intensity significantly reduced the development of the eggs by washing the eggs off of the leaves. We couldn't observe this effect in the field. Comparable rain events could be observes around 124 times in Germany in the last 14 years, representing one medium rain shower every 1.5 month. Heavier rain events were observed 15 times in the last 14 years, leading to one heavy rain per year and torrential rains were observes only four times, representing one torrential rain event every four years. Furthermore it must be considered that heavy rain events often occur only for a very short time period lasting for a few minutes and only seldom for twenty minutes as in our experiment. Due to this we can assume that rain, even heavy rain showers cannot reduce the population of the whiteflies.

We can summarise that the rain has an effect on the egg stage and on the adults, which are no longer protected by the wax layer, but not on the other developmental stages.

5.6 Conclusion

We assume that heavy rains will have no influence on the population development of the cabbage whitefly. Just torrential rains, which occurred in the last century only once, might have a negative influence on the survival and development of *Aleyrodes proletella*. But these heavy rains will also destroy the cabbage plants and the loss for the farmers due to the rain will be much higher than the loss due to the feeding and pollution of the pest.

6 Influence of drought on the development of *Aleyrodes proletella*

6.1 Abstract

To test the influence of droughts on the cabbage whitefly, adult *Aleyrodes proletella* were deployed on plants which are then stressed with three different water levels (drought-stress: <15% water holding capacity; normal: 40-50% water holding capacity; water-stressed: >80% water holding capacity). A further arrangement has the plants water-stressed before deploying the insects. With increasing water level the plants' biomass above and below ground increased significantly while the C/N-ratio decreased under the dry treatment. In the first part of the experiment the water level had no significant influence on the egg-laying and the development of the eggs and the larvae. In the second part of the experiment the number of eggs laid und hence the number of larvae and developing adults declined with decreasing water levels and the animals exposed to the dry treatment would be smaller in size. We could find no correlation between the C/N-ratio and the number of eggs, thus we assume that the change in the plant nutrients is not the limiting factor for the insects. In the second part of the experiment, we found a correlation between the plant size and the number of eggs laid. The plant size seems to be an important factor for the population development of the cabbage whitefly.

6.2 Introduction

The Intergovernmental Panel on Climate Change (Hartmann et al. 2013) predicts that extreme events like droughts will occur more often in future. Not only in summer the probabilities of droughts are increasing, but mainly in spring and in autumn droughts are to be expected. In the last years, especially in April droughts were visible. In April 2007 the rain was only at 6% of the average monthly precipitation, in April 2009 at 49%. In March 2011 the precipitation did not exceed 19% of the monthly average and March 2014 was very dry as well (30%). In 2011 also the autumn was very dry. Beside the manifestation in temperature and precipitation regime, droughts can also bear an important indirect impact on insects (Pritchard et al. 2007). Droughts change the nutrients in leaves and plant saps and thereby change the insects' hosts. Normally, droughts are reducing the nitrogen level in plants and are increasing the carbon level (Staley et al. 2007). Changing concentrations of elements (carbon, nitrogen, phosphorus) may affect herbivores, them being often limited by the availability of nitrogen and negatively affected by high contents of carbon, in regard to structural (e.g. lignin) and chemical defence (Mattson 1980). Besides carbon and nitrogen although the leaf chemicals (Schädler et al. 2007) are important. Droughts weaken the plants, making them more attractive for herbivores (Fuhrer 2003). Heavy droughts can also decrease the amount of VOCs, that are produced by the plant to communicate with other plants, attract beneficials or have antibacterial or antifungal effects (Laothawornkitkul et al. 2009). Many insects react to droughts favourably, but the different feeding guilds react to drought differently: Gall builders react negatively, while chewing insects do not react at all. Mining insects profit slightly, whereas phloem feeding insects even flourish (Fuhrer 2003) due to a higher concentration of amino acids in the phloem (Mengel 1991). As especially heavy droughts lead to a higher viscosity of the phloem (Mengel 1991), this extreme condition negatively affects all feeding guilds (Staley et al. 2006). A drought in spring would have a negative effect on herbivores, mykophages, omnivores and predators (Frampton et al. 2000).

Droughts can also change the species community or the prey-predator-interaction. Staley et al. (2006) could show that the parasitation rate on *Stephensia brunnichella* is increased under drought conditions. Yet, also the opposite can be found: Parasitoids under tropic conditions react negatively to drought, leading to a higher pest population (Hance et al.

2007). Drought can also decrease the density of beneficials (Rosenzweig et al. 2001), e. g., spiders and beetles (Thomson & Hoffmann 2010), while lady beetles are more common in dry fields (Thomson & Hoffmann 2010). It does not only influence the various feeding guilds differently, the habitat is also important. Thus, insects which live in the soil or develop in the soil, like the carrot fly *Psila rosae* suffer more under drought (Burn 1984).

A surplus of water has negative effects on plants as well, because it causes anaerobe conditions in the root area (Brunhold et al. 1996), killing fine roots and inducing decreased photosynthesis and growth. The concentration of carbon dioxide in the tissue increases, while the levels of nutrients like nitrogen, phosphor and potassium decline (Brunhold et al. 1996).

The arguments for choosing the cabbage whitefly as a model organism for our experiments are twofold: The population of this species has increased in the last decade and it has become one of the most important pest species in cabbage cultivation. With the assumption, the relevance of *Aleyrodes proletella* will show even more in the future, it is important to test the reaction of this species under drought conditions to then compile robust forecast models. Based on data which is available on other sucking insects, the whiteflies will presumably react positively to drought. Existing data, however, does not allow assumptions on how they will react to extreme droughts or plants under water stress.

6.2.1 The cabbage whitefly *Aleyrodes proletella*, (Fam. Aleyrodidae, Order Homoptera)

belongs to the family of Aleyrodidae, which are distributed worldwide, with a focus in the tropical regions. Especially in warmer climates with low rainfall *A. proletella* is a serious cabbage pest (Leite et al. 2005). Cabbage whiteflies have spread heavily in the last ten years (van Alebeek 2008) and prefer warm temperatures for their development. Optimal developmental temperatures range between 28-33 °C. Especially in warm summers and autumns mass occurrences are observed. (See also chapter 2.5.1.1.)

6.3 Material and Methods

6.3.1 Experiment

The cabbage whiteflies for the experiment were taken from the rearing of the Institute of Plant Disease and Plant Protection in Hanover. The insects were reared on Brussels Sprout at temperatures of 20 °C and light conditions of 18/6 (light/darkness).

The Brussels sprout (*Brassica oleracea* (L.) var. *gemmifera* DC. ”Hilds ideal®“) plants were grown two months in greenhouses at average temperatures of 20 °C. After this time the height of the plants and their leaf diameter were measured and the number of the leaves were counted as a parameter for plant developmental stage and to make plants more comparable. Afterwards, adult whiteflies and adult cabbage aphids were deployed in clip-cages on different leaves of the plants The plants were fertilised weekly with Wuxal® (AGLIKON), liquid fertiliser. The experiments were conducted in a climate chamber with a constant temperature of 21 °C (± 1 °C), a humidity of 50% and long-day-conditions (LD 16/8).

To test the influence of drought- and water-stress on the development of *Aleyrodes proletella*, an experiment with three different water treatments of the soil were performed: in which on one part the plants were stressed due to drought (<15% water holding capacity) and in the other due to flooding (>80% water holding capacity). The third treatment served as a control (40-50% water holding capacity). The water capacity was measured with the TDR-Bodenfeuchtesensor Fieldscout TDR 100 Soil moisture (Spectrum Technologies Inc.). In the first part of the experiment (Experiment No. 1), two adult female whiteflies were clipped on the plants and on the same day the water- or the drought-stressing started. The whiteflies were given one week to lay eggs after which they were removed and the eggs counted. Additionally, eggs and the adults were counted every third day to follow their development to larvae and later on to adults. Larvae that developed from the eggs were recorded in the different developmental stages. For each water level, a set of ten replicates was used.

In the second part of the experiment (Experiment No. 2), the insects were clipped on plants which were already two weeks water- and drought-stressed. From there on, the experiment proceeded like the aforementioned. At the end of both experiments the plant height and the above- and belowground biomass were measured and the number of leaves was counted. During the experiment the stomatal conductivity was measured using the leafporometer AP4 DELTA-T DEVICES-Cambridge-U.K. Ten replicates per water level were used as well.

6.3.2 C/N-analyses

To analyze the C/N-ratio in the leaves, two to three leaves of every plant were dried and ground to fine powder. The samples were analyzed at the Institute of Plant Nutrition (Universität Hannover) using a Micro-Dumas-Quantitative analysis of combustion, employing the CNS-device vario EL III Element Analyzer of the company Elementar 2003.

6.3.3 Statistical analysis

Data was visually checked for normality of residuals, creating histograms and box plots and was transformed and pooled for the replicates if necessary. The percentage data for the larval development and the C/N-ratio were arc sine square root transformed and the counting data for the leave number, the biomass and the eggs were square root transformed

Main emphasis of the experiment was on the relationships between different water levels, the plant parameters and the insect development. The effects of the water levels and on the insects were tested with an ANOVA. Every ANOVA which yielded significant results was followed by a post-hoc-test (Tukey's Test). IMB SPSS 19 was used for all statistical analyses.

The relationships of plant biomass, C/N-ratio and insect life data were evaluated determining Pearson’s correlation coefficient across values averaged per genotypes.

6.4 Results

6.4.1 Impact of drought stress on plants

The three different water treatments had a significant effect on the plant size ($F_{1,2} = 90.72$; $p < 0.001$). The results show that plants growing under drought stress (<15% water holding capacity of the soil) were much smaller than plants under normal water conditions (40-50% water holding capacity) or under water stress (>80% water holding capacity). The plants under drought stress showed no growth at all and got even smaller due to the missing water pressure in the stem (**Fig. 28**) The water treatment had also a significant effect on the number of leaves ($F_{2,21}$ = 4.29; p = 0.05). In the drought stressed treatments less leaves were found compared to the normal and water-stressed plants. But the experiment (comparison between experiment No.1 and No.2) had an even greater significant effect on the leave number ($F_{1,21}$ = 13.84; p = 0.014; **Fig. 54 Addendum**)

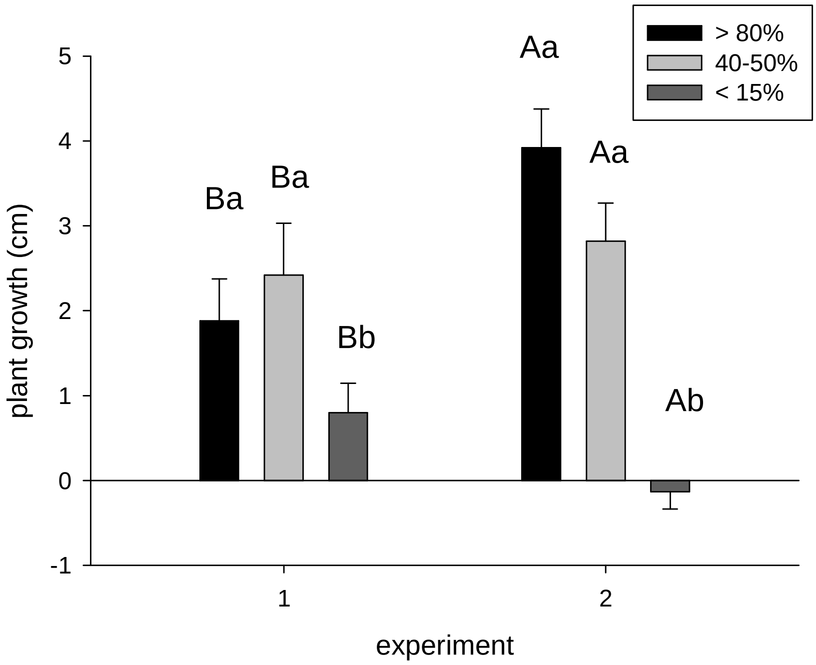

Fig. 28: Influence of water levels on plant growth during the experiment in the two different experiments (Experiment No. 1: Plants were stressed after colonisation by insects; Experiment No. 2: Colonisation took place after stressing of the plants). n = 10 for each experiment and treatment. Different characters representing significances (α ≤ 0.05). Capitals representing comparison between experiments, small letters within the experiment

The water treatment had a significant effect on the leaf length. In the first experiment (Experiment No. 1) the leaves in the drought treatment were significantly smaller ($F_{2,28}$ = 2.85; p = 0.076), with a leaf length of 6.95 cm ± 0.18 cm (mean ± standard error). The leafs in the normal treatment and in the water-stress treatment had nearly the same length (8.12 cm ± 0.40 cm; 8.28 cm ± 0.40 cm, respectively). In experiment No. 2 the leaves were significantly smaller ($F_{2,29}$ = 4.70; p = 0.018) in the drought stressed treatment as well, with a leaf length of 7.06 cm ± 0.26 cm (mean ± standard error). The leaves in the normal treatment had a length of 8.3 cm ± 0.27 cm (mean ± standard error) and the leaves in the water-stressed treatments a length of 8.49 cm ± 0.40 cm (mean ± standard error). In both cases the growth in size was calculated to avoid effects of different plants sizes at the beginning of the experiment.

The different water treatments had significant influence on the above- ($F_{2,60} = 25.89$; $p < 0.001$) and below- ($F_{2,59} = 99.84$; $p < 0.001$) ground biomass, both fresh and dry. With increasing water capacity the biomass increased (**Fig. 29; Fig. 55 Addendum**). It was also obvious, that those plants under the high water treatment were bigger and had more leaves and the leaves seemed even greener than the leaves in the other treatments.

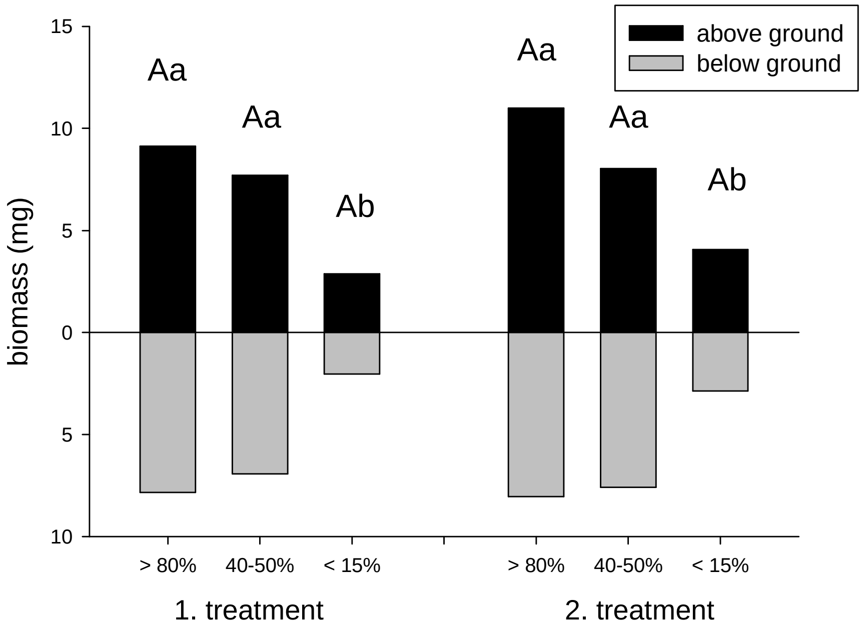

Fig. 29: Influence of water capacity and experiment on the biomass above and below ground (dry) (experiment No. 1: Plants were stressed after colonisation by insects; experiment No. 2: Colonisation took place after stressing of the plants). n = 10 for each experiment and treatment. Different characters representing significances ($\alpha \leq 0.05$). Capitals representing comparison between experiments, small letters within the experiment.

The different water treatments had a significant effect on the stomatal conductivity ($F_{2,29} = 16.44$; $p < 0.001$). With increasing water holding capacity of the treatment the stomatal conductivity in the leaves increased. (**Fig. 30**)

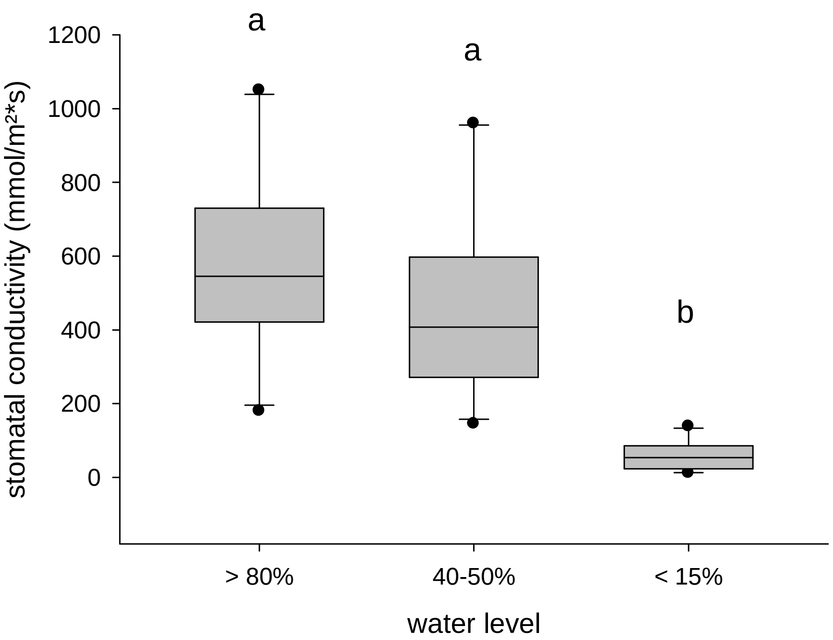

Fig. 30: Influence of water treatment on stomatal conductivity in the second experiment, representing median, upper and lower quartile, upper and lower whisker and aberrations. n = 10 for each treatment. Different characters representing significances ($\alpha \leq 0.05$).

Our analysis of the C/N-ratio showed that the experiment had a significant effect on this ratio ($F_{1,59} = 4.95$; $p = 0.03$). Therefore, the ratio for every experiment was analyzed separately. In the first experiment the C/N-ratio increased with increasing water treatment ($F_{2,28} = 16.86$; $p < 0.001$; **Fig. 31(A)**). In the second experiment the water capacity had no significant effect ($F_{2,29} = 0.43$; $p = 0.66$). The C/N-ratio was highest under the normal water capacity and nearly the same under the water stressed treatment. Just under the drought stressed treatment the C/N-ratio decreased (**Fig. 31(B)**).

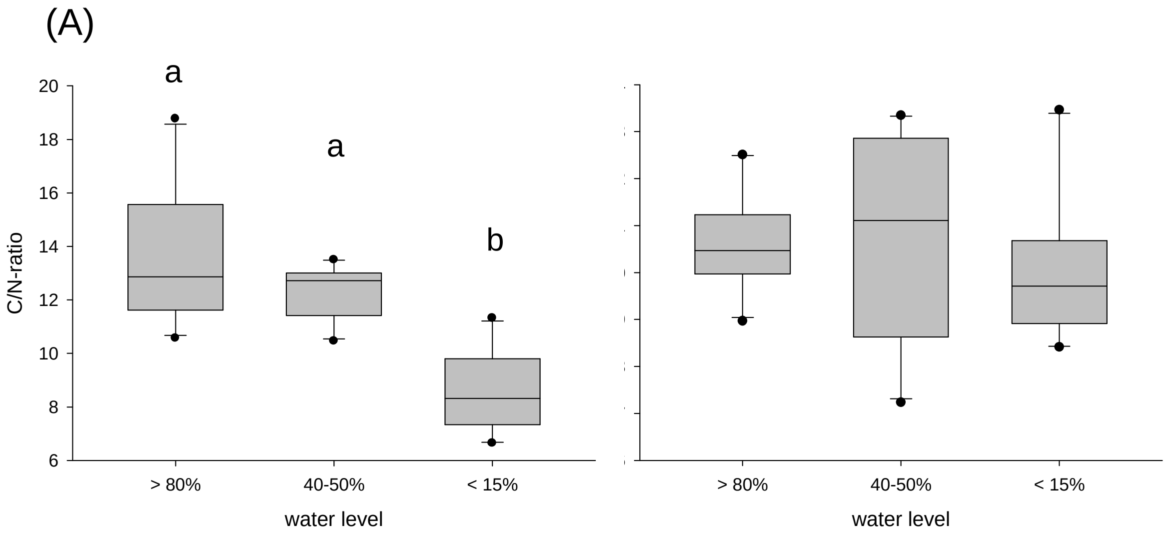

Fig. 31: Influence of the different water treatments in the C/N-ratio in the leaves (A) experiment No.1 insects were clipped on not yet stressed plants) (B) experiment No. 2 (insects were clipped on already stressed plants). n = 10 for each experiment and treatment. Different characters representing significances (α ≤ 0.05). Graphs without characters show no significances.

6.4.2 Impact of drought stress on insects

Independent of whether insects were already present on the plant when drought stress occurred (Experiment No. 1), or colonising plants experiencing already drought stress (Experiment No. 2) the number of eggs laid per day ranged between 0 and 56. While the experiment had a highly significant effect on the egg-laying of the females ($F_{1,59} = 7.88$; $p = 0.007$), the different water treatments had not ($F_{2,59} = 1.89$; $p = 0.16$). Experiment No. 1 revealed nearly no differences in egg-laying ($F_{2,28} = 0.56$; $p = 0.58$) since the plants were not stressed until the insects were clipped. In Experiment No. 2, where the plants had been stressed before the insects were clipped, the egg-laying decreased significantly with decreasing water capacity ($F_{2,28} = 0.64$; $p = 0.006$; **Fig. 32**).

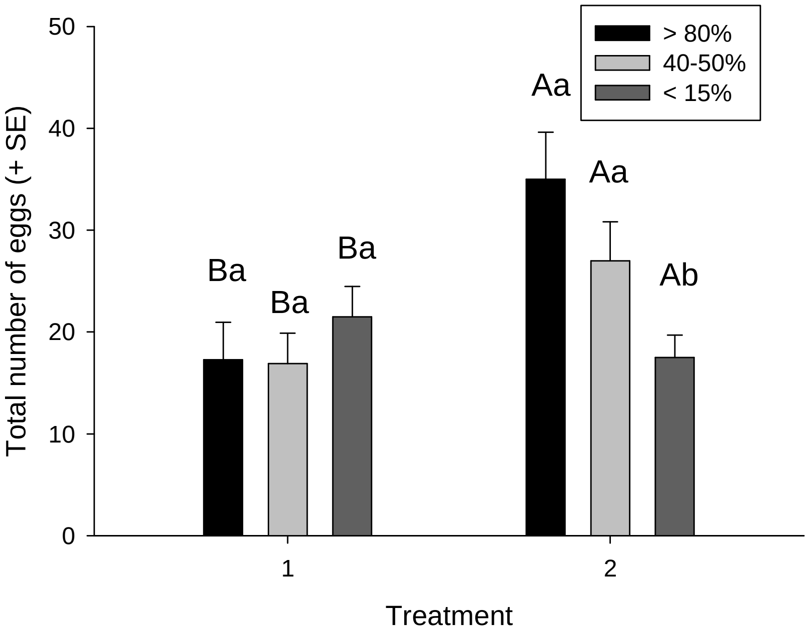

Fig. 32: Influence of experiment and water capacity on the egg-laying of two females over eight days (experiment No. 1: Plants were stressed after colonization by insects; experiment No. 2: Colonization took place after stressing of the plants). n = 10 for each experiment and treatment. Different characters representing significances (α ≤ 0.05). Capitals representing comparison between experiments, small letters within the experiment.

As a consequence, the water treatment had no influence on the number of larvae (**Fig. 33 (A)**) and adults ($F_{2,28} = 0.72$; $p = 0.50$; $F_{2,28} = 0.49$; $p = 0.62$, respectively; **Fig. 33 (B)**) in experiment No. 1, but it had an effect in experiment No. 2 ($F_{2,28} = 6.79$; $p = 0.004$; $F_{2,28} = 5.57$; $p = 0.01$, respectively).

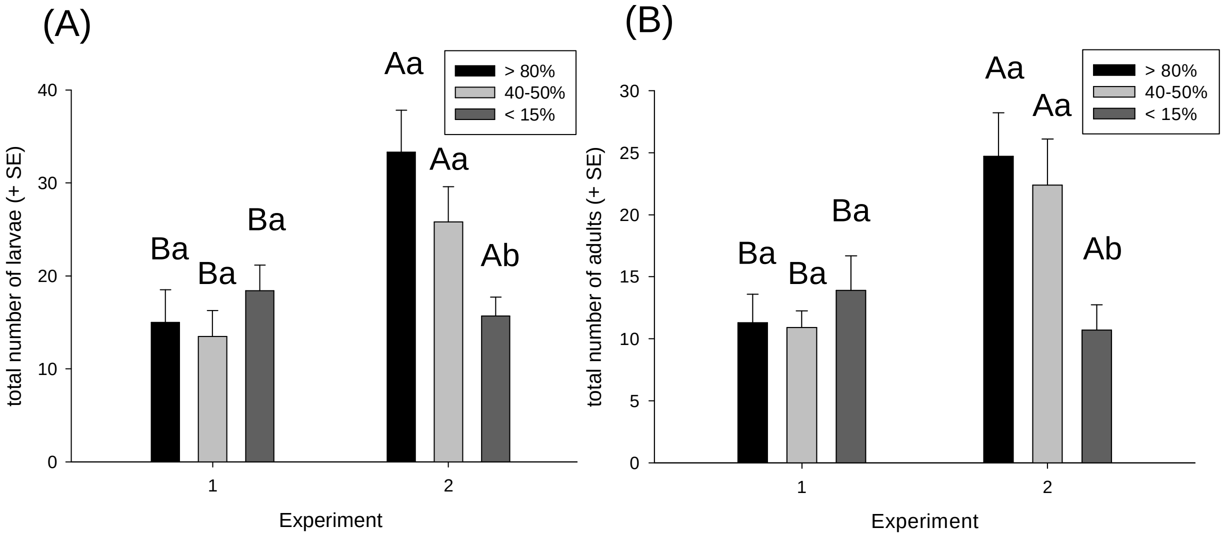

Fig. 33: Number of (A) larvae depending on water treatment and experiment (B) Number of adults, that emerged of the eggs laid on the experimental plants(experiment No. 1: Plants were stressed after colonisation by insects; experiment No. 2: Colonisation took place after stressing of the plants). n = 10 for each experiment and treatment. Different characters representing significances (α ≤ 0.05). Capitals representing comparison between experiments, small letters within the experiment.

The experiments had a significant influence on the development from eggs to larvae ($F_{1,58} = 7.95$; $p = 0.007$) but not from the larvae to the adults ($F_{2,58} = 1.31$; $p = 0.26$). In the first experiment 79.28% ± 4.46 (mean ± standard error) of the eggs developed to larvae (on the >80% water capacity level: 74.62% ± 10.79; on the 40-50% water capacity level: 77.93 ± 7.47 and on the <15% water capacity level: 85.28% ± 3.67) and in experiment No. 2 93.71% ± 1.85 (mean ± standard error) of the eggs developed to larvae (on the >80% water capacity level: 94.83% ± 2.17; on the 40-50% water capacity level: 95.29 ± 2.36 and on the <15% water capacity level: 91% ± 4.63). The differences between the treatments and their impact on the development from larvae to adults were not as big. In experiment No. 1 85.53% ± 10.34 (mean ± standard error; on the >80% water capacity level: 76.58% ± 10.96; on the 40-50% water capacity level: 83.9 ± 4.45 and on the <15% water capacity level: 71.11% ± 9.25) and in the second experiment 76.28% ± 3.5 (mean ± standard error; on the >80% water capacity level: 75.08% ± 4.72; on the 40-50% water capacity level: 84.94 ± 3.17 and on the <15% water capacity level: 68.8% ± 8.45) of the larvae developed to adults. In both experiments the water treatment had no significant effect on both the development of the larvae and the adults.

In the end of experiment No. 2 the size of the exuviae was measured to evaluate if the plants' stress did influence their size. The results show that the whiteflies were biggest under the normal water treatment and smallest growing up on drought-stressed plants ($F_{2,19} = 6.28$; $p = 0.009$; **Fig. 34**).

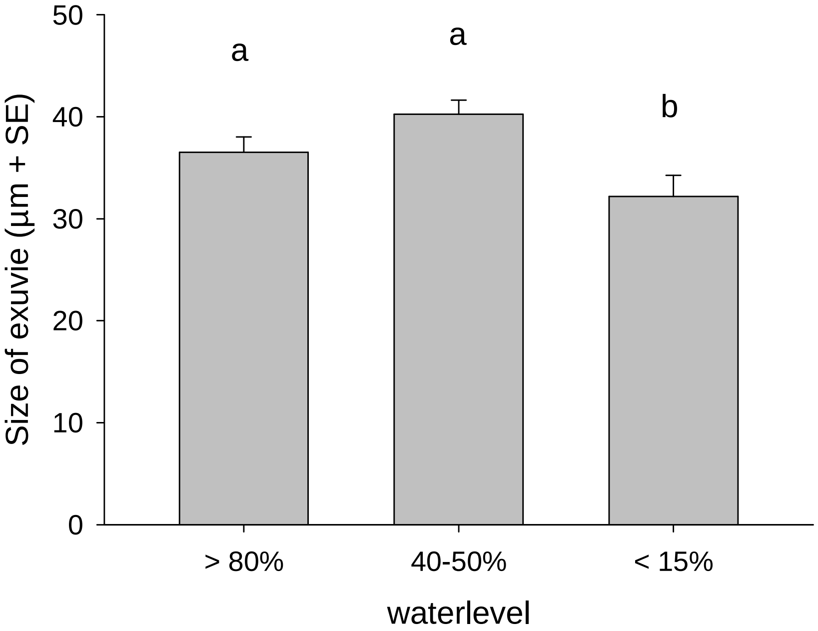

Fig. 34: Influence of water treatment on the size of the exuviae in experiment No. 2 (colonisation took place after stressing of the plants, n= 8 per water level, showing median and quartile). n = 10 for each treatment. Different characters representing significances (α ≤ 0.05).

6.4.3 Correlations

To study the important correlations the experiments were separated and analysed each at its own, but for better comparison they'll be discussed together. In experiment No. 1 the plants were water-stressed after the colonisation of the insects took place. In experiment No. 2 the plants were water-stressed before the colonisation took place.

The different plant parameters were expected to significantly correlate with each other, e.g., the aboveground biomass was correlated with the belowground biomass in experiment No. 1 and experiment No. 2 ($r = 0.772$; $p < 0.001$; $r = 0.811$; $p < 0.001$; respectively; **Fig. 35**). With an increase in the aboveground biomass the belowground biomass also increased.

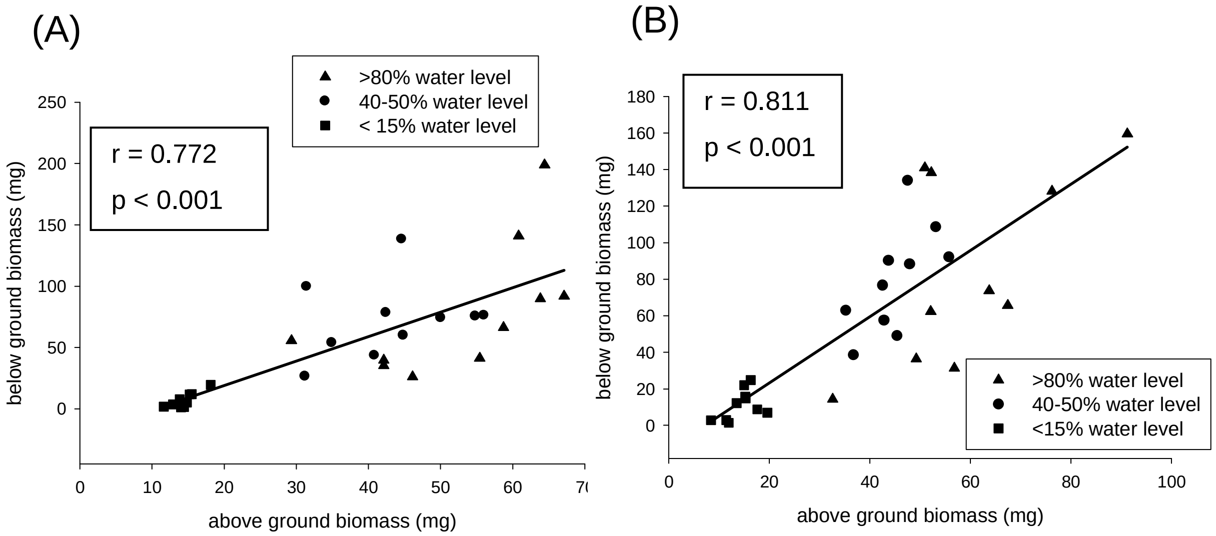

Fig. 35: Correlation between above and below ground biomass in the (A) experiment No. 1 (plants were stressed after colonisation) and (B) experiment No. 2 (plants were stressed before colonisation by insects took place). n = 10 for each experiment and treatment.

The C/N-ratio in the leaves was measured after the experiments: It did correlate with the size of the plants (r = 0.726; p < 0.001) and the number of leaves at the beginning of the experiment (r = 0.518; p < 0.001). It also correlated with the plant growth parameters, which were measured at the end of the experiment as well. With an increasing size of the plant at the beginning of the experiment the C/N-ratio further increased (**Fig. 36 (A)**). In experiment No. 2 in contrast to experiment No. 1, the C/N-ratio was not correlating with the plant parameters, e.g., the aboveground biomass (r = 0.126; p = 0.51; **Fig. 36 (B)**).

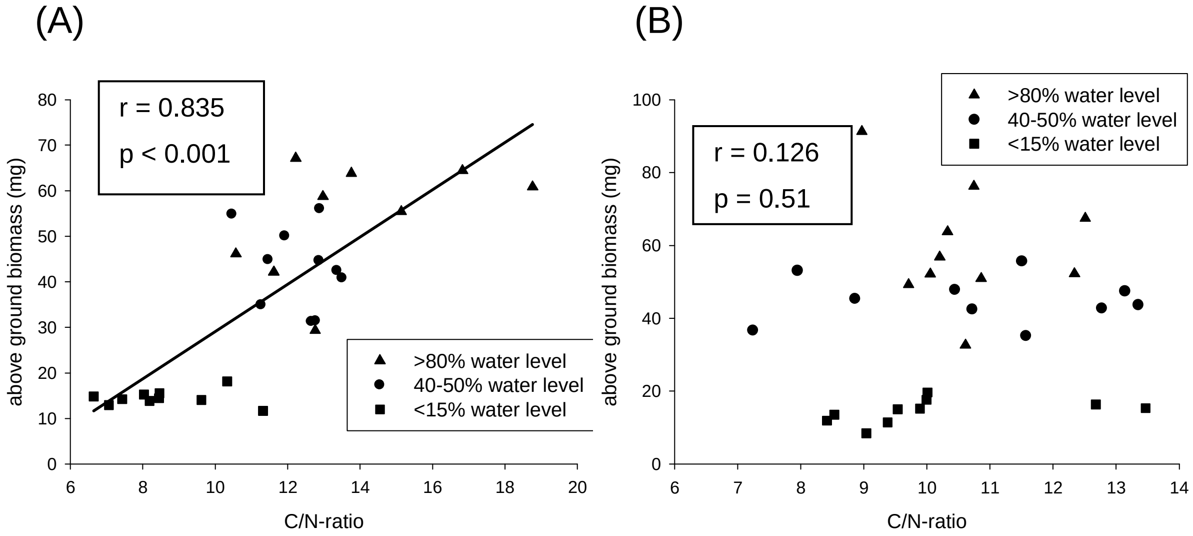

Fig. 36: Correlation between C/N-ratio and the aboveground biomass (A) in the first experiment (plants were stressed after colonisation by insects) and (B) in the second experiment (colonisation took place after stressing of the plants). n = 10 for each experiment and treatment.

In experiment No. 1 the number of eggs was correlated with the number of larvae and the number of adults ($r = 0.953$; $p < 0.001$; $r = 0.882$; $p < 0.001$; respectively; **Fig. 56 Addendum**). With an increasing number of eggs the number of adults increased. As in experiment No. 1, the number of the eggs was correlated with the numbers of larvae ($r = 0.982$; $p < 0.001$) and adults ($r = 0.91$; $p < 0.001$) in experiment No. 2. The number of adults and larvae were correlated as well ($r = 0.931$; $p < 0.001$). With an increasing number of eggs, the number of adults increased (**Fig. 58 Addendum**).

But the number of eggs was not correlated with the plant growth parameter in experiment No. 1 (**Fig. 37(A)**). The number of eggs and larvae in experiment No. 2 was correlated with plant parameters especially the biomass ($r = 0.559$; $p = 0.001$; $r = 0.570$; $p < 0.001$, respectively). With an increasing amount of aboveground biomass the number of eggs increased (**Fig. 37(B)**).

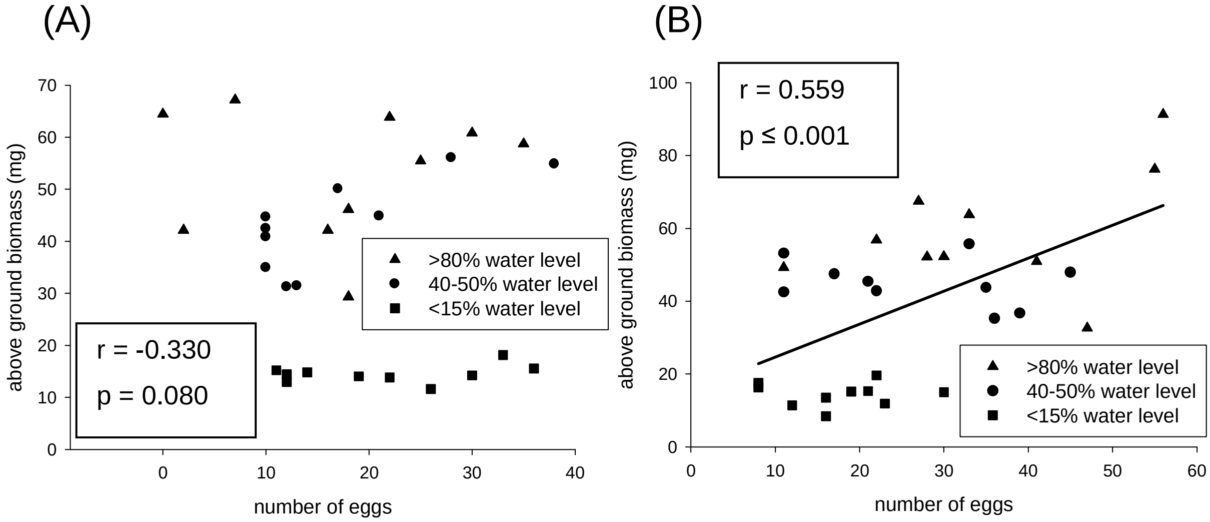

Fig. 37: Number of eggs correlated with the fresh aboveground biomass (mg) (A) experiment No. 1 (plants were stressed after colonisation by insects) experiment No. 2 (colonisation took place after stressing of the plants). n = 10 for each experiment and treatment.

In the first experiments the number of adults was slightly correlated with the plant size at the start (r = -0.409; p = 0.028; **Fig. 38 (A)**) and the end of the experiment (r = 0.-439; p = 0.017; **Fig. 58 Addendum**). If the plants were bigger at the beginning of the experiment as well as in the end, more adults developed.

The number of adults is supplementary to the measured plant parameter correlated with the plant growth (r = 0.387; p = 0.035). With increased plant growth, the number of adults increased as well (**Fig. 38 (B)**).

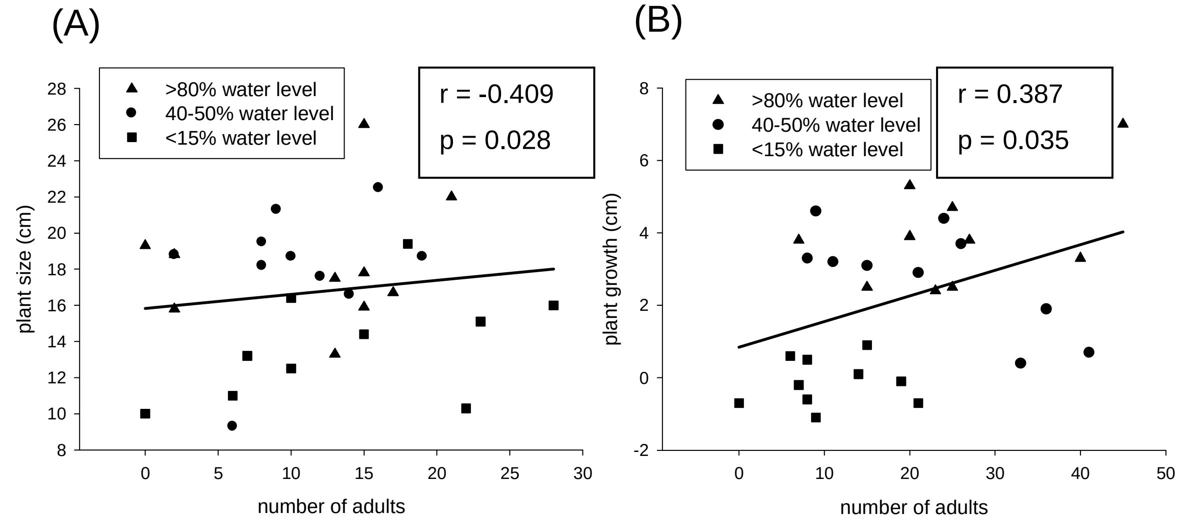

Fig. 38: (A) Number of adults correlated with the plant size at the beginning of the experiment in experiment No. 1 (plants were stressed after colonisation by insects) (B) correlation between number of adults and the plant growth during the experiment in experiment No. 2 (colonisation took place after stressing of the plants). n = 10 for each experiment and treatment.

The number of eggs, larvae and adults was not correlated with the C/N-ratio in both parts of the experiments (**Fig. 39**).

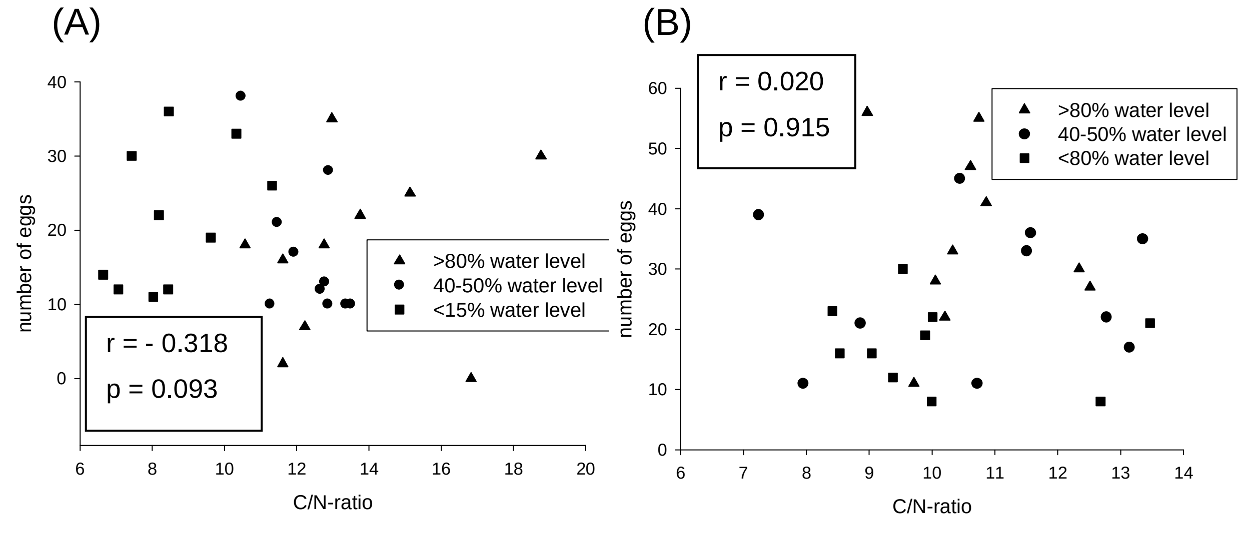

Fig. 39: C/N-ratio correlated with the number of eggs A) in the first experiment (plants were stressed after colonisation by insects) (B) in the second experiment (colonisation took place after stressing of the plants). n = 10 for each treatment and experiment.

As expected the stomatal conductivity correlates with all the plant parameters, e.g. the aboveground biomass ($r = 0.723$; $p < 0.001$; **Fig. 40**). With increasing stomatal conductivity the above ground biomass increased.

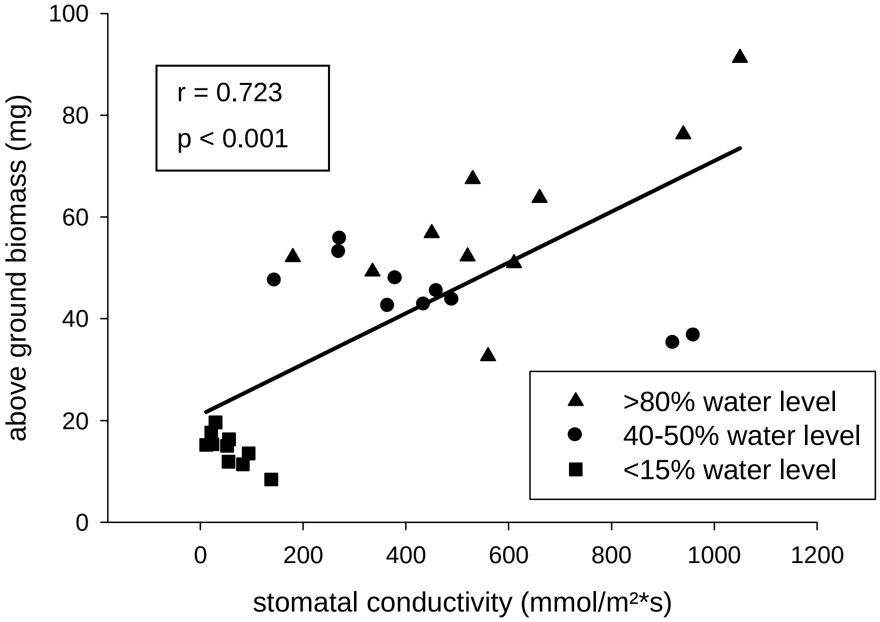

Fig. 40: Correlation between stomatal conductivity and above ground biomass in experiment No. 2 (colonisation took place after stressing of the plants). n = 10 for each treatment.

Hence with increasing stomatal conductivity the number of animals (eggs, larvae and adults) increased ($r = 0.746$; $p < 0.001$; $r = 0.764$; $p < 0.001$; $r = 0.746$; $p < 0.001$, respectively; **Fig. 41**). Due to the fact that the stomatal conductivity is correlated with the plant growth parameters and the number of whiteflies are also, this correlation was expected.

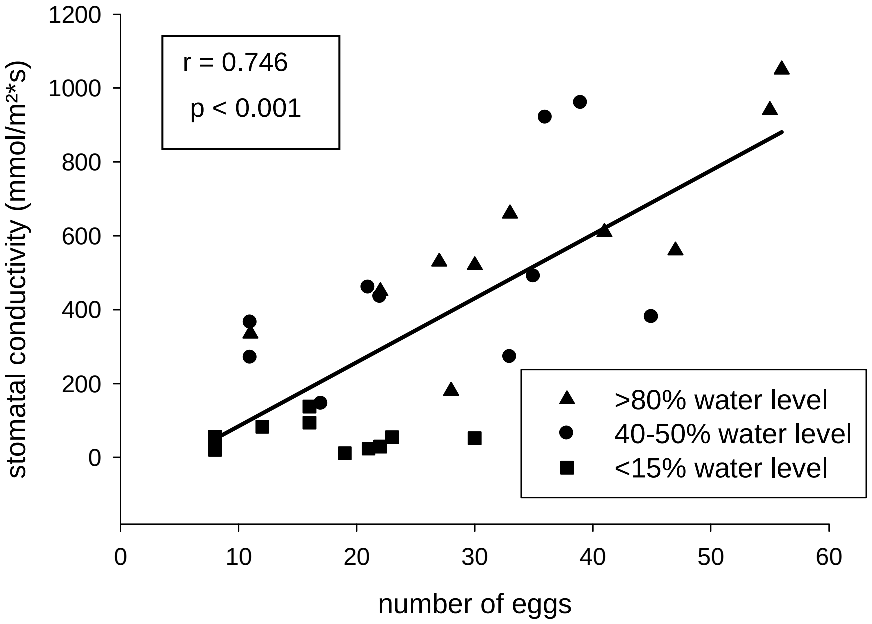

Fig. 41: Correlation between the number of eggs and the stomatal conductivity in treatment No. 2 (colonisation took place after stressing of the plants). n = 10 for each treatment.

The size of the exuviae did correlate with the development of the larvae (r = 0.454; p = 0.044). With increasing larval development time, size of the exuviae, increased as well (**Fig. 42**).

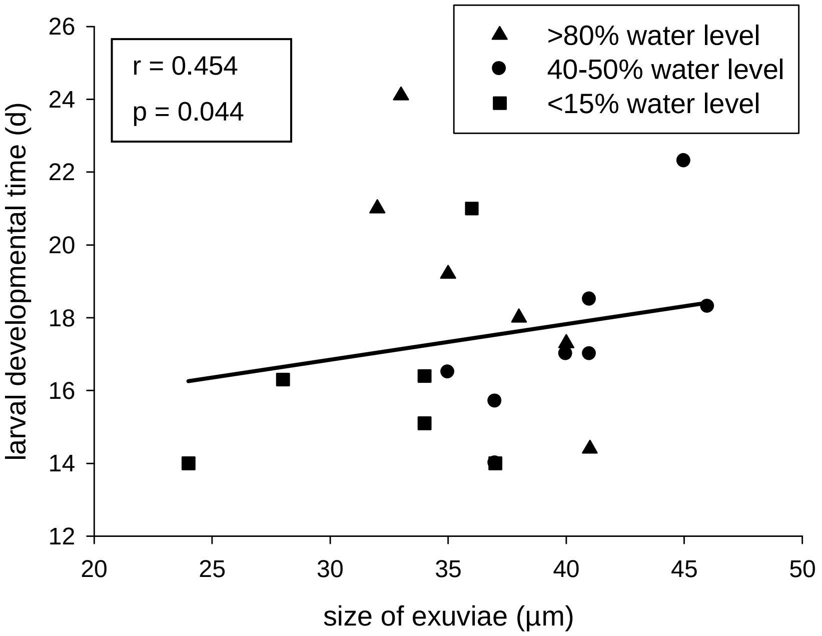

Fig. 42: Correlation between the size of the exuviae and the larval development in treatment No. 2 (colonisation took place after stressing of the plants). n = 10 for each treatment.

6.5 Discussion

The water level had a significant effect on plant growth. Plants under the wet and the normal treatment were bigger, had more leaves and a higher above- and belowground biomass compared to plants under the drought treatment. Plants under the wet treatment were slightly bigger than those under normal treatment. The green colour of the leaves also seemed more intense although this wasn't measured. Plants under the dry treatment didn’t grow at all or got smaller due to water loss in the stem tissue and early wilting and dying of the lower leaves was observed.

Surprisingly, the results showed the plants to flourish best under high soil humidity, while actually the opposite was to be expected due to rotting of the roots and anaerobic conditions (Brunold 1996). As a result of the anaerobe conditions, a poisoning by the accumulation of specific metabolites and a poor intake of nutrients for both root and shoot should have occurred (Liao & Lin 2001). Apparently, the experiment failed to create anaerobic conditions, so that the plants were able to grow very well and use all the water without facing the problems of rot due to missing oxygen. To create anaerobic conditions, it would have been necessary to use planting cylinders, which hold the water above the soil surface. It is likely that the plants would have died quickly under these conditions. We expected a small size of the plants under dry conditions, since a lack of water generally leads to wilting and dying (Veihmeyer & Hendrickson 1927; Stuhlfauth et al. 1987; Baher et al. 2002). Furthermore, the root weight of the plants grown under dry conditions was expected to be higher, to counter the low amount of water. Several studies show, that plants store more biomass belowground than aboveground in face of water limitation (Masinde et al. 2005) or reduce the aboveground biomass instead of root biomass (Zhang et al. 2008). Drought reduces the net photosynthesis and the stomatal conductivity and hence the biomass (Naderikharaji et al. 2008). But other studies like the one of Kage et al. (2004) also found no differences in the ratio of shoot and root biomass of cauliflower after water limitation.

The results showed that the C/N-ratio in the leaves of the first experiment was lowest in the dry treatment and nearly the same in the normal and the wet treatment, whereas the ratio was highest in the wet treatment. In the second experiment, the C/N-ratio in the leaves was also lowest in the dry treatment but slightly higher in the normal treatment than in the wet one.

It was assumed that plants under water stress have a lower C/N-ratio due to the less growth. As a consequence of limited water in the soil, the leaves close their stomata leading to decreased carbon assimilation (Faria et al. 1998; Liu & Stützel 2002). And as a consequence of the water limitation, the plants are not able to take up sufficient amounts of nutrients from the soil (Rouphael et al. 2012). Studies on pepper plants showed no influence of limited water supply on the C/N-ratio (Estirate et al. 1994). Furthermore, Huluka et al. (1994) found no different impacts of various irrigation systems on the C/N-ratio in cotton leaves.

Another source of differences could be an increase in nitrogen in the leaves of the drought-stressed plants (Huberty & Denno 2004). Staley et al. (2007) found drought to increase the amount of nitrogen in the leaves, whereas it would decrease the amount of carbon.

In general, drought stress makes plants more vulnerable to insect attacks, with sucking insects reacting particularly positive (Fuhrer 2003). The infestation on Summer squash (*Curcurbita pepo*) by *Bemisia tabaci* and consequently the silvering of the leaves for example occur mainly under drought stress (Paris et al. 1993). Infestations of *Bemisia argentifolii* on cotton have shown to be more intense on water-stressed plants compared to well-watered plants (Flint et al. 1995). Many insects prefer drought-stressed plants for oviposition like the Beet Armyworm (*Spodoptera exigua*) (Showler & Moran 2003). But heavy droughts have negative effects on all feeding guilds (Staley et al. 2006; Schoeneweis 1986; Mattson & Haack 1987). Reasons for this phenomenon may be increased nutrient and especially nitrogen levels (Rhoades 1983; White 1984), decreased plant defences (Rhoades 1983) and a generally better environment for the pests (Bregon 1983).

Significant differences in the intensity of egg-laying appear in the executed experiments. In experiment No. 1, in which the insects were clipped on not-stressed plants, the amount of eggs was nearly the same in all treatments. In the second experiment, the egg-laying decreased with decreasing water level. Altogether, the rate of egg-laying was higher in the second experiment. The insects of experiment No. 2 were clipped two weeks later on the plants compared to the insects in experiment No. 1. Due to the fact that the water capacity in the control level (40-50% water holding capacity) was the same in both experiments, we assumed the same amount of egg-laying in both treatments. The higher amount of eggs and in consequence the larvae and the adults in the experiment No. 2 might be due to abiotic factors, which we didn't take into account. In contrast to our results, Flint et al. (1995) found that *Bemisia tabaci* preferred drought stressed plants. And Isaacs et al. (1998) could find no difference in the preference of *Bemisia tabaci* on differently watered melons (*Cucumis melon*).

The results of the first experiment show that the different water supply of the plant has no significant effect on the development of the eggs and larvae to adults. Once the eggs are laid they develop to adults. It has been proven for *Trialeurodes vaporariorum* that the eggs are provided by water through the egg pedicel (Byrne et al. 1990). At the beginning of the experiment, the plant tissue was able to provide enough water for the eggs. Also, in the second experiment, the tissue water was enough for the egg development. It is likely that a certain amount of drought stress favours the colonisation of herbivores, but that after a long drought, the amount of pest insects decrease (Mattson & Haack 1987). In farmland experiments Frampton et al. (2000) found that drought decreased the number of herbivores. Insect response to drought seems to be species- or at least feeding-guild specific, whereas leaf-miners for example react species-specific to drought (Staley et al. 2006).

In the second experiment the stress level due to water loss was so high that the insects suffered and reduced egg-laying. An explanation for the bad performance of herbivores on plants under water stress might be that the reduction of turgor and water content impede the insect in exploiting the increased amount of nitrogen (Huberty & Denno 2004). An elevated viscosity of the plant sap would hinder them to take up enough amino acids. The oviposition rate of the sawfly *Diprion pini,* e.g., correlates with the water content in the needles of the host tree (Pasquier-Barre et al. 2001). The increase in pest outbreaks on water-stressed plants may also be an indirect effect. The dry and warm conditions promote the development of the insects (Larsson 1989). The experiments' results support this thesis their setup did not promote the insects' environment, but stressed the plants. In contrast to the results of Rhoades (1983), who found plant defence to decrease under water stress, or Laothawornkitkul et al. (2009), who could show that VOCs, which are part of the plants defence system, are reduced by droughts, several authors found opposite effects and an increase in plant defensiveness. Under stress conditions plants metabolise more secondary compounds to repel insects (Baher et al. 2002; Stuhlfauth et al. 1987; Tang et al. 1995, Inbar et al. 2001). The reduced egg-laying raises the question if the female is so weakened, that it is not able to lay any more eggs on the stressed plants or that it suspends egg-laying in order to find a better host. The preference-performance hypothesis suggests that females of phytophagous insects prefer oviposition places which support the best feeding ground for their offspring (Gripenberg et al. 2010; Videla et al. 2006). Skinner (1996) could show that *Bemisia argentifolii* prefers well watered plants for egg-laying. Females of the whitefly *Bemisia tabaci* also prefer to oviposit on host plants favourable for the larval development, supporting the preference-performance-hypothesis (Jiao et al. 2012).

The results of the size of the exuviae support the thesis of Huberty & Denno (2004) insofar the insects are not sufficiently able to use nutrients under drought stress. It was found that the exuviae were biggest under normal water treatment and smallest under the dry treatment. Without finding significances, the data shows that the developmental rate from eggs to larvae and from larvae to adult is smallest on the drought stressed plants. The host plants do not provide sufficient nutrients or water for the development of the larvae. It might also be possible that a change in the secondary compounds cause the poorer development. Mao et al. (2004) could show that the larvae of sweet potato weevil (*Cylas formicarius*) had a significantly higher mortality under drought.

The nitrogen level is lowest under the dry treatment leading to malnutrition of the larvae and pupae. An increased drying of the soil leads to an immobilisation of soil nutrients, since the pores are filled with air and exacerbate the transport of nutrients to the roots (Nye &

Tinker 1977). Although the C/N-ratio had no influence on the number of eggs laid nor on the hatching success, it could have a negative impact on the performance of the larvae. This assumption is supported by the fact that the size of the exuviae correlates with larval development. It was observed, that pupae under dry treatment hatched one day earlier compared to the other treatments. In other studies, the pupae of *Spodoptera littoralis* had a higher body weight and were bigger in dry treatment (Walter et al. 2012). In that study however, the plants were not as heavily water-stressed as were our plants and mere moderate stress might even enhance the performance of the herbivores (Scheirs & De Bruyn 2005). Water-stress influences phytophagous insects depending on their feeding preferences: Chewing and leaf-mining insects perform worse on stressed plants, whereas sucking and boring insects profit from stress (Koricheva et al. 1998). A moderate amount of drought stress favours the development of the larvae of *Brevicoryne brassicae* on oil rape, but under heavy stress the aphids became restless and rejected the heavy drought-stressed plants (Miles et al. 1982). The plant stress hypothesis predicts that insects perform better on stressed plants (White 1974), whereas the plant vigour hypothesis predicts that insects prefer vigorous plants (Price 1991). Several studies did show herbivorous insects to prefer stressed plants (De Bruyn 1995; Saikkonen et al. 1995; Tisdale & Wagner 1991), yet other studies (Cornelissen et al. 2008; McQuate & Connor 1990; Carr et al. 1998) and results of this paper promote the plant vigour hypothesis.

6.5.1 Correlations

Several similarities and some significant differences were found in the two experiments. In both the above-ground and below-ground biomass was significantly positive correlated. This was to be expected, yet it has often been found that plants under drought-stress develop a higher root biomass to counteract the water deficit (Liu & Stützel 2004). In experiment No. 1, the C/N-ratio in the leaves was positively correlated with the plant size and the biomass, whereas it did not correlate in experiment No. 2.

The number of eggs in both experiment did correspond with the number of larvae and adults. Since the eggs are the basis for the number of adults, this was also to be expected. Nevertheless, it might have been possible that some eggs or larvae suffered high mortality resulting in a lacking correlation.

In the first experiment the number of eggs did not correlate with plant biomass, while in the second experiment it did. This difference in the egg laying could be a consequence of the drought. The plants in the second experiment were stressed two weeks before the insects were clipped, leading to already visible drought effects. In experiment No. 1 the number of adults did positively correlate with the plant size before the experiment and the leaf size. In the second experiment the number of adults was positively correlated with the plant growth. In both experiments no correlation between the number of whiteflies, regardless of stage, and the C/N-ratio was found. It is unusual that the number of insects is not correlated with the carbon or nitrogen content in the leaves. In general, plant palatability increases with a decreasing C/N-ratio (Mattson 1980; Hartley & Jones 1997). Generalist as well as specialist herbivores should react positively to increased nitrogen (Coley et al. 2006; Mattson 1980; Schädler et al. 2007). However, some studies found a negative correlation between number of herbivores and nitrogen concentration in the leaves (Kay et al. 2007; Valladares & Lawton 1991). A possible explanation for such a negative correlation is a degradation of the host quality by the herbivore (Valladares & Lawton 1991). As a result, an initially high-quality, preferred host may become an inferior one. For instance, Schädler et al. (2007) showed that due to their function as nitrogen sink, the number of aphids per plant was negatively correlated to the nitrogen content of their host plant in a controlled greenhouse study. Also, environmental factors could explain the results. Thus, we suggest that the leaves with a high nitrogen ratio have a low ratio of secondary compounds. This could explain the missing correlation between the egg numbers and the C/N-ratio, due to the fact that specialist are attracted by secondary compounds and use them for host-plant location and host-plant identification (Chew 1979; Feeny et al. 1983; Honda 1986; Pereyra & Bowers 1988).

6.6 Conclusion

The results suggest the population of the whitefly *Aleyrodes proletella* to decline under long drought periods. But it is likely that the whiteflies will adapt quickly conditions of limited water supply. Experiments with *Drosophila melanogaster* could show, that larvae which developed under drought stress, are more resistant to dry conditions they encounter as adults (Aggarwal et al. 2013). Furthermore, vegetables are regularly irrigated to avoid yield loss and therefore provide optimal conditions for whitefly development.

7 Impact of cold winters compared to mild winters on the development and synchrony of the cabbage whitefly *Aleyrodes proletella* and the parasitoid *Encarsia tricolor*

7.1 Abstract

The predicted temperatures increases will regard especially the cold extremes, leading to warmer nights and warmer winters. Those mild winters may have an important effect on the population development of the cabbage whitefly and the synchrony between it and its natural enemy the parasitoid *Encarsia tricolor*. The development of *Aleyrodes proletella* is mainly controlled by the temperature, while the diapause of the wasp is controlled by the photoperiod. An experiment with mini-greenhouses was designed, representing conditions close to agricultural realities to test the influence of mild winters compared to cold winters. These greenhouses provided nearly natural conditions, but were closed to other species and would allow to control the temperatures via a heating device. Results showed that the whiteflies had a reproducing diapause in December and in the beginning of January. After this diapause the egg-laying started earlier in the heated greenhouse compared to the unheated, but surprisingly more adults survived in the cold houses than in the heated. In both the heated and the unheated houses we found no living *Encarsia tricolor*. In the field none of the larvae or the mummies on the lower leaves of Brussels sprout plants survived and only adult females of *A. proletella* were found on the upper leaves at the end of the winter.

7.2 Introduction

In Germany the temperature increased about 0.9 °C in the last hundred years. Temperature increase will be probably in the cold extremes leading to warmer winters and warmer nights (Rosenzweig et al. 2001) and to a shift in the differences of day and night temperatures. A temperature increase of 3 °C in winter is expected (Kromp-Kolb 2003). An increase in the average winter temperature and an early beginning of spring is already visible (Ahas et al. 2002).

A warmer winter can have several effects on insect populations. It may lead to a higher initial population due to lower mortality during winter and an earlier beginning of population development in spring (Bale et al. 2002; Fuhrer 2003; Harrington et al. 2007). Another factor influencing the population development might be the promotion of asexual clones and anholocyclic life cycles of aphids as reported for the green peach aphid *Myzus persicae* or the grain aphid *Sitobion avenae*. They survive better under warmer conditions (Bale et al. 2002) and are more fertile, building up bigger populations under these conditions. The winter temperature has also a direct effect on the phenology of aphids (Zhou et al. 1995). Warmer winters are crucial for immigrating species allowing them to colonise new areas early and more intensively (Ward & Masters 2007) or they may even be able to overwinter in regions which have been too cold in the past (Cannon 1998), so that they can reach host plants early and in a more vulnerable stage.

The model species for the following experiments is the cabbage whitefly *Aleyrodes proletella*. The population size of the whitefly increased rapidly in the last ten years and it has advanced to be one of the most important pest species in cabbage (van Albeek 2008). The females of this species overwinter on oil rape plants, cabbages stalks which remain on the field or wild Brasscia plants (Richter 2010). In spring they started to lay eggs as soon as temperatures are sufficient.

Encarsia tricolor is the main specialized natural enemy of the whitefly occurring in temperate regions such as Lower Saxony. The parasitoids overwinter as diapausing pupae; the end of the diapause is triggered by the photoperiod. This species has the potential to become important for the integrated plant protection against whiteflies (Herz 2012).

It is likely that pest and parasitoid react differently to a temperature increase in wintertime causing an asynchrony between prey and parasitoid. Most parasitoids like *Encarsia tricolor* survive the winter in a diapause stage, reducing all metabolic functions. The end of diapause is triggered by the photoperiod and not by temperature (Tobin et al. 2008). But warm winters and springs might lead to an earlier ending of the diapause (Tobin et al. 2008). The whiteflies in contrast overwinter as females without a diapause and their activity starts with increasing temperatures. If winter becomes milder, the activity of the whiteflies will start earlier than the activity of *E. tricolor*.

Such asynchronies can already be observed between pest species and their host plants (Thomson & Hoffmann 2010). Due to the warming in the last century many spring plants blossom one or two weeks early (Parmesan 2006), and if the hatching time of aphids is heritable (Komazaki 1986; Mittler & Wipperfurth 1988; Komatsu & Akimoto 1995; Dixon 2003) this causes an asynchrony between herbivore and host. Dixon (2003) could show that aphids which hatch before or after bud-burst are less fit than aphids that hatch at bud-burst. This phenomenon is leading to a high mortality of the aphids in spring (Dixon 2003). Furthermore, asynchronies between prey and parasitoid can be observed, with a decreased rate of parasitism on caterpillars in a more variable climate (Stireman et al. 2005).

As the diapause of *Encarsia tricolor* is triggered by the photoperiod and not by temperature, warmer winters would lead to an asynchrony between the whiteflies and their parasitoid so that aphid populations would start to grow before parasitoids leave the overwintering mummy stage. To evaluate if this is the case, we developed a semi-field experiment in a protected eco-system, yet close to natural conditions. In it both species and their population development would be monitored under simulated conditions of warm winters with nearly no freezing and under normal winter conditions with temperatures under the freezing point.

7.2.1 The cabbage whitefly *Aleyrodes proletella*, (Fam. Aleyrodidae, Order Homoptera)

is a common pest of Brassicaceae in Europe. The importance of the species is increasing since the 1970th and especially in the last year the species has spread heavily (van Alebeek 2008). The species overwinters on oil rape plants, on kale plants or on herbs like tetterwort (*Cheledonium majus*) as mated females or as pupae (Richter 2010). (See also chapter 2.5.1.1)

7.2.2 The parasitoid *Encarsia tricolor*, Fam. Aphelinidae, Order Hymenoptera

Encarsia tricolor is an autoparasitoid of whiteflies that occur in Europe and Russia. The mummies overwinter in their hosts and in late spring the adults hatch. The basal developmental temperatures and the developmental time are not known for *Encarsia tricolor*. Also the lower lethal temperature threshold is unknown. (See also chapter 3.2.2.)

7.3 Material and Methods

7.3.1 Experiment

The cabbage whiteflies for the experiment were taken from the rearing of the Institute of Plant Disease and Plant Protection in Hanover. The insects were reared on Brussels Sprout at temperatures of 20 °C and light conditions of 18/6 (light/darkness).

To test the influence of cold winters compared to mild winters small greenhouses were constructed which represent mini-ecosystems. These 12 greenhouses were made of steel frames with a surface area of 4 m² (2x2 m) and a height of 2 m. The lower part was stringed with UV-permeable gauze to allow air-ventilation and the upper part and the roof were stringed with UV-permeable foil. Half of the houses were equipped with a heating device. At the beginning of September eight ten-week-old cabbage plants were placed in each of the greenhouses and buried into the soil. Then 6 female 3-day-old whiteflies per plant were clipped on the Brussels sprouts. The whiteflies for this experiment were reared outside three months to allow the insects to adapt to field conditions. Each month the mortality and egg-laying of the whiteflies was recorded. In three randomly chosen heated and three unheated houses *Encarsia tricolor* mummies on leaves were placed additionally. The whole winter the temperature was recorded using Tinytag Data logger. The experiments run in winter 2010/2011 and 2011/2012.

In addition to this experiment, ten plants in the field (experimental field of the Institute for Plant Protection and Plant Disease, University of Hanover) with *Aleyrodes* larvae and *Encarsia tricolor* mummies were chosen and every month the number of eggs, larvae, pupae, hatched adults and mummies were counted.

7.3.2 Statistical analysis

Data were visually checked for normality of residuals, creating histograms and box plots and if necessary transformed and pooled for the replicates. The percentage data for the mortality of the adults and the development of the larvae and eggs were arc sine square root transformed. To show the influence of the heating devices bar charts were created for the experiments in winter 2010/2011 and scatter plots for the results of the winter 2011/2012. Due to the fact that several problems occurred in the experiments an accurate statistical analysis was not implemented.

Main emphasis of the experiment was on the relationships between influence of the heating and the different month on the mortality and the development of the whiteflies.

7.4 Results

7.4.1 Winter 2010/2011

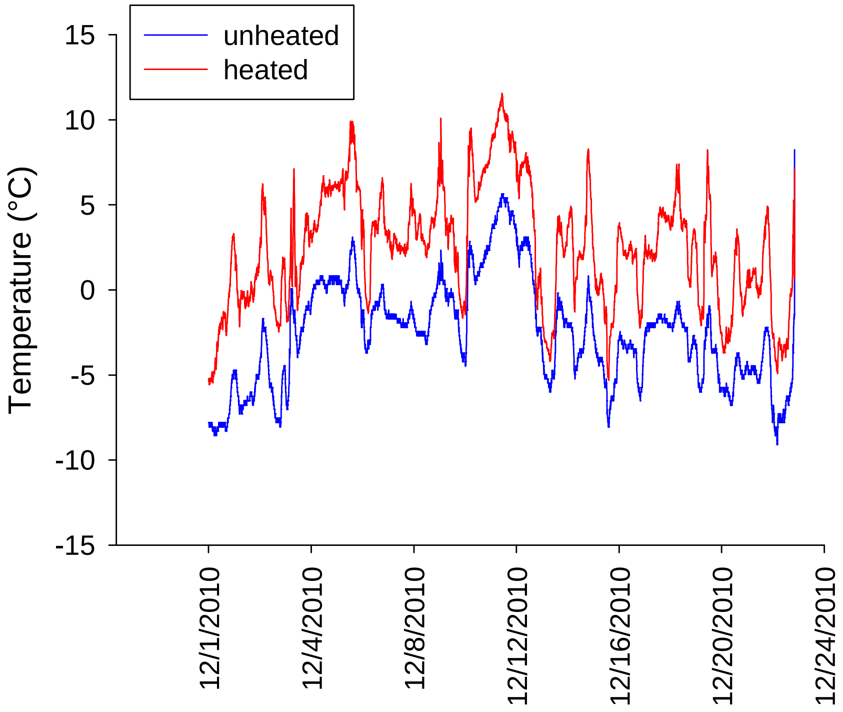

Fig. 43: Comparison of the heated and unheated greenhouses in December 2010.

In the winter of 2010/2011 the temperatures ranged from -9 °C up to 5 °C. In the heated greenhouses temperatures were 3-4 °C warmer on average than in the unheated houses. Nevertheless, in spite of heating temperatures as low as -5 °C did occur there also (**Fig. 43**). The temperatures in November, January and February were comparable to the winter 2011/2012 (**Fig. 48**). The lower developmental temperature for *Aleyrodes proletella* is 6.88 °C and the lethal temperature is unknown. The lower developmental temperature and the lethal temperature for *Encarsia tricolor* are unknown, either. The lower developmental temperature for *Diaeretiella rapae*, another parasitoid in temperate regions, is 3.5 °C and the lethal temperature is not investigated.

7.4.1.1 The cabbage whitefly

After the first month (November), the counting did not indicate significantly different numbers of adults in the heated and unheated houses. The number of adults was even slightly higher in the unheated houses. In December and January only a few living adults were found in the unheated houses, but none in the heated ones (**Fig. 44 (A)**). All other specimen had perished. The amount of eggs decreased rapidly during January both in the heated and in the unheated greenhouses. In November some females still laid eggs leading to an egg amount of 120% compared to the number of eggs at the beginning of the experiment. In December the number of eggs decreased in the unheated houses, while it increased in the heated houses. In January only a few eggs were left (**Fig. 44 (B)**). These eggs could have not been additionally laid, because all adults had died.

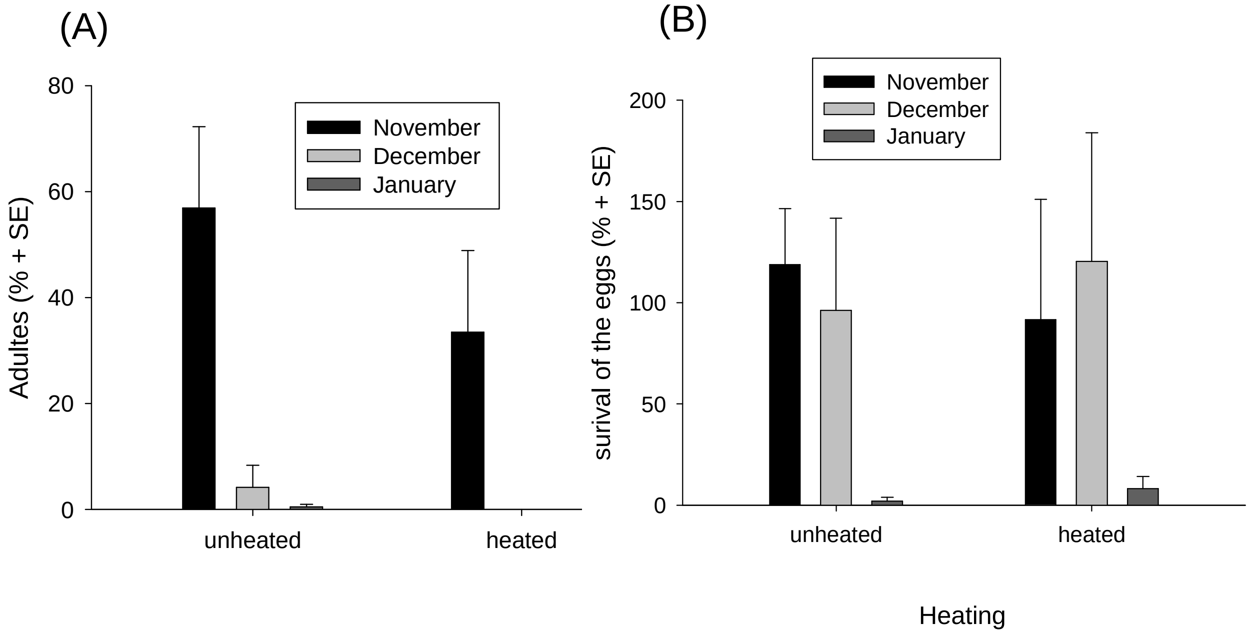

Fig. 44: (A) Amount of living adults of *Aleyrodes proletella* (B) Amount of eggs laid by *Aleyrodes proletella* in the heated and unheated greenhouses in winter of the first year. n = 6 for each treatment.

The amount of larvae was very high in November in the unheated houses, indicating that several eggs hatched successfully and developed to larvae. In December still a lot of eggs hatched, but January no larvae were to be found anymore. In the heated houses the hatching success was high as well, but not as high as in the unheated once in November, whereas it was higher in December. Both in heated and unheated greenhouses no L1-larvae were found in

January (**Fig. 45 (A)**). Nearly all L3-larvae survived in November in the unheated house, whereas only 70% survived in the heated one. In December no L3-larvae were found in the unheated houses, but about 20% in the heated ones. In January few L3-larvae were found in both the unheated and the heated houses (**Fig. 45 (B)**). The L3-larvae in the unheated houses in January were newly developed larvae and not surviving larvae of the previous month.

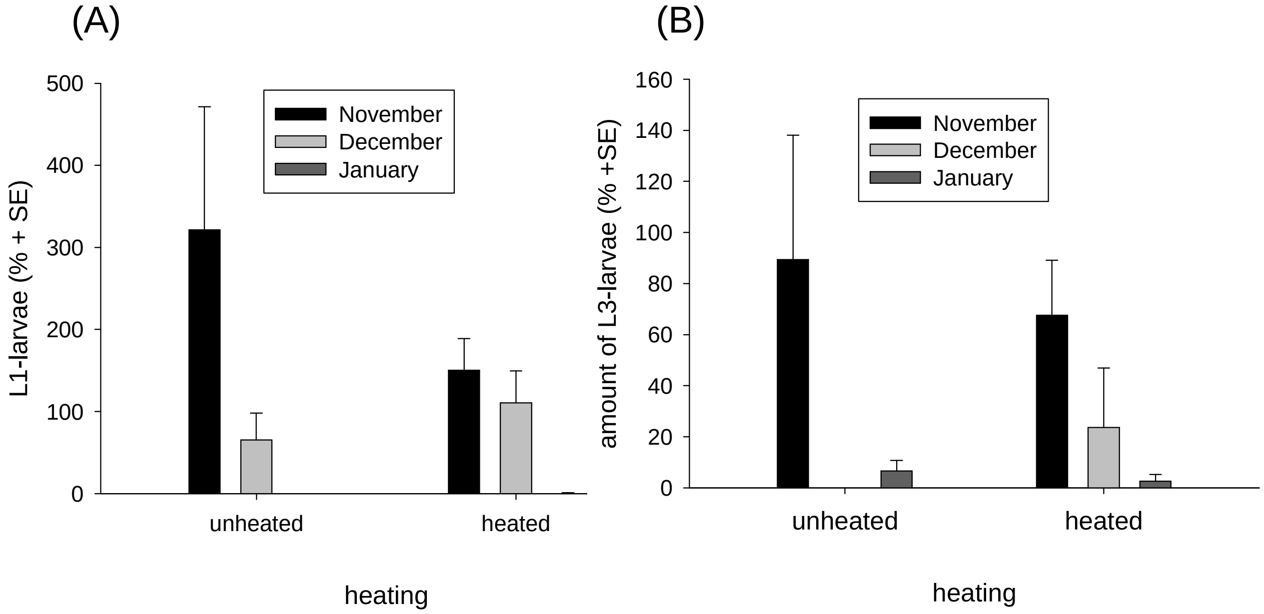

Fig. 45: (A) Amount of L1-larvae of *Aleyrodes proletella* (B) Amount of L3-larvae of *Aleyrodes proletella* in the heated and unheated houses in winter of the first year. n = 6 for each treatment.

7.4.1.2 Parasitoids

In the first year no *Encarsia tricolor* could be found after the winter.

7.4.2 Winter 2011/2012

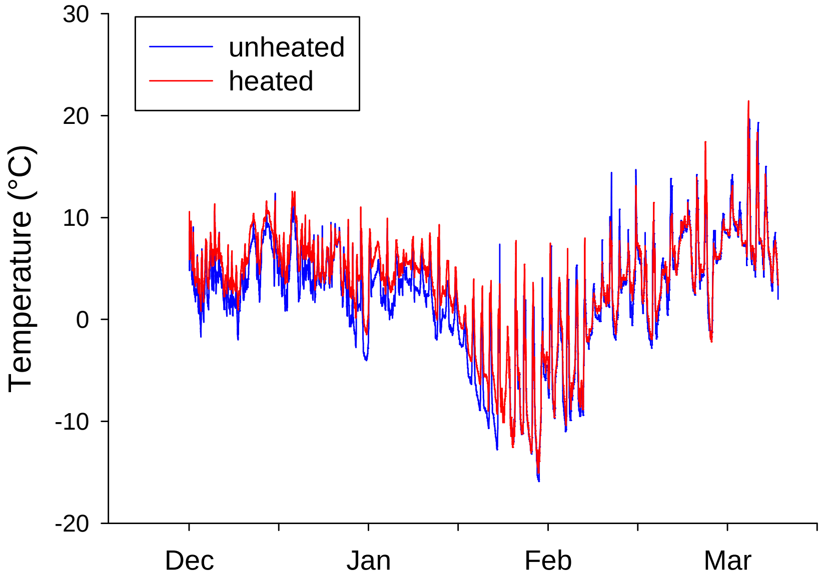

Fig. 46: Temperatures in winter comparing heated and unheated greenhouses. The red line illustrates the average temperature in the heated houses and the blue line the average temperature in the unheated houses.

In the winter 2011/2012 the temperatures ranged from 0 °C up to 10 °C in December and January. At the beginning of February the temperatures dropped down to -17 °C. In the heated houses the temperature was on average 3-4 °C higher compared to the unheated greenhouses **(Fig. 46, Fig. 47)**. Nevertheless in February temperatures down to -10 °C occurred in the heated houses for two weeks during night time with temperatures as cold as -16 °C in the unheated houses.

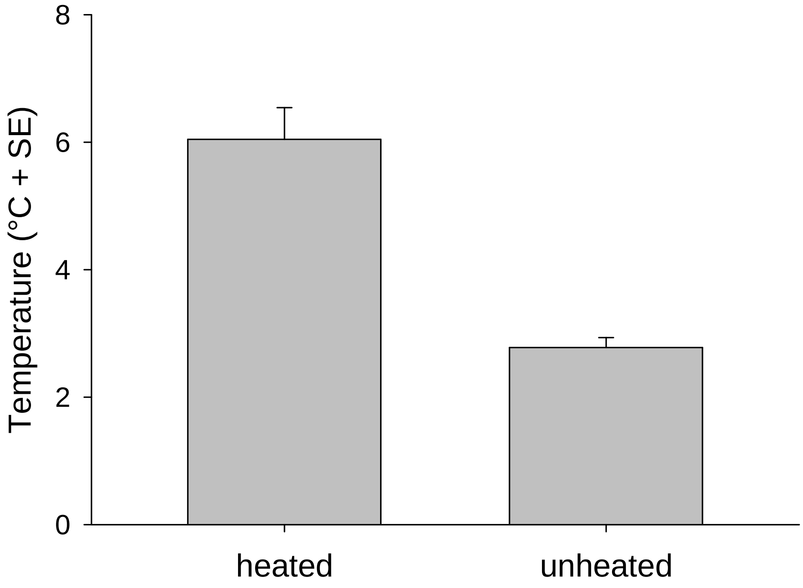

Fig. 47: Temperature difference between the heated and the unheated greenhouses in December 2011.

7.4.2.1 The cabbage whitefly

The number of adults decreased over the winter. They survived longer in the unheated houses than in the heated ones. In November all adults were still alive but after one month the survival rate dropped to 58% in the heated houses and to 80% in the unheated. In February and March nearly no living adults remained in the heated houses, while in the unheated still 69% (13% respectively) survived (**Fig. 48**).

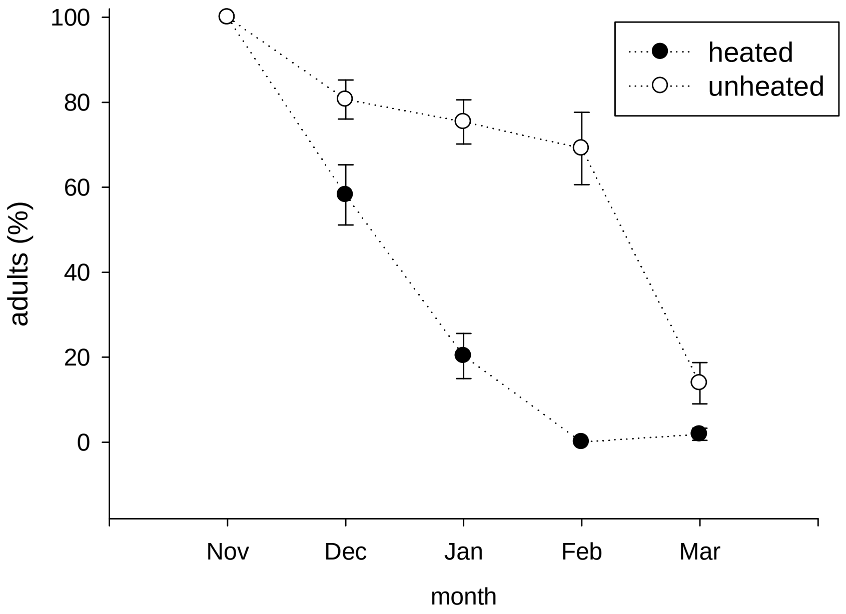

Fig. 48: Number of the adults of *Aleyrodes proletella* which survived in the second winter comparing the heated and unheated greenhouses. The data were collected on different plants, i.e., a decrease must not necessarily show mortality. n = 6 for each treatment.

The number of laid eggs increased with preceding months. There were more eggs in the heated greenhouses. In November in both heated and unheated houses no eggs were found and it seemed as if the females were in an egg-laying diapause. Then in December we found five eggs per plant in the heated houses and 1.5 eggs in the unheated ones. In January we could observe 3 eggs in the unheated and about 4 eggs in the heated houses. In February the number of eggs increased in the unheated houses to 4.5 eggs per plant and in the heated it was stable with 4 eggs per plant. In March the females started to reproduce especially in the unheated houses, where 14 eggs per plant could be found (**Fig. 49**).

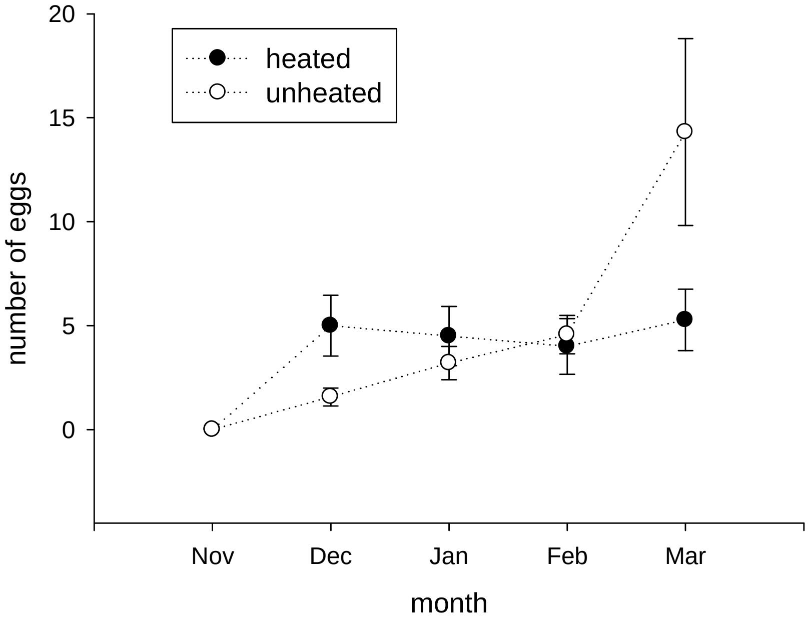

Fig. 49: Egg-laying of *Aleyrodes proletella* during the second winter comparing heated and unheated greenhouses. The data were collected on different plants, i.e., a decrease must not necessarily show mortality. n = 6 for each treatment.

No L1-larvae were found in November and in December only one larva was found in the heated house. In February the number of larvae increased significantly in the heated houses, while in the unheated still no larvae were found. In the unheated houses the first larvae emerged in March, whereas the number in the heated houses decreased (**Fig. 50**). At this point L3-larvae were found in the unheated houses for the first time. We found 4.3 larvae per plant in the heated houses and less than one in the unheated ones (**Fig. 51**). By the end of March several Brussels sprouts plants in the heated houses blossomed.

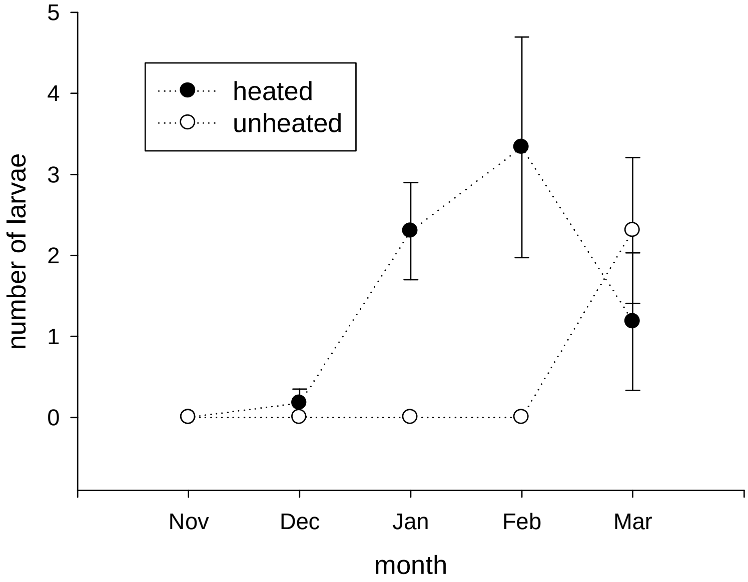

Fig. 50: Development from eggs to larvae of *Aleyrodes proletella* in the second winter comparing heated and unheated greenhouses. The data were collected on different plants, i.e., a decrease must not necessarily show mortality. n = 6 for each treatment.

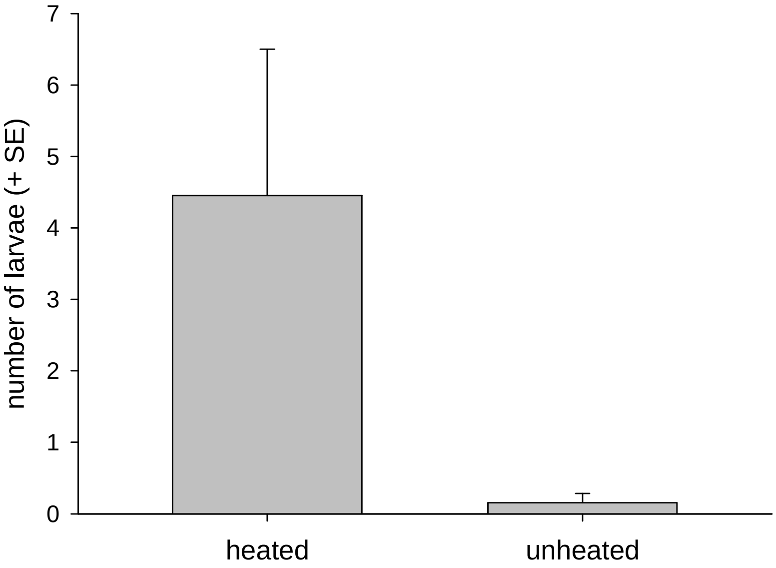

Fig. 51: The development of L3-larvae of *Aleyrodes proletella* in the second winter in heated and unheated greenhouses. The data were collected on different plants, i.e., a decrease must not necessarily show mortality.

7.4.2.2 Parasitoids

In the second year no *Encarsia tricolor* were found in the greenhouses, either.

7.4.3 Development of the whiteflies in the field

At the first counting at the beginning of December nearly no whitefly egg clutches on the lower leaves of the plants and only few L1-larvae were found, but several pupae and mummies with *E. tricolor.* Several whitefly adults on the lower leaves were registered, yet it was assumed that they had hatched recently and did not use the leaves as oviposition site, although the upper leaves were populated by many adults. So did adults with egg clutches but nearly no larvae and pupae. In average we found 6 L3-Larvae per leaf, 25 pupae per leaf, 28 mummies per leaf and 6 adults per leaf.

At the second counting in January half of the leaves had died and on these leaves only few living pupae and mummies could be registered. On the other leaves also all of the mummies and pupae had died and no egg clutches or L1-larvae were to be found. Still there appeared adults, which seemed recently hatched. At this counting there were 2 L3-larvae per leaf, which is 10% of the number in the beginning, 9 pupae (37%) per leaf, 9 mummies (40%) per leaf and 3 adults per leaf. No adult parasitoids were to be found in the field during the observation period.

At the third counting in February all leaves had wilted and all the mummies and pupae on them had died. No living whiteflies were recorded. In this month we only found living females in the upper leaves of the other cabbage plants than the experimental plants (**Fig. 52**).

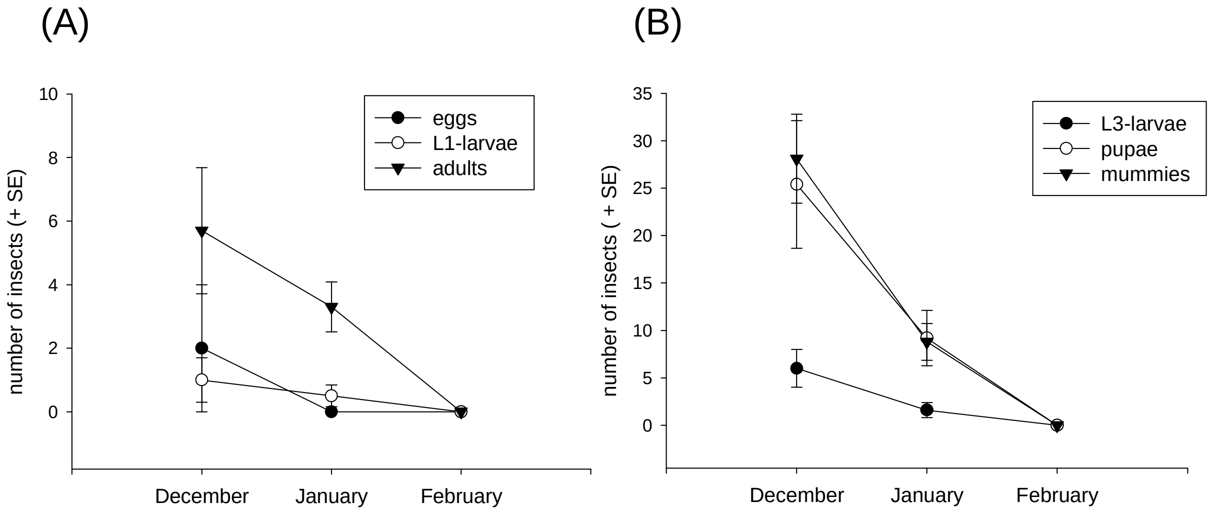

Fig. 52: (A) Number of eggs, L1-larvae and adults of *Aleyrodes proletella* (B) Survival and development of the whitefly larvae and the *Encarsia tricolor* mummies on cabbage leaves in the field in the second winter To evaluate the amount of insects, plants were labeled and the living insects were counted monthly. n = 10 for each treatment.

7.5 Discussion

7.5.1 Overwintering under semi-field conditions

The results indicate the whiteflies to have an egg-laying diapause in December and the first weeks of January. In January even adults which were brought to the nursery, with long-day conditions and temperatures of 20 °C, stopped laying eggs. Only after three weeks in the nursery, egg-laying started again. At the end of February the females started to lay eggs again, but mainly in the heated houses. In other whitefly species, e.g., the bayberry whitefly *Parabemisia myricae*, the reproduction is also reduced in winter (Swirski et al. 1986). The results in our experiments are in consensus with Adams (1986b) who found that the ovarian development decreases between September and December and that body fat increased during this time. The critical photoperiod that will induce this egg-laying diapause is LD 15.5/8.5 hours (Adams 1985). Under this conditions 60% of the females went into egg-laying diapause (Iheagwam 1977). This reproductive diapause is independent of temperature and can be induced in face of temperatures of up to 15 or 20 °C (Iheagwam 1977). It is also important if the whiteflies live under constant short-day-conditions or if they live under developing short-day-conditions from long-day-conditions; The first case results in a weak inhibition of ovarian development, while in the second scenario the pre-emergence oogenesis is completely inhibited (Adams 1985b). The peak photoperiodic sensitivity is in the third larval instar (Adams 1985b). The termination of the diapause is in contrast to its induction temperature-dependent (Adams 1986).

In the heated greenhouses the developmental rate of the larvae was accelerated. The number of L3-larvae was also higher in the heated houses. The adults survived better in the unheated houses.

In contrast to *Aleyrodes proletella*, the adults of the cotton whitefly *Bemisia tabaci* are most prone to cold while the eggs are less vulnerable (Bosco & Caciagli 1998). Yet, those specimen are common in regions with less than 5 frost days per winter, whereas our whiteflies were taken from the field in Hanover and already adapted to cold temperatures. In other regions like California, *Bemisia tabaci* overwinters in an active stage (Mayberry & Perring 1992; Mallah et al. 2001). In an experiment with *Bemisia tabaci* biotype B the mortality of eggs, which were exposed 10 hours to -10 was 86.6%, and the mortality of nymphs and adults was even higher (88.4 and 100%, respectively; Lin et al. 2007). Although *Bemisia tabaci* is a close relative to the cabbage whitefly, it is a tropical species and a comparison with other species of the temperate region would be useful. The grain aphid *Sitobion avenae*, which is common in Germany, has a cold torpor point of 0.5 °C after a short period of cold hardening (Powell & Bale 2006). Thus, 80% of the nymphs and 68% of the adults can survive temperatures below -8 °C (Powell & Bale 2004). Aphides acclimated to cold can survive even temperatures as low as -12 °C after cold hardening (Powell & Bale 2005). In the field the aphids suffer mortality at temperatures below -4 °C (Williams 1980). The lower lethal temperatures (LLT_{50}) for the *Myzus persicae* range from -12.7 to -13.9 °C (Hazell et al. 2010), with first-born nymphs surviving temperatures of -15.9 °C (Clough et al. 1990). The host-alternating aphid *Pemphigus bursarius* overwinters as asexual hiemalis in the soil and as adult on poplars. The hiemalis have a LLT_{50} of -13.5 °C and can survive this temperature for up to 18 days (Phillips et al. 2000). The super-cooling point changes with the season, leading to an LT_{50} of -6.9 °C in October and -12.2 °C in January for *Brevicoryne brassicae* (Saeidi et al. 2012). In autumn the amount of glycerol or other alcohols like mannitol increases in insects, effectively serving as an antifreeze agent (Sømme 1964; Block et al. 1990). *Aleyrodes proletella* is the most cold tolerant whitefly species. In other outdoor studies as well as in our study the populations of whiteflies thinned dramatically in winter and increased rapidly again in spring (Gerling 1984, Richter 2010).

No parasitoids were recorded in both the heated and the unheated houses in spring. Normally the parasitic wasp overwinters as mummy in the host on fallen leaves (Nucifora 1985), e.g., in *Encarsia quaintancci*, *E. pergandiella*, *Eretmocerus haldemani* and all parasitoids of *Trialeurodes abutilonea*. *Encarsia formosa*, a close relative, needs frost-free habitats to overwinter. Even temperatures of 10 °C for 13 days reduce its hatching success by about 45%; the hatching success of mummies exposed to 2 or 5 °C respectively declined rapidly after three days (Lacey et al. 1999). But other studies could show that the adults can survive temperatures of 5 °C for several days (Kajita 1983). The parasitoid *Aphidius ervi*, which is used in Integrated Pest Management in Germany (Katz, unpublished) and *Aphidius rhopalosiphi* overwinter as diapausing mummies and can survive long term exposures of 0 down to -10 °C (Langer & Hance 2000). The parasitoid *Aphidius colemani* even has a super-cooling point of -22 °C (Colinet et al. 2007). Another common parasitoid in Lower Saxony, the wasp *Diaeretiella rapae*, suffers a mortality of 55% after 32 days with temperatures under 5 °C (Silvia et al. 2013).

The longer the exposure to cold, the more the water content (water mass/ dry mass) increased in overwintering *Aphidius colemani* mummies, leading to a starving of the mummies (Colinet et al. 2006 b). A short rise in temperature can lead to a recovery of the parasitoids (Colinet et al. 2006 a), but in this paper’s experiments the low temperatures continued for several days.

During the experiments it was not possible to hold the temperatures above 0 °C, due to very cold night temperatures. We assume that the low temperatures in the houses were too cold for *Encarsia tricolor* leading to a mortality of all individuals. In fallen leaves they are protected from very low temperatures.

7.5.2 Overwintering in the field

On the leaves we chose for our counting, mainly larvae and pupae were registered. The adults settled on the upper leaves for overwintering, because they prefer fresh leave material. Over the course of the winter most leaves died and the larvae and pupae on them died as well, due to a lack of nutrient availability. In the field under cold conditions the whiteflies seem the overwinter completely as mated females. Living females were found even after nights with temperatures as low as -18 °C. The survival at these cold temperatures may be due to a protection of the whiteflies by the leaves, because the living insects on our field were hiding in the core of the kale plants and the animals on the lower and less protected leaves were dead. Furthermore is the amount of glycerol or other alcohols like mannitol increased in insects in winter, effectively serving as an antifreeze agent (Sømme 1964; Block et al. 1990). Males are more vulnerable to cold temperatures and only few of them survive the winter (Adams 1985). One explanation for this observation could be the smaller body size of the males. The Bergmann Rule postulates that bigger animals are better protected under cold circumstances due to the smaller surface in relation to the volume (Meiri 2010). Regarding other whitefly species, it has been found that merely larvae and females overwinter (Swirski et al. 1986). In the field, whiteflies overwinter regularly on cabbage plants, like Brussels sprout or kale, which are harvested late and often on oil rape plants (Richter 2010).

In the field we found no surviving parasitoids on our test plants. In this winter the temperatures had fallen down to -18 °C and the mummies on the lower leaves were not protected from the cold. In the field the parasitoids overwinter mainly on fallen leaves, which provide frost-protected habitats. Due to the fact that *Encarsia tricolor* and *Diaeretiella rapae* live under the same climatic conditions we assume that the lethal temperatures are similar in both species. *Diaeretiella rapae* suffers a high mortality after 32 consecutive days with temperatures under 5 °C (Silvia et al. 2013) and it is likely that *Encarsia* mummies also have a high mortality at temperatures under 0 °C. The resettlement in the field might occur from individuals which overwintered on frost-free places.

7.6 Conclusion

Since the whiteflies in heated greenhouses, in spite of higher mortality, started earlier with the egg-laying and their larvae would developed faster, we assume that the whiteflies will be able to build up bigger populations and appear earlier in spring after mild winters. No parasitoids survived the experiment, but we assume that this shows no general trend. If the break of the diapause of the parasitoid *Encarsia tricolor* depends on the photoperiod, this will lead to an asynchrony between prey and predator.

We propose to repeat the experiments by bringing heavily infested plants into the greenhouses and clip several adults in clip-cages on at least five leaves. This would allow a population development over the winter of free whiteflies with a choice for the adults regarding the plant part, e.g., leaf level and a controlled observation of the insects in the clip-cages. The parasitoid should as well be available in all developmental stages. Furthermore we would propose to infest plants on an experimental field with *Aleyrodes proletella* and *Encarsia tricolor* and to evaluate their numbers constantly.

Especially the heating device must be improved: Despite additional improvised insulation with bubble wrap, the temperatures in the heated greenhouses fell below -10 °C. Maybe, a stronger heating device with heat sensor opposite of the heating or even under floor heating would be useful, although a under floor heating does not reflect the cooling from the air naturally. With such a device a drying of the plants due to frozen soil would be avoided as well, also this would not represent natural conditions for the plant, but near natural conditions for the insects. Furthermore, the plants in the greenhouses must be effectively protected against voles. This can be achieved by mesh cages or by applying older plants which are not palatable for the voles. Also mesh dug in under the greenhouses or sound devices might be helpful.

For the overwintering in the field it would be useful to take half of the plants with whitefly larvae and mummies of *Encarsia tricolor* into the lab and study the rate of hatching under controlled conditions. Furthermore, it would be useful to open some of the mummies and study if they really contain larvae of the parasitoid. In spring trapping plants in the field could show resettlement with parasitoids.

We would also suggest to study the lower lethal temperatures for *Aleyrodes proletella* and *Encarsia tricolor* under controlled conditions in the lab to estimate the mortality in winter under freezing conditions and to assess if milder winters would favour asynchronisation.

8 Final Discussion

An increase of the population of the cabbage whitefly *Aleyrodes proletella* in the last decade and the results of our study, lead to the assumption that this insects are very robust against high temperatures and are promoted by an increase in the average temperature. Our results show that the whiteflies are robust to even very high temperatures of 42 °C and that also repeated heat waves, which might occur in the future in Germany and in Lower Saxony, have no negative influence on the population density. They are if anything even positive for *A. proletella* due to reducing of the developmental time. Furthermore the adults and the larvae are protected by the leaves due to evaporative cooling.

The rain, another climatic factor, has also just a slightly negative effect on the population development of the cabbage whitefly. The mortality was mainly due to washing off of the leaves and mechanical destruction of the egg clutches. Torrential rain was the only rain level, which had an important effect on the mortality of the adult whiteflies and such heavy rains are not likely to occur several times a year in Lower Saxony. Due to this the whiteflies will be able to compensate the loss in connection with the rain, quickly. But normally the whiteflies cease flying under bad weather conditions and hide under the leaves. The larvae are also protected by the leaves and the wax layer.

Associated with the heavy rains in summer are more frequent summer droughts. The negative effects of the drought, reduced egg-laying and a poorer larval conditions, won't be so distinct in the field, because the farmers will irrigate their plants to avoid harvest loss due to water shortage. The insects in out experiment hadn't had a chance to chose another plant for the oviposition and we assume that they will chose a more sufficient plant for oviposition in the field. In addition to it summer droughts are often associated with high temperatures and we therefore assume that the increase in temperature will outweigh the negative effects of the drought.

The mild winters which are expected in the future will as well have ambivalent effects on *Aleyrodes proletella*. On the one hand our results indicate that adults will suffer a higher mortality under warmer winters, on the other hand the egg laying is starting earlier and the larvae develop faster. Despite the losses of the adult in winter, we assume that the positive effects of the earlier egg-laying and the faster larval development will predominate.

All in all we assume that the importance of the cabbage whitefly as a pest species in cabbage will further on increase and become even more dramatic for cabbage farmers than today. There are only few effective pesticides against whiteflies available and the living on the lower side on the leaves, complicates the application on the cabbage plants. Hence it is important to evolve new ways of plant protection and develop a sufficient model to forecast the emergence of the whiteflies (**Fig. 53**).

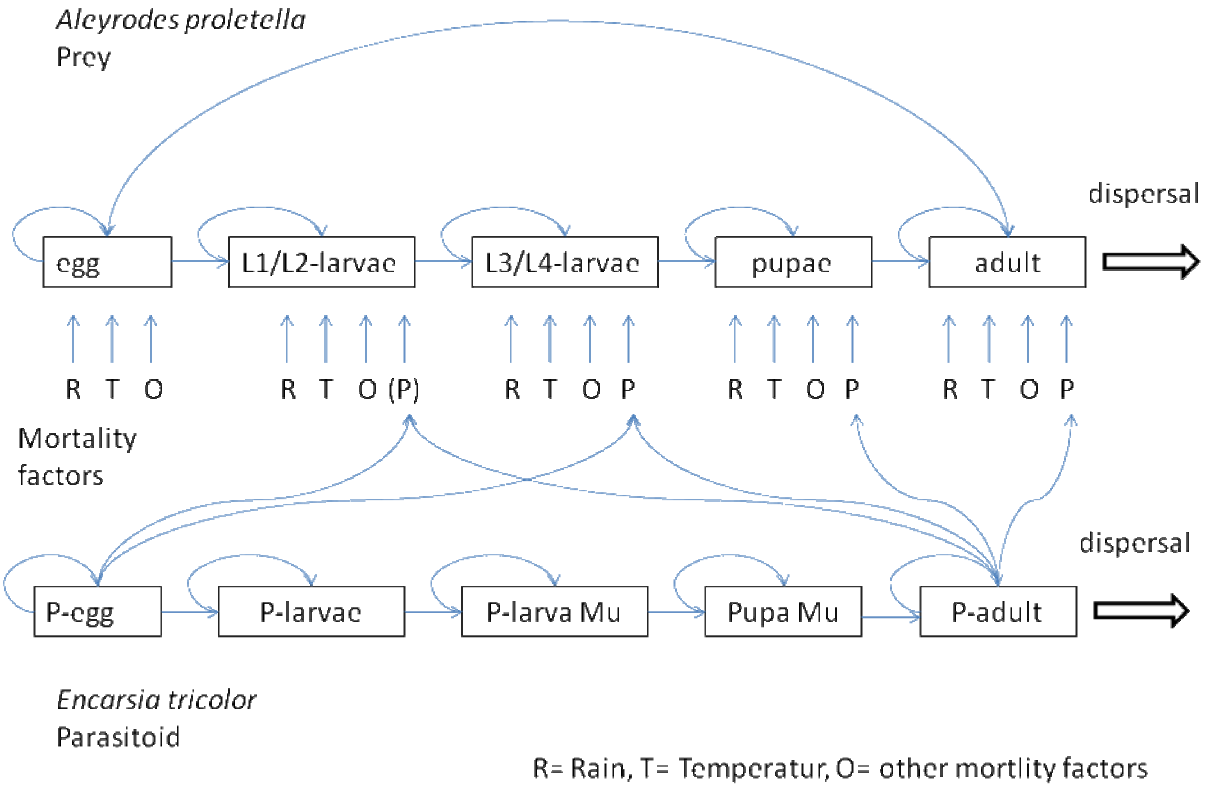

Fig. 53: Model on a daily basis to forecast the population development of *Aleyrodes proletella* under changing climatic conditions.

A forecast model will help the farmers and the plant protection commissioners to forecast the appearance of the whiteflies and calculate the instant on time on which pesticides can be used most successful or natural enemies can be released.

It might also be important to breed cabbage varieties which are resistant to the feeding of the whiteflies or which are not very palatable to them. Short observations show that they seem to prefer green kale and avoid purple varieties if it is possible. Changed cultivation methods may as well help to reduce the problems. Brussels sprout planting for a harvest later in the year reduces the infestation compared to an early planting and harvesting till beginning of November (Schultz et al. 2010). Moreover it is important to evolve pesticides which can perforate the wax layer and reach the larvae and pupae. It is also important to engineer crop protection sprayer, which can spray on the lower side of the leaf to reach as many insect as possible. Despite of this arrangements it will not be possible to get all insects and other ways of plant protection like beneficials will be necessary. This postulation is supported by the fact that the EU is discussing about a prohibition of neonicotinoids, one of the active ingredients against whiteflies.

One possibility in the control of *A. proletella* is the parasitic wasp *Encarsia tricolor*, which naturally occur in Lower Saxony. An close relative of *E. tricolor*, *E. formosa* is successfully used in greenhouses against *Trialeurodes vaporariorum*. Nowadays *E. tricolor* is not able to control whiteflies sufficiently enough, but this might change under a warmer climate. Our results indicate that the parasitoid is also robust against high temperatures. And although the break of the diapause is controlled by the photoperiod, some studies indicate that the diapause can also be broken by high spring temperatures (Tobin et al. 2008). In an experiment in Kassel, Germany *Encarsia tricolor* was successfully used in combination with mesh. The use of *Encarsia* reduced the infestation about 33% leading to an yield increase of 23% (Schultz et al. 2010) or even an reduction of 42% at an earlier release of the parasitoid (Liebig 2010). In southern Germany the use of *Encarsia tricolor* was even more successful leading to such an high decrease of whiteflies that a spraying with pesticides wasn't necessary any more (Hilgensloh 2010). This experiments indicate that the control with *E. tricolor* gains in importance in the future.

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10 Addendum

10.1 Zusammenfassungen der einzelnen Kapitel

10.1.1 Zusammenfassung: Einfluss wiederholter kurzzeitiger Hitzewellen auf *Aleyrodes proletella*

Die Klimaveränderungen, die im letzten Jahrhundert zu beobachten waren, werden sich auch in den folgenden hundert Jahren fortsetzen. Weltweit werden die Temperaturen ansteigen und das Niederschlagsregime wird sich verändern, außerdem wird es zu häufigeren Extremereignissen wie Starkregen oder Hitzewellen kommen. Besonders die Temperatur hat einen bedeutenden Einfluss auf die Entwicklung von Insekten und kann diese fördern oder verhindern, und sehr hohe Temperaturen können zu einer erhöhten Sterblichkeit führen. In bisherigen Studien wurde häufig lediglich der Einfluss einer bestimmten Höchsttemperatur getestet, wobei die Temperaturen in sehr kurzer Zeit anstiegen und es nicht klar ist, ob die Mortalität von der Temperatur oder dem schnellen Temperaturanstieg abhängt. Darüber hinaus wurde häufig nur ein Hitzeereignis getestet. Aus diesem Grund haben wir, um den Einfluss von hohen Temperaturen und Hitzewellen zu testen, ein Modell entwickelt, bei dem die Temperaturen langsam ab- und ansteigen. Dazwischen wird eine Spitzentemperatur von 30 (34, 36, 38, 40, 42 °C) gehalten. Die Tiere wurden diesen Temperaturen entweder in Petrischalen mit Blättern oder an lebenden Pflanzen ausgesetzt. Zusätzlich wurden diese Hitzezyklen 1, 3 oder 5 mal wiederholt, um den Einfluss von Hitzewellen wie sie in Niedersachsen auftreten könnten, zu testen und zu untersuchen, ob sich die Kohlmottenschildlaus an diese Bedingungen anpasst oder stärker unter ihnen leidet als unter einem einzelnen Hitzeereignis. Unsere Ergebnisse zeigen, dass die Kohlmottenschildlaus sehr robust gegenüber Hitze ist und sogar Temperaturen von 42 °C für acht Stunden überlebt. Mit zunehmender Wiederholung der Hitzezyklen stieg jedoch auch die Mortalität. Nach drei Zyklen mit Temperaturen über 38 °C lag die Mortalität der Weibchen bei 90%. Männchen reagierten noch empfindlicher auf die Hitze, nach zwei Zyklen mit Temperaturen über 38 % waren über 95% der Tiere tot. Die Eiablage sank bereits nach einem Zyklus von 38 °C drastisch, Temperaturen von 30 und 34 °C hatten jedoch keinen Einfluss auf die Oviposition. Bei einer Wiederholung der Versuche mit Tieren auf lebenden Pflanzen stellten sich die Ergebnisse jedoch anders da. Hitzewellen, unabhängig von Höhe der Temperatur und Wiederholung der Zyklen, hatten keinen Einfluss auf die Mortalität von Männchen und Weibchen. Es war ebenfalls kein Einfluss auf die Eiablage, die Entwicklung der Eier oder der Larven feststellbar. Lediglich die Entwicklungszeit der Eier verkürzte sich mit zunehmender Temperatur. Hitzewellen haben somit keinen negativen Einfluss auf die Kohlmottenschildlaus und, die hohen Temperaturen werden die Populationsentwicklung dieser Art eher fördern.

10.1.2 Zusammenfassung: Einfluss von wiederholter kurzzeitiger Hitzewellen auf die Glucosinulate

Die Temperaturerhöhung als Folge des Klimawandels wird direkte und indirekte Wirkungen auf die Insekten haben. Ein wichtiger indirekter Effekt wird die Änderung der Pflanzennährstoffe und der sekundären Pflanzeninhaltsstoffe sein. Eine Gruppe dieser Pflanzeninhaltsstoffe sind die Glucosinolate, die vor allem in Brassicaceaen vorkommen und zur Abwehr gegen Herbivoren dienen. Wir untersuchten, ob sich diese Pflanzeninhaltsstoffe unter wiederholten Hitzewellen, die durch an- und absteigende Temperaturen und einer Spitzentemperatur von 30 (34, 38 °C), die für drei Stunden gehalten wurde, simuliert wurden, verändern und somit ein Grund für die Änderung in der Populationsentwicklung der Insekten sein könnte. Die Simulation dieser Hitzewelle, die in Niedersachen auftreten könnte, wurde einmal und fünfmal wiederholt. Unsere Ergebnisse zeigen, dass die Menge der Glucosinolate unter hohen Temperaturen zunahm, wobei jedoch nur die Zunahme von 4-Methoxy-Glucobrassicin signifikant war. Die Menge der Glucosinolate nahm auch stärker nach einer Hitzewelle im Vergleich zu fünf Wellen zu. Den größten Einfluss auf die Veränderung der Glucosinolate hatte jedoch der Fraß des Schädlings *Aleyrodes proletella*. Dieser führte zu einer Verdreifachung der Glucosinulatmenge.

10.1.3 Zusammenfassung: Einfluss von Starkregen auf die Kohlmottenschildlaus *Aleyrodes proletella*

Neben der Temperatur ist Niederschlag einer der wichtigsten Klimafaktoren für Insekten. Die Klimaszenarion für Niedersachsen sagen eine Verschieben des Niederschlags in den Winter und häufigere Starkregenereignisse, unterbrochen von Trockenperioden, voraus. Studien zu dem konkreten Einfluss von Starkregen auf die Entwicklung von Insekten sind selten. Deshalb entwickelten wir eine Arena, um den Einfluss von Starkregen auf *Aleyrodes proletella* zu testen, in der die Insekten verschiedenen Regenleveln ausgesetzt waren. Wir untersuchten drei Regenlevel und setzten alle Stadien der Kohlmottenschildlaus mittlerem (0,6 l/min), starkem (2 l/min) und sintflutartigem (6 l/min) Regen aus. Der mittlere und der starke Regen hatten keinen Einfluss auf die Mortalität der Insekten, nur unter dem sinflutartigen Regen stieg die Mortalität auf 50% an, da die Tiere von den Blättern gewaschen wurden und starben. Die Anzahl der abgelegten Eier nach einem 20-minütigen Regenschauer sank unter dem sintflutartigen Regen um 50%. Der Schlupferfolg aus den Eier sank unter allen Regenlevel um circa die Hälfte, die Entwicklung der Larven und Puppen war jedoch nicht vom Regen beeinflusst. Wiederholung mit realem mittelstarkem Regen hatte keinen Einfluss auf *Aleyrodes proletella*.

10.1.4 Zusammenfassung: Einfluss von Trockenheit auf *Aleyrodes proletella*

Die Gefahr von Trockenperioden, auch im Frühling und im Herbst, wird zunehmen. Um den Einfluss von Trockenheit auf die Kohlmottenschildlaus *Aleyrodes proletella* zu testen, haben wir zuerst Insekten auf Pflanzen in Clip-Cages aufgebracht, die wir dann in drei Stufen Wasserstress ausgesetzt haben. Im zweiten Teil des Experiments haben wir *A. proletella* auf Pflanzen gesetzt, die bereits gestresst waren. Mit zunehmendem Wasserkapazität nahm die ober- und unterirdische Biomasse der Pflanzen zu und das C/N-Verhältnis nahm unter dem Trockentreatment ab. Im ersten Teil des Experiments hatte die Wasserkapazität keinen signifikanten Einfluss auf die Eiablage, die Entwicklung der Eier oder die Entwicklung der Larven der Kohlmottenschildlaus. Im zweiten Teil des Experiments nahm die Eiablage und, als Folge davon, die Anzahl der sich entwickelnden Larven und Adulten mit abnehmender Wasserverfügbarkeit ab. Die Tiere, die sich unter dem Trockentreatment entwickelten waren darüberhinaus kleiner. Wir fanden keine Korrelation zwischen dem C/N-Verhältnis und der Anzahl der abgelegten Eier, sodass wir davon ausgehen können, dass dies nicht der limitierende Faktor für die Entwicklung war. Im zweiten Teil des Versuchs fanden wir jedoch eine signifikant positive Korrelation zwischen der Pflanzengröße und der Anzahl der abgelegten Eier. Die Pflanzengröße scheint ein wichtiger Faktor für die Populationsentwicklung der Kohlmottenschildlaus zu sein.

10.1.5 Zusammenfassung: Einfluss von kalten Wintern im Vergleich zu milden Wintern auf die Entwicklung und Synchronisation der Kohlmottenschildlaus *Aleyrodes proletella* und des Parasitoiden *Encarsia tricolor*

Die zukünftigen Temperaturerhöhungen werden sich vor allem auf die Kälteextreme auswirken, was wärmere Nächte und wärmere Winter zur Folge haben wird. Die wärmeren Winter werden einen wichtigen Einfluss auf die Populationsentwicklung der Kohlmottenschildlaus *Aleyrodes proletella* und die Synchronität mit ihrem Parasitoiden *Encarsia tricolor* haben. Die Entwicklung der Kohlmottenschildlaus wird hauptsächlich von der Temperatur gesteuert, wohingegen die Diapause des Parasitoiden von der Photoperiode abhängt. Wir entwickelten ein Experiment mit Mini-Agrar-Ökosystem, das es ermöglicht, den Einfluss von milden Wintern im Vergleich zu kalten Wintern unter Halb-Freiland-Bedingungen zu testen. Die Gewächshäuser für das Experiment boten den Vorteil, dass in ihnen nahezu freilandähnliche Bedingungen herrschten, die Temperaturen in ihnen bis zu einem gewissen Grad regulierbar waren und andere Insekten ausgeschlossen wurden. Unsere Ergebnisse zeigen, dass die Kohlmottenschildlaus eine reproduktive Diapause von Dezember bis Anfang Januar hat. Nach Beendigung dieser Diapause begann die Eiablage in den geheizten Gewächshäusern früher als in den ungeheizten Gewächshäusern und auch die Larven entwickelten sich unter den warmen Bedingungen schneller. Entgegen unserer Erwartung überlebten jedoch mehr Adulte in den ungeheizten Häusern. Sowohl in den ungeheizten als auch in den geheizten Gewächshäusern konnten wir keine Larven der Schlupfwespe *Encarsia tricolor* finden. Im Freiland überlebten keine der Larven oder Mumien an den unteren Blättern. Nur die adulten Weibchen der Kohlmottenschildlaus überlebten an den oberen Blättern und im Herzen der Kohlpflanzen.

10.2 Additional graphs

10.2.1 Influence of drought on the development of *Aleyrodes proletella*

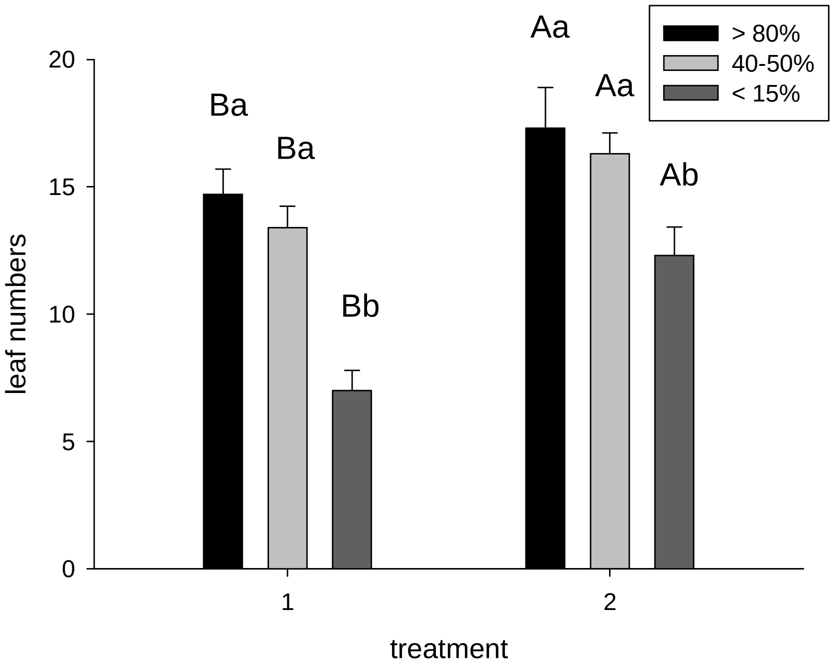

Fig. 54: Influence of the water level on the increase of the leaf number in the two different experiments (Experiment No.1: plants were stressed after colonisation by insects; experiment No. 2: colonisation took place after stressing of the plants). Different characters representing significances ($\alpha \leq 0.05$). Capitals representing camparison between experiments, small letters within the experiment.

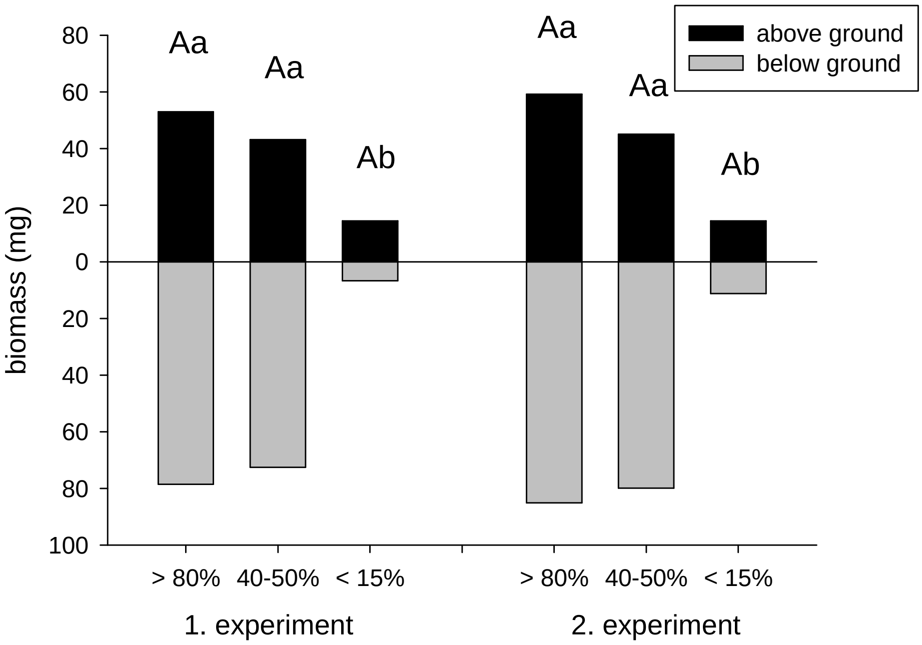

Fig. 55: Influence of water level and experiment on the above and belowground biomass (treatment one: plants were stressed after colonisation by insects; treatment 2: colonisation took place after stressing of the plants). Different characters representing significances ($\alpha \leq 0.05$). Capitals representing camparison between experiments, small letters within the experiment

10.2.1.1 First experiment

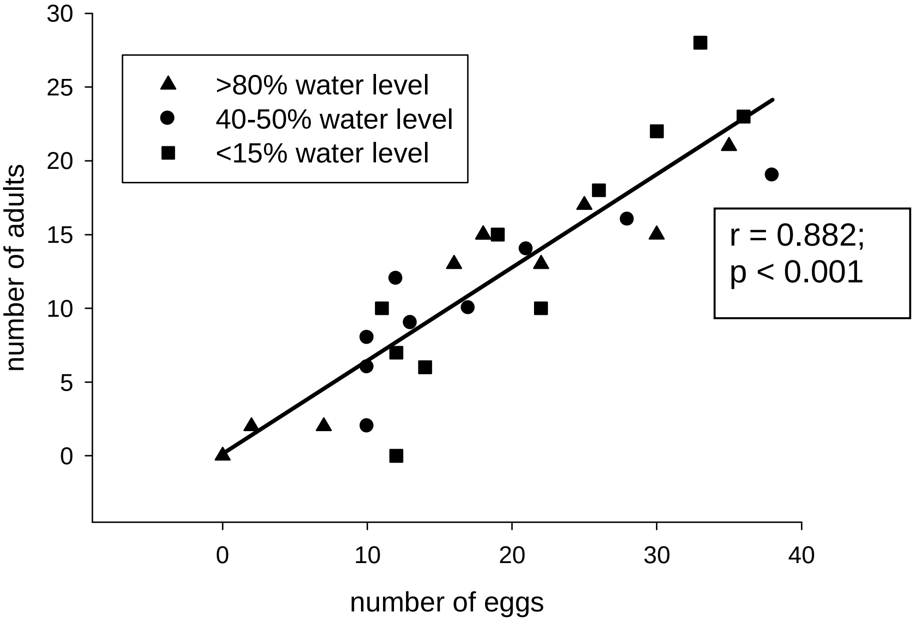

Fig. 56: Number of eggs correlated with the number of adults of *Aleyrodes proletella* in the experiment No. 1 (plants were stressed after colonisation by insects).

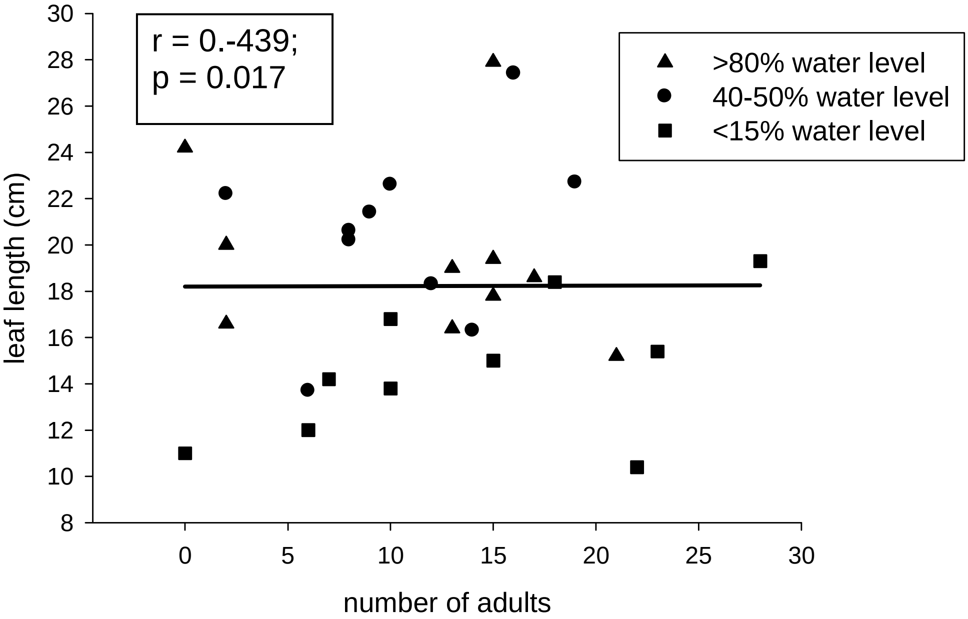

Fig. 57: Number of adults of *Aleyrodes proletella* correlated with the plant size at the end of the experiment No. 1 (plants were stressed after colonisation by insects).

10.2.1.2 Second experiment

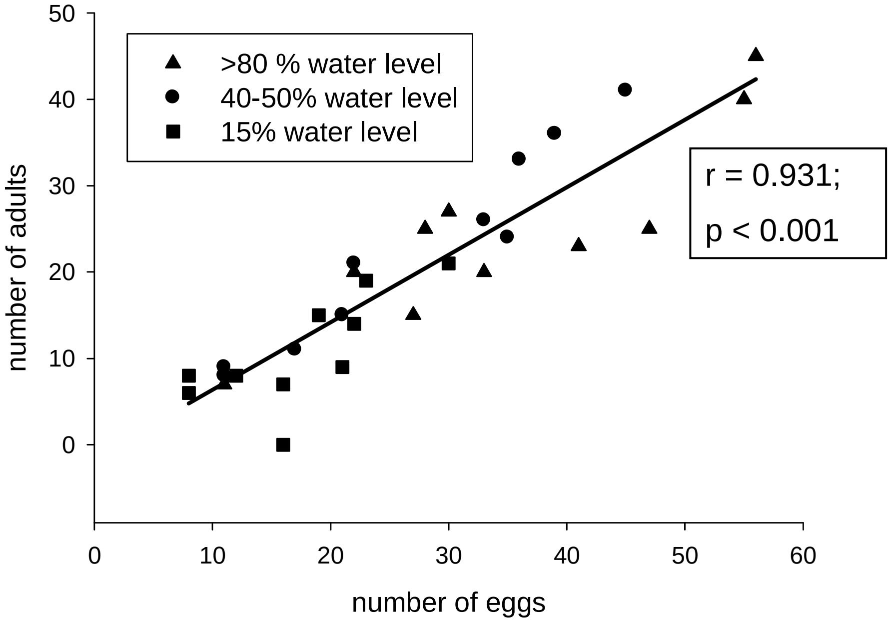

Fig. 58: Correlation between the number of eggs and the number of adults of *Aleyrodes proletella* in experiment No. 2 (colonisation took place after stressing of the plants).

10.3 List of tables

10.4 List of Figures

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12 Curriculum vitae

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*15.02. 1983

Education

4/2009 - 1/2015 **PhD thesis in Biology on the Institute of Plant Disease and Plant Protection, Leibniz Universität Hannover**
PhD thesis: Ompact of Climate Change on vegetable pest insects - *Aleyrodes proletella* as a model organism

10/2002 - 6/2008 **Diploma studies (equivalent to Master degree) in Biology at the University of Marburg**
Final mark: 1.1
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Diploma thesis: Plant genotopic effects on insect herbivory in poplar
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8/1993 - 6/2002 **Abitur at Städtisches Gymnasium Barntrup**
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Primary Subjects: Biology, German
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3/2008 - 6/2015	**Leasehold of a farm** cultivation of cereals, oil rape and sugar beet
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10/2005 - 4/2008	**Student assistant in the group of Prof. Brandl, Animal Ecology, University of Marburg** supervision of courses (phylogenetic systematics, ecology) supervision of bachelor students, leading of excursions (main focus: ornithology)