Lepidoptera in agricultural landscapes –
The role of field margins, the effects of agrochemicals and moth pollination services

von

Melanie Hahn

aus Landau

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Berichterstatter:

Dr. Carsten Brühl, Landau

Prof. Dr. Ralf Schulz, Landau

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You cannot get through a single day without having an impact on the world around you. What you do makes a difference, and you have to decide what difference you want to make.

Jane Goodall

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Overview

This thesis is written as a cumulative dissertation. After an introduction (chapter 1) and presentation of the objective of the dissertation (chapter 2), the subsequent chapters are based on peer-reviewed articles published in various journals (chapters 3 – 6, please see the list below). Thereafter, the main results of these publications are summarized and discussed in a broader context (chapter 7), and the conclusions as well as a short outlook are then presented (chapter 8).

Publications:

Paper 1:	**Hahn, M.**, Lenhardt, P. & Brühl, C.A. (2014): Characterization of field margins in intensified agro-ecosystems – Why narrow margins should matter in terrestrial pesticide risk assessment and management. Integrated Environmental Assessment and Management, 10(3): 456–462
Paper 2:	**Hahn, M.**, Schotthöfer, A., Schmitz, J., Franke, L.A. & Brühl, C.A. (2015): The effects of agrochemicals on Lepidoptera, with a focus on moths, and their pollination service in field margin habitats. Agriculture, Ecosystems and Environment, 207: 153–162.
Paper 3:	**Hahn, M.**, Geisthardt, M. & Brühl, C.A. (2014): Effects of herbicide-treated host plants on the development of *Mamestra brassicae* L. caterpillars. Environmental Toxicology and Chemistry, 33(11): 2633–2638
Paper 4:	**Hahn, M.** & Brühl, C.A. (submitted): The secret pollinators – Moth pollination with a focus on Europe and North America. Manuscript.

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Abstract

Modern agriculture is a dominant land use in Europe, although it has been associated with negative effects on biodiversity in agricultural landscapes. One species-rich insect group in agro-ecosystems is the Lepidoptera (moths and butterflies); however, the populations of a number of Lepidoptera species are currently declining. The aims of this thesis were to assess the amount and structure of field margins in agricultural landscapes, study the effects of realistic field margin input rates of agrochemicals (fertilizer and pesticides) on Lepidoptera, and provide information on moth pollination services.

In general, field margins are common semi-natural habitat elements in agro-ecosystems; however, data on the structure, size, and width of field margins is limited. An assessment in two German agricultural landscapes (4,000 ha each) demonstrated that many of the evaluated field margins were less than 3 m wide (Rhineland-Palatinate: 85% of margin length; Brandenburg: 45% margin length). In Germany, risk mitigation measures (such as buffer zones) to reduce pesticide inputs to terrestrial non-crop habitats do not have to be established by farmers next to narrow field margins. Thus, narrow field margins receive inputs of agrochemicals, especially via overspray and spray drift. These field margins were used as a development habitat for caterpillars, but the mean abundance of caterpillars was 35 – 60% lower compared with that in meadows. Caterpillars were sensitive to realistic field margin input rates of insecticide (pyrethroid, lambda-cyhalothrin) in a field experiment as well as in laboratory experiments. Moreover, 40% fewer *Hadena bicruris* eggs were observed on *Silene latifolia* plants treated with this insecticide compared with control plants, and the flowers of these insecticide-treated plants were less likely to be pollinated by moths. In addition, realistic field margin input rates of herbicides can also affect Lepidoptera. *Ranunculus acris* L. plants treated with sublethal rates of a sulfonylurea herbicide were used as host plants for *Mamestra brassicae* L. caterpillars, which resulted in significantly lower caterpillar weights, increased time to pupation, and increased overall development time compared with caterpillars feeding on control plants. These results might have been caused by lower nutritional value of the herbicide-treated plants or increased concentrations of secondary metabolites involved in plant defense. Fertilizer applications slightly increased the caterpillar abundance in the field experiment. However, fertilizers reduce plant diversity in the long term and thus, most likely, also reduce caterpillar diversity.

Moths such as Noctuidae and Sphingidae have been observed to act as pollinators for numerous plant species, including a number of Orchidaceae and Caryophyllaceae. Although in temperate agro-ecosystems moths are less likely to act as the main pollinators for crops, they can pollinate non-crop plants in semi-natural habitats. Currently, the role of moths as pollinators appears to be underestimated, and long-term research focusing on ecosystems is necessary to address temporal fluctuations in their abundance and community composition.

Lepidoptera represent a diverse organism group in agricultural landscapes and fulfill essential ecosystem services, such as pollination. To better protect moths and butterflies, agrochemical inputs to (narrow) field margins habitats should be reduced, for example, via risk mitigation measures and agro-environmental schemes.

Zusammenfassung

In Europa ist die moderne Landwirtschaft eine der häufigsten Formen der Landnutzung, allerdings wird sie auch mit negativen Auswirkungen auf die Biodiversität in Agrarlandschaften in Verbindung gebracht. Lepidoptera (Nacht- und Tagfalter) bilden eine artenreiche Gruppe in Agrarsystemen, doch die Populationen vieler Falterarten sind rückläufig. Zu den Zielen der vorliegenden Arbeit gehörte es, Feldsäume in Agrarlandschaften zu erfassen und zu charakterisieren, Effekte realistischer Eintragsraten von Agrarchemikalien (Dünger und Pestizide) in Feldsäumen auf Lepidoptera zu untersuchen und Informationen zu den Bestäubungsleistungen von Nachtfaltern zu sammeln.

Feldsäume sind zwar häufige semi-natürliche Habitatelemente in Agrarökosystemen, aber es gibt nur wenige Informationen über ihre Struktur, Größe und Breite. Daher wurden Feldsäume in zwei deutschen Agrarlandschaften (je 4.000 ha) erfasst und es zeigte sich, dass ein Großteil dieser Säume schmaler als 3 m war (Rheinland-Pfalz: 85% der Feldsaumlänge, Brandenburg: 45% der Feldsaumlänge). In Deutschland müssen Landwirte bei solchen schmalen Feldsäumen keine Maßnahmen zur Verminderung von Pestizideinträgen (z.B. Pufferzonen) umsetzen. Agrarchemikalien werden deshalb insbesondere durch Überspritzung und Abdrift in schmale Feldsäume eingetragen. In solchen schmalen Feldsäumen konnten zwar Raupen nachgewiesen werden, doch ihre mittlere Abundanz war um 35 – 60% niedriger als auf Vergleichsflächen (Wiesen). Im Rahmen eines Feldversuchs sowie in Laborexperimenten zeigte sich, dass Raupen sensitiv auf Insektizideinträge (Pyrethroid, Lambda-Cyhalothrin) regieren. Zudem wurden auf insektizid-behandelten *Silene latifolia* Pflanzen 40% weniger Eier von *Hadena bicruris* Faltern gefunden als auf unbehandelten Kontrollpflanzen und die Blüten der behandelten Pflanzen wurden seltener von Nachtfaltern bestäubt. Lepidoptera können neben Insektizid- auch von Herbizideinträgen beeinflussen werden. *Ranunculus acris* L. Pflanzen wurden mit subletalen Raten eines Sulfonylurea-Herbizids behandelt und dann als Futterpflanzen für *Mamestra brassicae* L. Raupen genutzt; dies führte zu signifikant geringeren Raupengewichten, einer verlängerten Zeit bis zur Verpuppung und einer verlängerten Gesamtentwicklungsdauer verglichen mit Raupen, die an Kontrollpflanzen fraßen. Ursachen hierfür waren möglicherweise ein geringerer Nährwert oder eine höhere Konzentration von Abwehrstoffen in den herbizid-behandelten Pflanzen. Düngereinträge führten zu einer geringfügigen Erhöhung der Raupenabundanz in dem Feldversuch. Langfristig reduziert Dünger jedoch die Pflanzenvielfalt und dadurch wahrscheinlich auch die Raupendiversität.

Nachtfalter wie Noctuidae und Sphingidae sind Bestäuber für zahlreiche Pflanzenarten, z.B. viele Orchidaceae und Caryophyllaceae. Obwohl sie in den Agrarökosystemen der gemäßigten Breiten wahrscheinlich keine bedeutenden Bestäuber für Kulturpflanzen sind, können Nachtfalter aber für die Bestäubung der Wildpflanzen in semi-natürlichen Habitaten von Relevanz sein. Dabei wird die Rolle der Nachtfalter als Bestäuber zurzeit vermutlich unterschätzt und es werden Langzeitstudien benötigt, um die zeitlichen Schwankungen in ihrer Abundanz und Artenzusammensetzung berücksichtigen zu können.

Lepidopteren bilden eine artenreiche Organismengruppe in Agrarlandschaften, die auch wesentliche Ökosystem-Dienstleistungen erfüllen. Um Nacht- und Tagfalter besser zu schützen, sollten Einträge von Agrarchemikalien in (schmale) Feldsaumhabitate reduziert werden, beispielsweise durch Maßnahmen zur Risikominderung von Pestiziden und Agrarumweltprogramme.

1 Introduction

1.1 Agriculture and biodiversity

In Europe, arable agriculture and grazing systems with domestic animals were developed approximately 7,000 to 10,000 years ago (Potts, 1991; Stoate *et al.*, 2001; Vos and Meekes, 1999); thus, agricultural land use has a long history. Over time, the management of agro-ecosystems was adapted to local and regional conditions, leading to a rich variety of traditional landscapes (Antrop, 2005; Berglund *et al.*, 2014; Jedicke, 1994; Meeus *et al.*, 1990; Plieninger *et al.*, 2006). Such landscapes were characterized by a mosaic of agricultural land and semi-natural structures that not only provided people with goods, such as food, fiber, and fuel (e.g., Berglund *et al.*, 2014), but also sustained a large diversity of habitats and species (e.g., Bignal and McCracken, 2000; Eriksson, 2013; Kretschmer *et al.*, 1997; Plieninger *et al.*, 2006; Potts, 1991). Currently, agriculture is a widespread form of land use, with croplands and pastures constituting approximately half of the area of EU27-states (Stoate *et al.*, 2009). Overall, agricultural landscapes harbor a significant proportion of European biodiversity (Robinson and Sutherland, 2002), including numerous endemic as well as threatened species, such as approximately 30 species listed in the Habitat Directive and approximately 40 species listed in the Birds Directive (European Environment Agency, 2010).

During the second half of the 20th century, agricultural production was characterized by increasing industrialization and intensification in a number of European regions (Robinson and Sutherland, 2002; Stoate *et al.*, 2001). The agricultural intensification has benefited from the development of new technologies and machines (e.g., tractors, harvesters) as well as from the widespread availability of agrochemicals, such as synthetic fertilizers and pesticides. This development led to changes in the structure of agricultural landscapes: for example, simplified crop rotations lowered the heterogeneity of agricultural habitats (Benton *et al.*, 2003). Furthermore, because of increased specialization in agricultural production, the number of mixed livestock and arable farms has been reduced throughout Western Europe, which has also resulted in less diverse agro-ecosystems (Robinson and Sutherland, 2002; Stoate *et al.*, 2001). In addition, field sizes have been increased at the expense of semi-natural landscape elements, such as hedgerows, to facilitate crop cultivation and increase machine operational efficiency (Burel, 1996; Stoate *et al.*, 2001) (Figure 1-1).

Figure 1-1 Example of a simplified agricultural landscape in Germany.

Farm sizes have also increased (e.g., from 36 ha (2000) to 56 ha (2010) per farm in Germany; Eurostat Statistics Explained, 2015), whereas the number of farms substantially decreased (e.g., from 904,700 farms (1975) to 285,000 farms (2013) in Germany; Statistisches Bundesamt, 2014a). Moreover, the use of synthetic fertilizers to optimize nutrient supplies for crop plants and the application of pesticides to reduce the abundance of pest organisms have altered agricultural management.

As a result of this intensification process, farmers have greatly increased their crop yields: in Britain, the average cereal yield increased from approximately 2 tons per hectare in 1945 to more than 7 tons per hectare in 2000 (Robinson and Sutherland, 2002). Similarly, the wheat yield in Germany increased from 3 tons per hectare in 1960 to 8 tons per hectare in 2013 (Statistisches Bundesamt, 2015).

However, in the course of this agricultural intensification, a number of organisms associated with farmlands and agro-ecosystems have shown declines in abundance and species richness, which have caused concerns over the effects of modern, intensified farming practices on biodiversity (e.g., Billeter *et al.*, 2008; Geiger *et al.*, 2010; Kleijn *et al.*, 2009; Krebs *et al.*, 1999; Robinson and Sutherland, 2002; Stoate *et al.*, 2001; Storkey *et al.*, 2012; Wilson *et al.*, 1999). The affected organism groups include plants (Clough *et al.*, 2014; Kleijn *et al.*, 2009; Storkey *et al.*, 2012; Wilson *et al.*, 1999), arthropods (Fox *et al.*, 2014; Hendrickx *et al.*, 2007; Heydemann and Meyer, 1983; Ollerton *et al.*, 2014; Wilson *et al.*, 1999), birds (Donald *et al.*, 2001; European Bird Census Council, 2014; Guerrero *et al.*, 2012; Krebs *et al.*, 1999; Wilson *et al.*, 1999) and mammals (Broughton *et al.*, 2014; Butet and Leroux, 2001; Gentili *et al.*, 2014; Stahlschmidt *et al.*, 2012; Wickramasinghe *et al.*, 2004; Wickramasinghe *et al.*, 2003). For example, many species in agricultural landscapes depend to a certain degree on natural and semi-natural habitats (Duelli and Obrist, 2003), and the occurrence and proximity of these landscape elements is beneficial for species richness (e.g., Hendrickx *et al.*, 2007). As described above, many semi-natural habitats have been lost because of increased land use intensity (e.g., Burel, 1996; Le Coeur *et al.*, 2002; Robinson and Sutherland, 2002), and it has been estimated that, for instance, the rate of hedgerow loss was approximately 14% in the Republic of Ireland between 1976 and 1982 (McAdam *et al.*, 1994), whereas approximately 740,000 km hedgerows were lost in France during the three decades after the 1970s (Pointereau and Bazile, 1995, cited in Le Coeur *et al.*, 2002). In addition, agrochemicals can affect various organisms within the fields (Geiger *et al.*, 2010) as well as in the remaining semi-natural habitats, such as field margins (e.g., Davis *et al.*, 1991; Schmitz *et al.*, 2014a).

Currently, the protection and preservation of biodiversity is a major political goal (e.g., Convention on Biological Diversity, Birds and Habitats Directives). Therefore, the effects of modern agriculture on biodiversity are of fundamental interest. Arthropods are of special concern because they not only represent a large proportion of species diversity (Duelli and Obrist, 2003) but also provide valuable ecosystem services, such as pollination and biological pest control (Power, 2010). Additionally, they are essential food sources for species at higher trophic levels, such as birds (Wilson *et al.*, 1999) and bats (Vaughan, 1997; Wickramasinghe *et al.*, 2004).

1.2 Field margins

1.2.1 Functions for agriculture and biodiversity

One of the most common semi-natural habitats for arthropods (and other organisms) in agricultural landscapes are field margins, which can be found at nearly all field edges (Marshall and Moonen, 2002). In certain landscapes, field margins represent the main part of the available semi-natural habitats (Marshall and Moonen, 2002). As a result of their widespread occurrence, the structure of field margins can differ between countries (e.g., Bäckman and Tiainen, 2002; Greaves and Marshall, 1987; Kühne *et al.*, 2000; Le Coeur *et al.*, 2002). In Germany, the term ***field margin*** is used for linear, semi-natural elements adjoining agricultural sites that are characterized by permanent vegetation consisting of non-crop plants (Kühne *et al.*, 2000) (Figure 1-2). The field margins can be vegetated with grasses, herbs, and shrubbery (hedgerows).

Figure 1-2 Examples of grassy field margins commonly found next to arable fields and vineyards in Rhineland Palatinate, Germany.

One reason for the permanence of field margins in agricultural landscapes over time is the important agronomic functions provided by these elements (Le Coeur *et al.*, 2002; Marshall and Moonen, 2002): For example, hedgerows were once used as natural fences to keep livestock within pastures and outside fields. Moreover, hedgerows are a source of wild fruits and wood, act as windbreaks to shelter crops, and reduce soil erosion. Grassy field margins enhance biological crop protection because they harbor predatory arthropods (Landis *et al.*, 2000; Thomas *et al.*, 1992; Welling *et al.*, 1994) and field margins vegetated with flowering plants are suitable habitats for pollinators (Bäckman and Tiainen, 2002; Ekroos *et al.*, 2008) and can improve crop pollination. Furthermore, field margins can act as buffer strips to protect ditches and streams from inputs of agrochemicals (Reichenberger *et al.*, 2007), and they offer the potential for carbon sequestration (Falloon *et al.*, 2004).

Figure 1-3 Bird’s nest at the top of a single tree on a grass margin next to vineyards.

In addition to these agronomic functions, field margins benefit agricultural landscape biodiversity because they provide a less disturbed habitat compared with agricultural sites (e.g., no ploughing) and are a source of food resources (e.g., flowering plants: Bäckman and Tiainen, 2002), nesting sites (e.g., solitary wasps: Holzschuh *et al.*, 2009; small mammals: Bence *et al.*, 1999; birds: Aebischer and Blake, 1994, see Figure 1-3), and overwintering sites (e.g., beetles and spiders: Pywell *et al.*, 2005; Thomas *et al.*, 1991). Overall, approximately 65% of the arthropod species living in an agriculturally managed landscape seem to rely on the presence of semi-natural habitats (Duelli and Obrist, 2003). A survey in three landscapes in Germany found approximately 550 arthropod species inhabiting grassy field margins (Ross-Nickoll *et al.*, 2004). The results of a literature review demonstrated that about 650 species have been observed in grassy and herbaceous field margins and more than 1,250 species have been observed in field margins vegetated with hedgerows (Hahn *et al.*, 2013) (Table 1-1).

Table 1-1 Number of observed species in grassy and herbaceous field margins and hedgerows based on ten studies (Barthel, 1997; Feber *et al.*, 1996; Lewis, 1969; Merckx *et al.*, 2010b; Molthan, 1990; Ross-Nickoll *et al.*, 2004; Stachow, 1988; Tischler, 1948; Welling *et al.*, 1994; Zwölfer *et al.*, 1984). Results are shown for the most common organism groups. Table modified from Hahn *et al.* (2013).

	grassy and herbaceous field margin	hedgerow	both habitats
Araneae	211	81	34
Coleoptera	141	261	48
Collembola	46	-	-
Diptera	103	241	22
Hemiptera	-	175	-
Hymenoptera	106	249	13
Lepidoptera	43	216	25
Neuroptera	-	10	-
Orthoptera	15	8	4
Pulmonata	-	27	-
Total	665	1,268	146

In addition to their habitat function, field margins can also act as corridors that facilitate the movement of species through agricultural landscapes and link different habitats (e.g., Holzschuh *et al.*, 2009).

Despite these agronomic and ecological functions of field margins, agricultural intensification has resulted in a loss and degradation of these habitats. For example, approximately 50% of hedgerow stock has been removed in Great Britain since 1945 (Robinson and Sutherland, 2002; see also Le Coeur *et al.*, 2002 for further examples). Moreover, because of their position next to agricultural fields, field margins can receive inputs of pesticides and fertilizers (e.g., Rautmann *et al.*, 2001; Tsiouris and Marshall, 1998).

1.2.2 Agrochemical inputs

Pesticides are used against organisms that reduce crop yields, such as by competing with crops for resources or making harvesting more difficult (weeds) and feeding on the crops (insect herbivores). The application of pesticides against weeds (herbicides), fungi (fungicides), and pest insects (insecticides) on agricultural sites is a common management practice of farmers. In Germany, the most commonly applied pesticides are herbicides (approximately 54,000 tons in 2013), followed by products acting against fungi, bacteria or viruses (approximately 28,100 tons in 2013) and insecticides (approximately 4,500 tons in 2013) (Bundesamt für Verbraucherschutz und Lebensmittelsicherheit, 2014).

In general, field margins receive inputs of pesticides especially from two pathways (Figure 1-4).

- ***Overspray:*** when farmers spray pesticides on arable fields, the spray cones of two nozzles have to overlap to ensure a full application rate (100%); however, if the last nozzle is placed at the field edge, parts of the adjoining field margin are sprayed with 50% of the in-crop application rate (Figure 1-4) which is known as overspray (Schmitz *et al.*, 2013).
- ***Spray drift:*** the movement of smaller pesticide droplets or particles through the air to areas outside the intended agricultural sites is known as spray drift, which occurs during or soon after pesticide application. The drift rates differ with crop type and distance to the crop (Ganzelmeier *et al.*, 1995; Rautmann *et al.*, 2001).

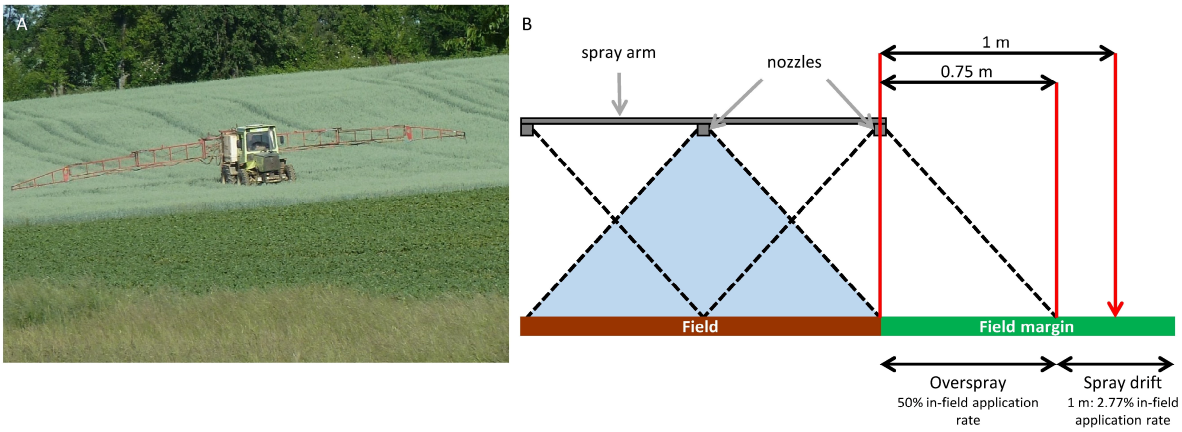

Figure 1-4 (A) Pesticide application in an arable field. (B) Example scheme of the potential pesticide inputs in arable field margins via overspray and spray drift. Figure modified from Hahn *et al.* (2013). Photo taken by C. Brühl.

To reduce the exposure of field margins to pesticides, product-specific risk mitigation measures (RMMs) may be defined during the registration of the pesticide. Such RMMs can include in-field buffer zones to adjacent non-target areas, such as field margins, and/or the usage of low-drift-nozzles during pesticide application (Bundesamt für Verbraucherschutz und Lebensmittelsicherheit, 2015). In Germany, a distinction is made between RMMs to protect aquatic habitats ("NW-Auflagen") and RMMs to protect terrestrial non-target habitats (“NT-Auflagen”) (Bundesamt für Verbraucherschutz und Lebensmittelsicherheit, 2015). However, the latter are not relevant for all terrestrial habitats. For instance, when terrestrial habitats are less than 3 m wide, they are not considered non-target areas; therefore, RMMs do not have to be applied by farmers (Bundesamt für Verbraucherschutz und Lebensmittelsicherheit, 2015; Kühne *et al.*, 2000). For this reason, the first meter of a narrow (= less than 3 m wide) cereal field margin can receive more than 30% of the in-field rate of a pesticide via spray drift and overspray (Figure 1-4) because farmers do not have to maintain a distance to the field margin during the pesticide application (Schmitz *et al.*, 2013). It was argued that such an exception was necessary because farmers would probably remove existing field margins completely otherwise and refuse to create new margins (Kühne *et al.*, 2000). Although the width of field margins is of major importance regarding the impact of pesticide inputs, there is only limited information available focusing on the amount and width of field margins in German agricultural landscapes (in particular: Kühne *et al.*, 2000).

Next to pesticides, fields are also treated with mineral fertilizers to enhance the nutritional growing conditions for the crop plants. For instance, approximately 1.6 million tons of nitrogen (N), 0.3 million tons of phosphate (P_2O_5) and 0.4 million tons of potassium oxide (K_2O) were sold in 2013 in Germany (Statistisches Bundesamt, 2014b). Depending on the application technique, one survey showed that up to 75% of the field application rate of fertilizers can be found in adjoining hedgerows (Tsiouris and Marshall, 1998).

1.2.3 Effects of agrochemical inputs in field margins

In general, pesticides and fertilizers can negatively affect the biodiversity of agro-ecosystems. For example, in agricultural landscapes, the species richness of vascular plants and birds is negatively related to fertilizer usage (Billeter *et al.*, 2008; Kleijn *et al.*, 2009), and pesticide applications reduce the diversity of wild plants and carabids in fields as well as the diversity of birds in the surrounding areas (Geiger *et al.*, 2010).

In field margins, the deposition of fertilizer and inputs of herbicides results in a decline in plant species and affects plant community composition (Kleijn and Snoeijing, 1997; Kleijn and Verbeek, 2000; Marshall and Moonen, 2002; Schmitz *et al.*, 2014a; Stoate *et al.*, 2001). Arthropods can be adversely affected by agrochemical inputs in different ways. Insecticides can directly target arthropods in field margins and cause lethal effects (e.g., caterpillars: Davis *et al.*, 1991; beneficial insects: Langhof *et al.*, 2005). Furthermore, insecticides might affect arthropods sublethally or act as a repellent and reduce oviposition on treated plant surfaces or cause antifeedant effects against larvae (e.g., Lepidoptera: Blair, 1991; Gist and Pless, 1985; Longley and Sotherton, 1997; Seljasen and Meadow, 2006). Because herbicides and fertilizers can alter the abundance and diversity of field margin vegetation, they can impact arthropods either due to changes in the availability of host plants (butterflies: Longley and

Sotherton, 1997) or due to changes in vegetation structure (e.g., spiders: Haughton *et al.*, 1999). In addition, as herbicides alter plant chemistry, they might influence the host plant quality for herbivores (Kjær and Elmegaard, 1996). Furthermore, the reduced availability of plants and arthropods might also have adverse effects on vertebrates that feed on them (e.g., birds or bats) (Figure 1-5).

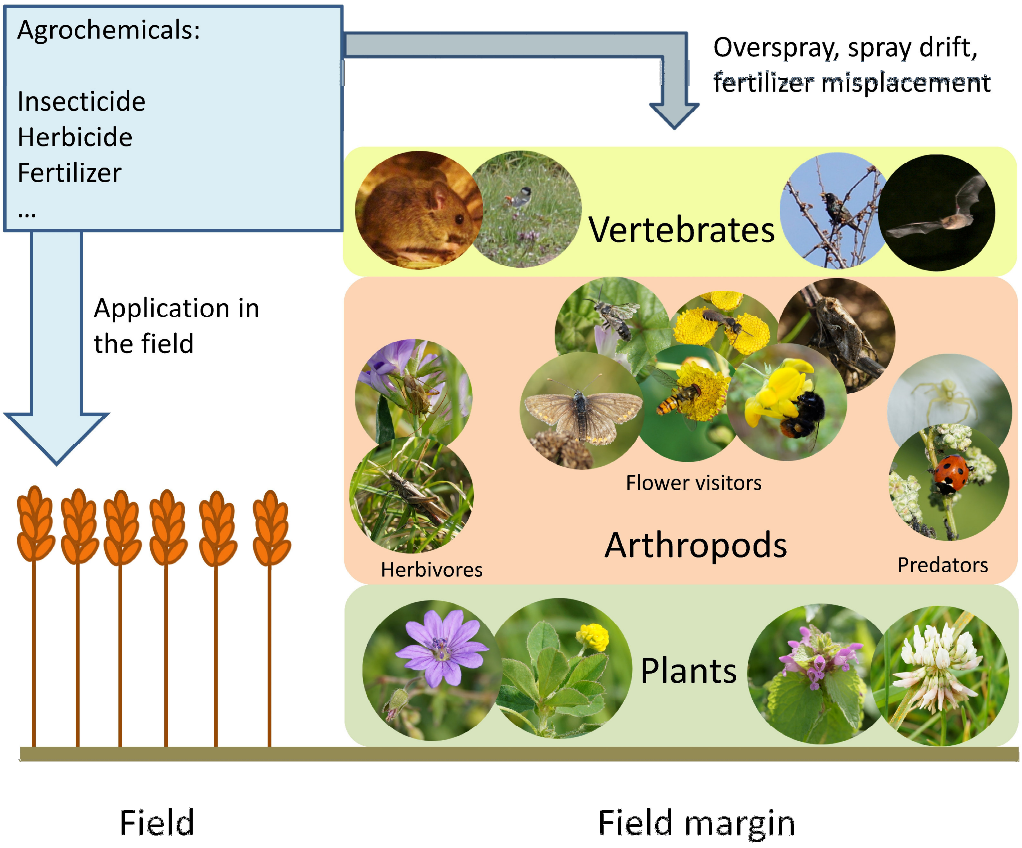

Figure 1-5 Field margins can receive inputs of agrochemicals from adjoining agricultural sites, which can influence the habitat quality of field margins and the available resources (e.g., food) for various organism groups (e.g., plants, arthropods, vertebrates). Agrochemicals might affect the organism groups directly (e.g., lethal herbicide effects on plants) or indirectly (e.g., via changes in food availability). Bat photo taken by L. Hartmann.

1.3 Non-target arthropods and pesticide risk assessment

To avoid or reduce the negative effects of pesticides on the environment, each pesticide is submitted to a registration process in which potential threats to, e.g., non-target organisms should be identified. In 2009, a new regulatory framework for the registration of pesticides was published (Regulation No. 1107/2009; European Commission, 2009), and it explicitly requires the consideration of the pesticide effects on non-target species, including behavior effects, but also their impacts on biodiversity and the ecosystem (European Commission, 2009: article 4, paragraph 3e). Therefore, new guidance documents on the terrestrial ecotoxicology have to be developed (EFSA, 2015).

The current risk assessment methodology for terrestrial non-target arthropod (NTA) species is based on the results of the ESCORT[1] 1 and ESCORT 2 workshop (Barrett *et al.*, 1994; Candolfi *et al.*, 2000), which recommended a tiered approach. This tiered approach begins with simple laboratory tests (tier 1) representing conservative (worst case) assumptions to assess the effects of pesticides on selected test species. In the case of NTAs, the parasitoid wasp *Aphidius rhopalosiphi* and the predatory mite *Typhlodromus pyri* are used as test species (Candolfi *et al.*, 2000). If these simple test systems reveal a potential risk, higher tier studies can be performed. These studies should include additional test species (e.g., the lacewing *Chrysoperla carnea* or the ladybird *Coccinella septempunctata*; Candolfi *et al.*, 2000). Furthermore, the design of these higher tier studies is often more complicated than the tier 1 tests (e.g., using natural substrates in the laboratory or conducting (semi-) field studies), but they are thus also more realistic regarding the testing conditions.

However, current risk assessments are focused on beneficial arthropods (EFSA, 2015). Therefore, all of the suggested terrestrial arthropod test species can be classified as predators or parasitoids (feeding mostly on aphids). Although predators and parasitoids are of great agronomic value because they feed on pest organisms, they represent only a fraction of the arthropod species found in agricultural landscapes and field margin habitats. Against the background of the species declines in agricultural landscapes, the current selection of test species might be not appropriate to protect biodiversity because the negative effects of pesticides on arthropods have been recognized within fields (Geiger *et al.*, 2010), in adjoining field margin habitats (e.g., Davis *et al.*, 1991, de Jong *et al.*, 2008), and in whole agricultural landscapes (Brittain *et al.*, 2010).

In a literature search on species occurring in field margins (Table 1-1), numerous arthropods could be classified as phytophagous, such as moths and butterflies (Lepidoptera; all species from Table 1-1), grasshoppers (Orthoptera; approximately 50% phytophagous species (10 species), further 35% (7 species) feed partly on plant material), and a number of bugs (Hemiptera; approximately 70% phytophagous species (120 species), further 20% (36 species) feed partly on plant material). Phytophagous arthropods are an essential element in the food webs of agricultural landscapes because they transform plant biomass and represent prey for predatory organisms. Phytophagous arthropods may be affected by pesticides via direct contact because of overspray or spray drift as well as through consumption of contaminated plant material, changes in host plant quality through previous contact with herbicides and induced plant defense (Kjær and Elmegaard, 1996), and the loss of suitable host plant species.

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[1] European standard characteristics of non-target arthropod regulatory testing

1.4 Moths in agricultural landscapes

A common phytophagous insect group in agricultural landscapes is Lepidoptera, which includes moths and butterflies. Overall, approximately 180,000 Lepidoptera species have been described worldwide (Hamm and Wittmann, 2009), and they account for approximately 10% of all known insect species (Willmer, 2011). However, although Lepidoptera belong to one of the most studied arthropod groups, the majority of Lepidoptera research has focused on diurnal butterflies (New, 2004), which represent approximately 10% of the Lepidoptera species (Shields, 1989). The remaining species are classified as moths and have predominantly crepuscular and nocturnal lifestyles. For example, of the 3,500 Lepidoptera species occurring in Germany (Karsholt and Razowski, 1996), only approximately 185 (5%) species are butterflies (Rhopalocera inclusive Hesperiidae, BfN, 1998).

Lepidoptera are holometabolous insects that undergo a complete metamorphism (e.g., Scoble, 1995), including the following stages: egg, caterpillar (larvae), pupa, and adult (Figure 1-6).

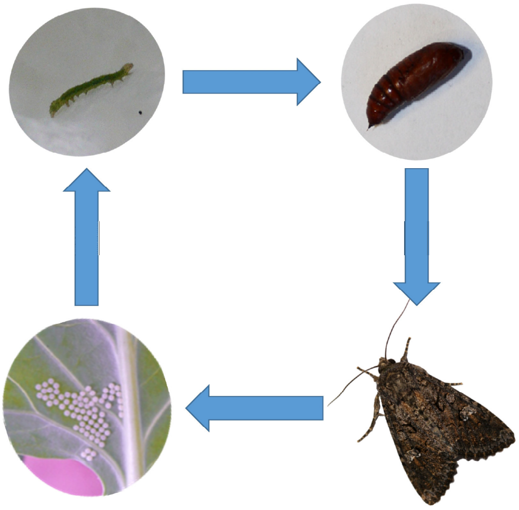

Figure 1-6 Different development stages (egg, caterpillar, pupa and adult) for the cabbage moth *Mamestra brassicae* (Noctuidae). Moth photo taken by M. Geisthardt.

In general, caterpillars are the feeding stage in Lepidoptera (Scoble, 1995), and they gather energy for their development into an adult and subsequent reproduction. The caterpillars of most species feed on plant material, such as leaves, flowers, fruits, seeds or roots. Caterpillars seem especially vulnerable to stressors in agricultural landscapes because they are immobile compared with most adult moths and dependent on the availability of suitable host plants. Thus, a loss of plant diversity or changes in plant communities most likely affect caterpillars if the host plants are involved (Longley and Sotherton, 1997). Although certain caterpillar species can feed on a variety of plant species (polyphagous species, such as *Mamestra brassicae*, Rojas *et al.*, 2000, Figure 1-6), others are specialized. For example, caterpillars of the moth species *Hadena bicruris* (Noctuidae) feed on the developing seeds of certain plant species of the genus *Silene* (Caryophyllaceae), particularly *Silene latifolia* (Bopp and Gottsberger, 2004) (Figure 1-7). Specialized Lepidoptera species can be especially vulnerable to changes in their caterpillar host plant's abundance and appear to decline more strongly compared with less specialized species (Kotiaho *et al.*, 2005).

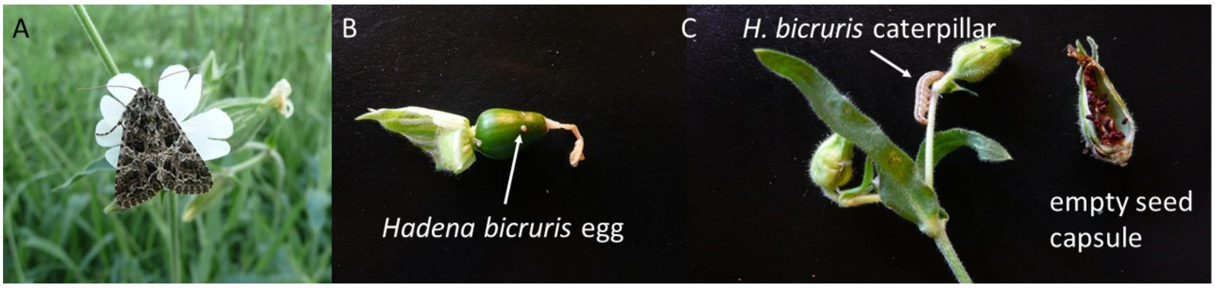

Figure 1-7 (A) Adult *Hadena bicruris* moth on *Silene latifolia* flower. (B) Egg of *H. bicruris* on a seed capsule of *S. latifolia*. (C) *H. bicruris* caterpillar searching for a new seed capsule.

Some moth species do not feed as adults as their proboscis is absent or vestigial (Scoble, 1995), and they rely completely on the resources gathered in their caterpillar stage (e.g., *Lasiocampa quercus*). However, a large number of Lepidoptera species visit flowering plants and feed on nectar (Scoble, 1995). Because of this flower visiting behavior, Lepidoptera are considered potential pollinators (Abrol, 2012; Allen-Wardell *et al.*, 1998). Declines in honey bees, which represent the most important pollinators of crops, and the potential consequences of climate change on pollination services have increased the attention to non-bee pollinators (Allen-Wardell *et al.*, 1998; Christmann and Aw-Hassan, 2012; Potts *et al.*, 2010), such as Lepidoptera. Furthermore, certain plant species are even specialized for moth pollination, including numerous plants in the genus *Silene* (Kephart *et al.*, 2006). These plant species are often characterized by nocturnal flowering times and intense flower scents (e.g., *S. latifolia*, Figure 1-7). In general, two groups of flower visiting moths can be distinguished: hawkmoths (Sphingidae) hover in front of flowers as they feed, whereas other moths often settle down (settling moths) before drinking nectar (Willmer, 2011). Nocturnal pollinator systems have been less frequently studied relative to diurnal systems, although this does not indicate that they are less important (Devoto *et al.*, 2011). Because moths are among to the most common nocturnal flower-visiting insects, their role as pollinators is of special interest (e.g.,Willmer, 2011). However, little information on moth pollination is available.

Several studies have shown strong declines in moth and butterfly populations in recent decades (Conrad *et al.*, 2004; Conrad *et al.*, 2006; van Swaay *et al.*, 2013). In addition to climate change, the effects of agricultural intensification, such as a loss of habitat and input of agrochemicals, are often discussed as causes for these declines (Fox, 2012; Fox *et al.*, 2014; van Swaay *et al.*, 2013).

Table 1-2: Factors influencing Lepidoptera based on 42 studies (for details on the studies and effects, see Appendix 10.1). +: positive factor (green), o: neutral factor (yellow), -: negative factor (red); wr: influencing factor without clear relationship (blue). Numbers in cells represent the number of studies in which the respective relationship was found, whereas letters (a-z) refer to the studies in Appendix I (chapter 10.1). Grey fields: no information regarding the factor was found in the studied literature. This table is modified from Hahn *et al*. (2013), including additional information.

Influencing factor	+	o	-	wr
Plant species richness/flower abundance	11[a]	2[b]		1[c]
Vegetation structure/height	3[d]	1[e]	1[f]	2[g]
Presence/ proportion of forests or woody habitats	1[h]			
Percentage of semi-natural habitat in agricultural landscapes	1[i]	1[j]		1[k]
Field margins/hedges	8[l]	1[m]		
"Ackerschonstreifen"/headlands	5[n]			
"Blühstreifen"/beetle banks/grass strips	3[o]	1[p]		
Agricultural intensification	1[q]	2[r]	4[s]	
Isolation/fragmentation			1[t]	
Organic agriculture	7[u]	3[v]		
Pesticides		2[w]	9[x]	
Fertilizer	3[y]		1[z]	

A literature search revealed that high plant species richness and flower abundance have a predominantly positive effect on Lepidoptera (Hahn *et al*., 2013) (Table 1-2). This result is not surprising because the majority of caterpillars and a number of adult Lepidoptera depend on the availability of plant resources. Landscape elements, such as field margins, conservation headlands and flower strips, are habitats for various plant species and also have a positive influence on Lepidoptera. This result indicates that field margins can represent a development and foraging habitat for Lepidoptera in agricultural landscapes. However, when Lepidoptera occur in field margins, they might also be affected by agrochemicals (see, e.g., Longley and Sotherton, 1997, for effects of agrochemicals on butterflies). In general, pesticides are a factor showing a mainly negative effect on Lepidoptera (Table 1-2). For example, inputs of insecticides can directly affect non-target Lepidoptera species (e.g., Cilgi and Jepson, 1995; Davis *et al*., 1991). In addition, herbicides and fertilizers can affect the plant community in field margins (Schmitz *et al*., 2014a) and may change the distribution of host and nectar plants. Moreover, caterpillars could also potentially be affected by changes in the quality of their host plants.

Because of their widespread occurrence and ecological roles (herbivores, flower visitors and pollinators, and prey organisms), moths represent a suitable organism group for studying the effects of agrochemicals on species in agro-ecosystems.

2 Thesis

2.1 Objective

This thesis focuses on the occurrence and characteristics of field margins in agricultural landscapes and their role as potential habitats for moths (Lepidoptera) with an emphasis on the possible effects of agrochemical inputs (herbicides, insecticides, and fertilizers) on caterpillars and adult moths. The effects were assessed in laboratory, semi-field, and field experiments. In addition, because moths are considered pollinators, their pollination services were evaluated in a literature search.

2.2 Thesis structure

As a first step, field margin habitats were quantified and characterized in two agriculture intensive areas in Germany. Thus, the width of field margins was of particular interest because little data are available on field margin widths in Germany, and the width of field margins is responsible for the amount of agrochemical inputs to these habitats.

Paper 1: Hahn, M., Lenhardt, P. & Brühl, C.A. (2014): Characterization of field margins in intensified agro-ecosystems – Why narrow margins should matter in terrestrial pesticide risk assessment and management. Integrated Environmental Assessment and Management, 10(3): 456–462.

Subsequently, the occurrence of caterpillars in small field margins and the effects of different agrochemicals on caterpillars and adult Lepidoptera were studied in various experiments. These studies analyzed the direct toxic effects, sublethal effects, repellent effects, and host plant quality effects.

Paper 2: Hahn, M., Schotthöfer, A., Schmitz, J., Franke, L.A. & Brühl, C.A. (2015): The effects of agrochemicals on Lepidoptera, with a focus on moths, and their pollination service in field margin habitats. Agriculture, Ecosystems and Environment, 207: 153–162.

Paper 3: Hahn, M., Geisthardt, M. & Brühl, C.A. (2014): Effects of herbicide-treated host plants on the development of *Mamestra brassicae* L. caterpillars. Environmental Toxicology and Chemistry, 33(11): 2633–2638.

Pollination is a crucial ecosystem service in natural habitats and in agro-ecosystems. Because moths are considered potential pollinators, information on their pollination service has been summarized according to a literature search.

Paper 4: Hahn, M. & Brühl, C.A. (submitted): The secret pollinators – Moth pollination with a focus on Europe and North America. Manuscript.

3 Characterization of field margins in intensified agro-ecosystems – Why narrow margins should matter in terrestrial pesticide risk assessment and management

Paper 1

This chapter presents the author’s final version of the article

Hahn, M., Lenhardt, P. & Brühl, C.A. (2014): Characterization of field margins in intensified agro-ecosystems – Why narrow margins should matter in terrestrial pesticide risk assessment and management. Integrated Environmental Assessment and Management, 10(3): 456–462

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Abstract – Field margins are important semi-natural habitats in agro-ecosystems, but they can be negatively affected by pesticide inputs via direct overspray and spray drift. In Germany, risk mitigation measures (like buffer zones) to reduce pesticide inputs in terrestrial noncrop habitats do not have to be put in place by farmers next to narrow field margins (<3 m width). Because data on structure, size, and width of field margins are scarce, we identified field margins in 2 German agricultural landscapes (Rhineland-Palatinate [RLP], Brandenburg [BB]; 4000 ha each) using digital orthophotos and geographical information systems. In RLP, most of the field margins were less than 3 m wide (85% of margin length and 65% of the margin area), whereas in BB narrow field margins account for 45% of the margin length and 17% of the margin area. Hedgerows were only occasionally recorded. Hence, narrow grassy field margins can represent a large part of the available seminatural habitats adjoining agricultural sites and potentially act as corridors between further habitat patches. For this reason, these margins should be protected from pesticide inputs, at least in landscapes under intensive agricultural use. Field margins are also the main, so-called non-target habitat protected by the terrestrial risk assessment for plants and arthropods. With many (narrow) margins not considered relevant for risk management, the current practice for protecting the biodiversity from negative effects of pesticides seems questionable. More data on field margin constitution in Germany and other European countries is necessary to critically assess the current practice of pesticide risk assessment and management on a larger scale.

3.1 Introduction

Agriculture is a leading land use in Europe covering almost 50% of the total European Union (EU) 27 land area (Stoate *et al.*, 2009). Next to their value for agricultural production, agro-ecosystems also harbor a significant proportion of European biodiversity (Robinson and Sutherland, 2002). Thereby, many species rely on the availability of semi-natural landscape elements (Duelli and Obrist, 2003). These landscape elements also include field margins that are terrestrial habitats occurring in some form at all field edges and can constitute the majority of semi-natural habitats in some landscapes (Marshall and Moonen, 2002). However, despite their widespread existence, the exact definition of field margins varies between different countries and authors (Kühne and Freier, 2001; Marshall and Moonen, 2002). Greaves and Marshall (1987) described the principal components of a field margin as field boundary, boundary strip, and crop (edge). The field boundary was defined as "barrier such as hedge, fence or wall, the hedge bank if present with its herbaceous vegetation, and any associated water course such as ditch or drain" (Greaves and Marshall, 1987). In Germany, field margins often differ from this definition because they consist only of a grassy strip between the agricultural site and a road (Figure 3-1). Hence, in the present study, the term field margin refers to linear, permanent vegetation strips of grassy, herbaceous, and/or woody off-field habitats directly adjacent to agricultural fields (Kühne and Freier, 2001; Schmitz *et al.*, 2013). This definition includes structures like permanent grass strips as well as hedgerows.

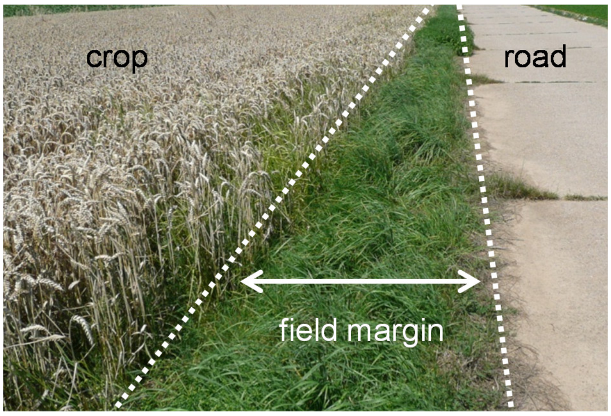

Figure 3-1 Exemplary field margin between a cereal field and a road.

The origins of field margins are diverse; hedgerows can be planted and are thus man-made elements, or they can develop spontaneously, or they can be relicts of ancient woodlands (Burel, 1996). Field margins exist in agro-ecosystems because they fulfill different functions (or fulfilled them in the past). For instance, they can provide agronomic benefits such as hedgerows acting as windbreaks and protecting adjacent crops (Marshall and Moonen, 2002). Moreover, numerous studies have shown that field margins are habitats for a wide range of plant and animal species (Kühne *et al.*, 2000; Pollard and Holland, 2006; Ross-Nickoll *et al.*, 2004), and therefore, these elements benefit biodiversity. Furthermore, these elements can also link other semi-natural habitats to form a corridor network (Holzschuh *et al.*, 2009; Le Coeur *et al.*, 2002).

However, because of increased mechanization in agricultural management, field sizes have been increased in the past decades (Robinson and Sutherland, 2002), and many field margins were removed or reduced in their size.

In addition, the quality of the remaining field margins can be affected by agricultural intensification. When field margins are exposed to inputs of pesticides applied at the adjoining field, these inputs can be detrimental to the inhabiting plant and animal species (Gove *et al.*, 2007; Longley and Sotherton, 1997; Schmitz *et al.*, 2013). To prevent or reduce negative effects of pesticides, product-specific risk mitigation measures (RMM) can be defined during the registration of the pesticide. RMM comprise for example in-field buffer zones to adjacent non-target areas like ditches, field margins, and/or the usage of low-drift-nozzles during the pesticide application (BVL, 2013). In Germany, risks are differentiated between RMM to protect aquatic habitats ("NW-Auflagen") and those to protect terrestrial non-target habitats ("NT-Auflagen") (BVL, 2013). However, the RMM are not relevant for all terrestrial habitats. For instance, terrestrial habitats less than 3 m wide are not considered as non-target areas, and hence, RMM do not have to be applied by farmers (BVL, 2013; Kühne *et al.*, 2000). It was argued that, without such an exception, farmers would probably remove existing field margins completely and refuse the creation of new ones (Kühne *et al.*, 2000). Because field margins smaller than 3 m width are not regarded as non-target areas in Germany, farmers do not have to keep a distance during the application and field margins can receive pesticide inputs via spray drift (see Table 3-1) and via overspray (Schmitz *et al.*, 2013). The overspraying of field margins can occur because the spray cones of neighboring nozzles on a spray arm have to overlap to apply the full 100% field rate of the pesticide. As the last nozzle of the spray arm is placed over the field edge during the application, not only the field but also the parts of the field margins receive an overspray (for details and a schema see Schmitz *et al.*, 2013).

Table 3-1 Selected basic drift values for a single application regarding the ground sediment (% of the application rate [90th percentiles]) calculated by Rautmann *et al.* (2001).

	Spray drift [%]		
Distance to field [m]	Field crops	Fruit crops (early)	Fruit crops (late)
1	2.77	No data	No data
3	0.95	29.20	8.02
5	0.57	19.89	3.62
10	0.29	11.81	1.23

Quantitative data on the structure, size, and especially the width of field margins are scarce (see van der Zanden *et al.*, 2013, for an example of modeling linear elements in the large scale). However, these data are important because they can be used to make judgments on the likely exposure of margins to, for example, pesticide drift and consequent impact on population persistence. Hence, the aim of the present study was to identify field margins in intensified agricultural landscapes and to characterize them concerning their width, the adjoining crops, and the presence of woody structures like hedgerows. The assessment was based on colored digital high resolution orthophotos.

3.2 Methods

Study regions

Field margins were assessed in 2 regions in Germany: one in the southern part of Rhineland Palatinate (RLP) and one in the eastern part of Brandenburg (BB) (Figure 3-2). Both regions are under intensive agricultural use. In the study area of RLP, different crops are cultivated with a dominance of vineyards and arable fields with rather small-sized acreages (Figure 3-2). In contrast, in BB only arable fields can be found and field size is considerably larger compared to RLP (Figure 3-2).

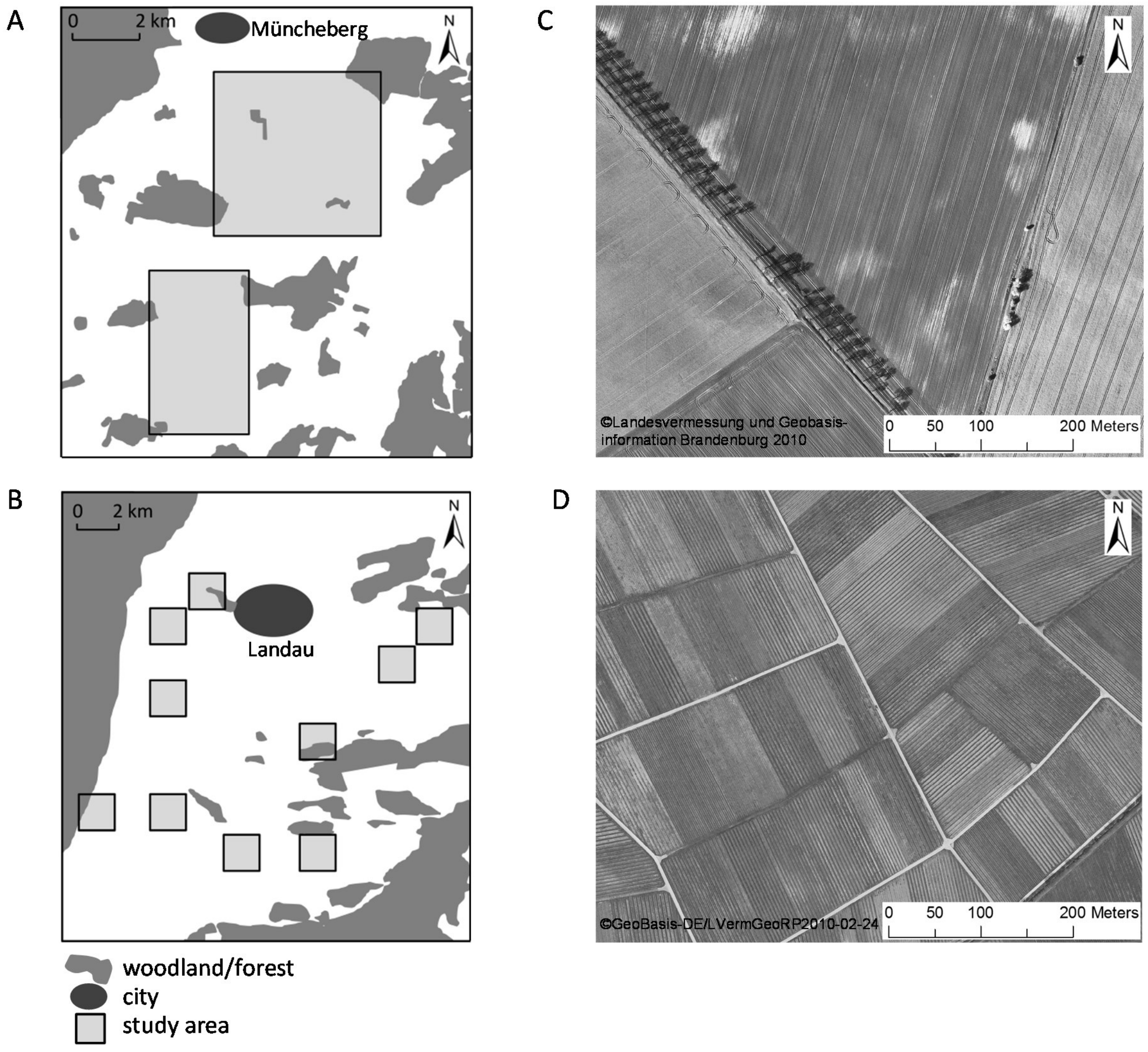

Figure 3-2 Simplified schematic of the studied landscapes in (A) Brandenburg and (B) Rhineland-Palatinate. The study areas chosen for the field margin characterization are sketched (overall 4000 ha per landscape). Exemplary sections are presented for the study regions Brandenburg (C) and Rhineland-Palatinate (D).

The present analysis is based on colored digital orthophotos (DOP) of the study areas with a resolution of 20 cm. The DOPs were generated in 2008/2009 for RLP and 2010 for BB and delivered by the German providers "Landesamt für Vermessung und Geobasisinformation Rheinland-Pfalz" (http://www.lvermgeo.rlp.de) and “Landesvermessung und Geobasisinformation Brandenburg” (http://www.geobasis-bb.de).

In RLP, 149 DOPs each covering 400 ha were available (59 600 ha). We decided to digitize field margins manually because an automatic detection, e.g., via a pixel-based classification approach, seemed to be too inaccurate (Cleve *et al.*, 2008) for a detailed assessment of narrow field margins. However, manual digitizing is rather time consuming and, therefore, a complete processing of all DOPs was not possible. Thus, a subgroup consisting of 10 DOPs (4000 ha, Figure 3-2) was randomly chosen for a detailed assessment of all field margins. As the agricultural landscape in RLP is small scaled, each DOP in RLP showed numerous field margins. In BB, agricultural sites were larger and a smaller amount of field margins per area occurred. In an area which was known from previous studies to be under intensive agricultural use (unpublished data), 2 larger survey sites were chosen, covering 2500 and 1500 ha, to represent this agricultural landscape (Figure 3-2). In both regions, 4000 ha of predominantly agricultural landscape were analyzed.

Because in RLP different crop types are cultivated in the study area (vineyards, arable crops, orchards), it was possible to compare characteristics of field margins next to these crop types in addition to the assessment of the overall availability of field margins. Vineyard and arable fields were represented well (ca. 30% and 50%, respectively) in the survey of 4000 ha. However, because orchards were found only in low densities and to improve database, the survey area for orchards was extended to all 149 DOPs available, covering an area of 59 600 ha.

Digitizing

Structures were defined as field margins if they were located at the edge of agricultural fields, had a (predominantly) linear shape, and were naturally vegetated and not planted with crops (on DOPs, sown crops appeared in different colors and as more homogeneous structures than naturally vegetated strips). The field margins were digitized using the geographical information system (GIS) software ArcGIS 9 (version: 9.3.1, Esri) and Quantum GIS 1.4.0 Enceladus (Quantum GIS Development Team).

By the use of GIS, it is not possible to compute length or width information based on polygons, and hence, this information had to be calculated in further steps. Length was determined by including lines running at the edge of fields and field margin (Figure 3-3). These lines were traced by the inner side of the field margin polygons and were the origin of multiple ring buffers generated by ArcGIS, which contained width information. The multiple ring buffers were established using the following distances: <1 m, 1 to 2 m, 2 to 3 m, 3 to 4 m, 4 to 5 m, 5 to 6 m, 6 to 8 m, 8 to 10 m, and >10 m. Later on, field margins were classified in these width categories. Therefore, each digitized margin section ended as soon as the margins' width crossed a buffer line, or in other words, as soon as a field margin section became broader or narrower than its current width class. In the 4000 ha study areas, off-crop structures wider than 10 m occurred at 8% (RLP) and 12% (BB) of the assessed field margin length and these wider structures could often be attributed to meadows. Meadows are managed in a different way than field margins (e.g., fertilizing) and, hence, it was decided to not include structures wider than 10 m in these analyses. When an agricultural site adjoined to an unpaved and vegetated dirt road, field margins included the strip between the field and the tracks of the tractor and/or car wheels. However, if such tracks were not clearly recognizable on the DOP, the whole vegetation strip was treated as field margin.

For the characterization of the digitized field margins an attribute table was used, in which information about adjoining crops (vineyard, arable crop, orchard) and the occurrence of hedgerows (definition: at least 3 shrubs and/or trees with touching branches) was noted for each field margin section. As soon as one or both of these attributes changed, a new field margin polygon was started (Figure 3-3).

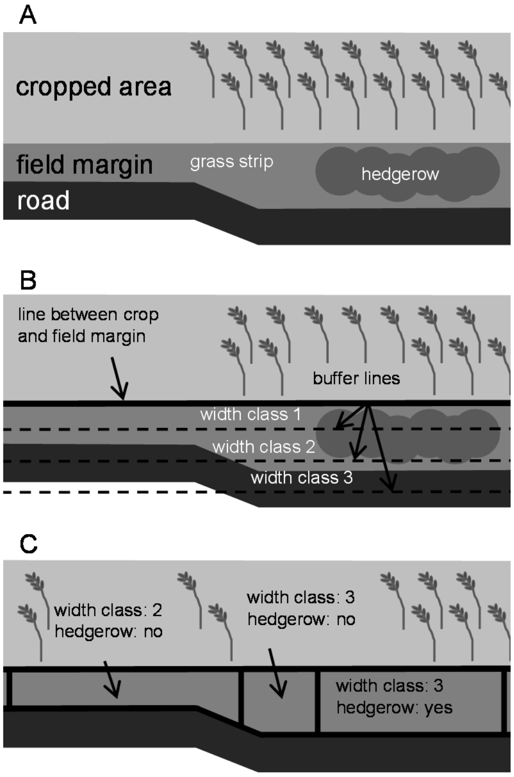

Figure 3-3 Schematic illustration of the digitizing method. (A) A hypothetic field margin consisting of 2 vegetation types, grassy parts and hedgerows, is shown. Information on field margin length is provided by a line between crop and field margin, whereas the width of the field margin is assessed using multiple buffer lines which represented different width classes (B). When the field margin characteristics concerning the width class or the vegetation type (or the adjoining crop type, not shown in the figure) change, a new field margin polygon has to be created (C).

3.3 Results

Field margins in RLP and BB

In the study region in RLP, approximately 477 km (119 m/ha) of field margins with a field margin area of 91 ha (226 m²/ha) were recorded (Figure 3-4A). Field margins smaller than 3 m width comprised approximately 85% (102 m/ha) of margin length and 65% (145 m²/ha) of the margin area (Figure 3-4A). Thereby, especially field margins with a width of 1 to 2 m were responsible for a great amount of total length (60 m/ha) and area (84 m²/ha). Field margins with a width between 3 and 10 m were rather scarce. Woody structures were only occasionally present (overall 8.3 km or 2.1 m/ha) and occurred almost exclusively on field margins wider than 3 m (Figure 3-4C).

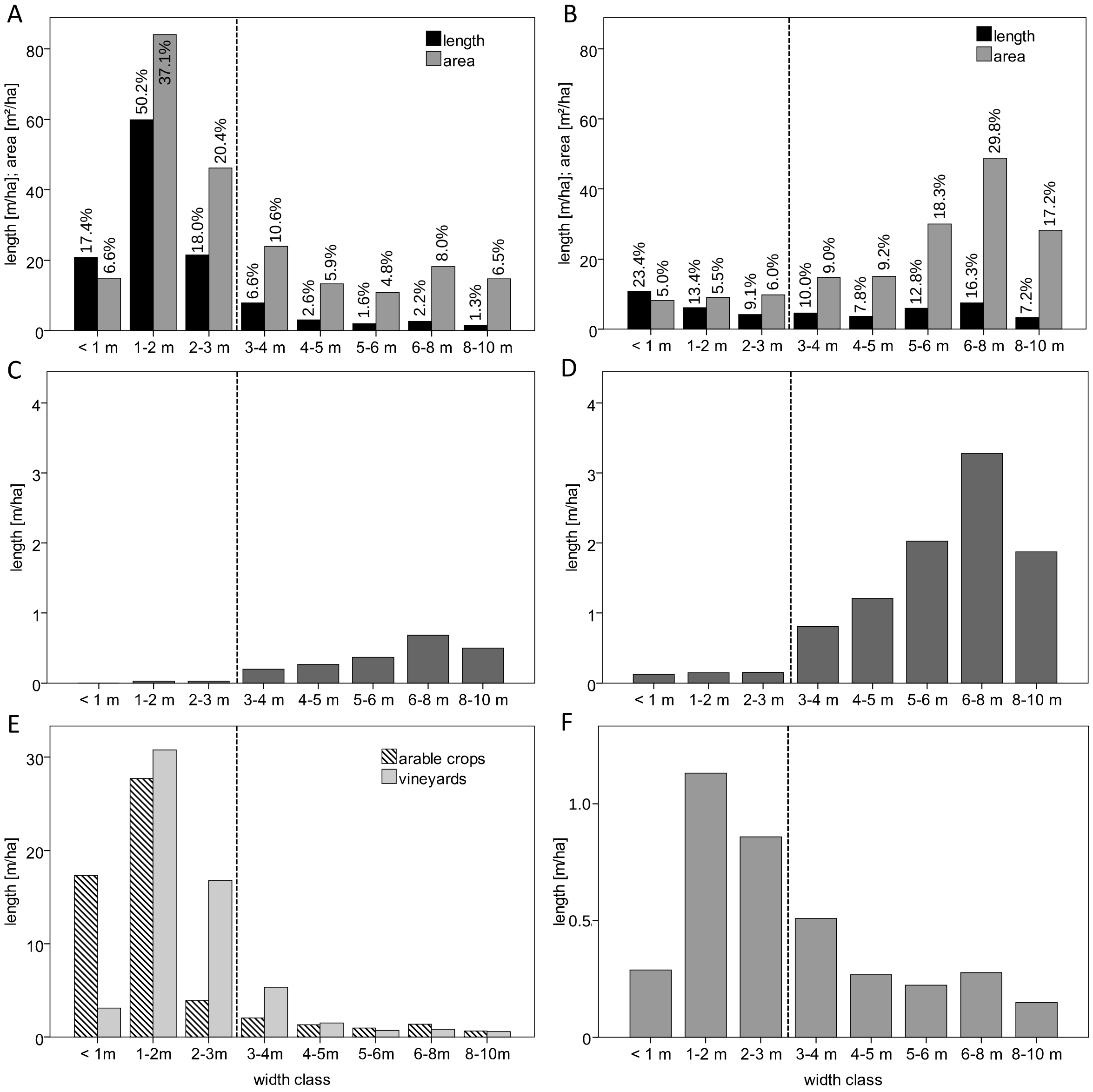

Figure 3-4 Results of the field margin assessments: 1) overall field margin length ([m/ha] and [%]) and area ([m²/ha] and [%]) per width class in the 2 study regions (A) Rhineland-Palatinate RLP and (B) Brandenburg BB; 2) length of hedgerows per width class in (C) RLP and (D) BB; 3) field margin widths of different crop types in RLP with (E) showing field margins next to arable crops and vineyards and (F) showing orchard field margins. (A–E) Based on assessments of 4000 ha agricultural landscape per study region, (F) extended data set for an area of 59 600 ha in RLP. Information for small (<3 m) and wide (≥3 m) field margins is separated by dotted lines.

In the study region in BB, field margin length and area was reduced (187 km or 47 m/ha; 65 ha or 163 m²/ha) in comparison to RLP. Field margin length was almost evenly distributed across all width classes (Figure 3-4B) with 45% of the length belonging to field margins smaller 3 m. With regard to the field margin area, the highest amount (83%) could be attributed to the wider margins (3–10 m). As in RLP, in BB woody structures were predominantly found on margins wider than 3 m (Figure 3-4D). The amount of these structures was 5 times higher than in RLP (nearly 40 km or 10 m/ha).

Comparison of different crops in RLP

Concerning the crop type, the studied field margins in RLP showed a different distribution of the width classes (Figure 3-4E and Figure 3-4F). Arable field margins were mostly smaller than 2 m, whereas vineyards were predominantly 1 to 3 m wide. Orchards represent a minor land use type compared with arable fields and vineyards in RLP. The identified orchard field margins were mostly between 1 to 4 m wide.

3.4 Discussion

There were considerable differences in the overall amount of field margins available in both study regions. The spatial distribution of linear landscape elements like grassy margins has been found to be rather heterogeneous in Europe (van der Zanden *et al.*, 2013). For this reason, the study areas in RLP and BB might be not representative for Germany as whole country but instead exemplify the situation in regions with intensive agricultural use. An enlargement of the study area to more than 4000 ha might improve the results of the field margin characterization, as a greater amount of field margins could be assessed. Because both study regions were located in intensively used and rather homogeneous agricultural landscapes, the study areas covered numerous field margins and were assumed to be representative for the chosen landscapes. Nonetheless, in more complex landscapes, an extension of the study areas might be reasonable. However, as manual digitizing of field margins is time-consuming, costs and benefits of enlarged study areas should be considered.

In RLP, the length of the field margins was more than twice the value of BB. This can be attributed to the varying field sizes in these regions because field margins were associated with the amount of field edges (Figure 3-2). However, field margins with a width of less than 3 m were common landscape features in both study regions. With 85% and 45% of the field margin length, these narrow features represent a large share of the field margins available in RLP and BB, respectively. In contrast to BB, where narrow field margins were of minor significance concerning the field margin area (17%), in RLP narrow margins form a major part of the field margin area with field margins between 1 and 3 m width accounting for nearly 60% of the area.

It is known that even narrow grass strips promote the occurrence of arthropod predators like carabids, staphylinids, or spiders by serving as overwintering habitat (Thomas *et al.*, 1991). Furthermore, narrow field margins are habitats for phytophagous arthropods like butterflies (Feber *et al.*, 1996; Field *et al.*, 2007) and grasshoppers (Bundschuh *et al.*, 2012). However, because of their width below 3 m these margins are not protected from pesticide inputs by German law, and hence, a large part of the non-crop habitat next to agricultural sites can be exposed to pesticides. Herbicide inputs, for example, can negatively affect exposed plant species via increased mortality, reduced biomass, or suppressed flowering (Gove *et al.*, 2007; Schmitz *et al.*, 2013). Next to the plants, this can have an effect on further organism groups like herbivores and pollinators. Butterflies, for instance, rely on host plants in their larval stage and nectar plants in their adult stage. Spraying field margins with herbicides have been observed to lead to declines in butterfly abundance (Feber *et al.*, 1996). In addition, insecticides can reduce the survival of caterpillars and can also affect them sublethally (Longley and Sotherton, 1997, and references therein).

Species richness (Link and Harrach, 1998; Ma *et al.*, 2002) and density (Bäckman and Tiainen, 2002) of organisms rise with increasing field margin width. Furthermore, it has been shown that sown strips can increase the plant diversity in adjoining field boundaries (Marshall *et al.*, 2006). One possible explanation for these observations is that disturbances via agricultural management, like inputs of fertilizers or pesticides, are reduced with increasing width and distance to the crop, respectively. For example, pesticide inputs of spray drift decrease with increasing distance to the field edge (Rautmann *et al.*, 2001) (Table 3-1). However, the width of field margins is not the only crucial factor affecting the received pesticide input. The crops cultivated on adjoining agricultural sites may also impact species occurrence in field margins because of different intensity of pesticide usage, as well as different application techniques in various crops. In a study regarding the occurrence of grasshoppers in field margins of varying width and next to different crops, it could be shown that field margins next to orchards were rarely used as habitats compared to arable fields or vineyards – even in 20 m wide field margins (Bundschuh *et al.*, 2012). A possible reason for this is that more pesticides are used in orchards and due to the application technique, in which the pesticide spray is blown upward to reach the upper parts of the trees, a high amount of pesticides reaches the field margins even in greater distances (Rautmann *et al.*, 2001). Next to arable fields, the field margins tend to be smaller than next to vineyards or orchards (Figure 3-4E and Figure 3-4F). The pesticide input via spray drift in field margins next to arable fields is lower compared to both other crops (vineyards and orchards) as a result of a downward directed pesticide application (Rautmann *et al.*, 2001). However, narrow arable field margins can receive high pesticide inputs via overspray. In combination with spray drift, 1 m wide cereal field margins can receive nearly 40% of the applied in-field pesticide input (Schmitz *et al.*, 2013). In RLP, more than 80% of the arable field margins were less than 2 m wide and are therefore exposed to high pesticide inputs.

Although narrow field margins are almost exclusively vegetated with grasses and herbs, wider field margins can be also grown with woody structures (Figure 3-4C and Figure 3-4D). In both study regions, the occurrence of such woody elements is rather low, especially in RLP with approximately 2 m/ha. Such landscape elements can benefit the biodiversity of agricultural habitats in various ways. Pollard and Holland (2006) describe hedgerows as one of the most important non-crop habitats for arthropods on farmland. Furthermore, they provide food sources, shelter, and nesting sites for birds (Hinsley and Bellamy, 2000) and act as landmarks and sheltered commuting roads for bats (Boughey *et al.*, 2011).

Field margins are assumed to act as corridors for species movements (Grashof-Bokdam and van Langevelde, 2005) and, hence, link other (non-linear) semi-natural habitats and might be crucial for populations to maintain a high genetic diversity. Especially in the small-scaled agricultural landscape in

RLP, grassy field margins form a dense network in the landscape and might provide suitable corridors for a range of species. As it has been shown for wasps, even narrow grassy field margins can benefit the movement of individuals (Holzschuh *et al.*, 2009). Next to wasps, butterflies also use corridors for their movements (Dover and Settele, 2009), and grassy strips can enhance the butterfly dispersal (Delattre *et al.*, 2013).

3.5 Conclusion

Our analysis demonstrated that narrow field margins (<3 m width) were dominant landscape elements in the studied agro-ecosystem in RLP, whereas wider field margins, that represent the non-target habitat for terrestrial risk assessment and the following RMM, were comparatively rare. This situation might be similar in further areas under intensive agricultural use in Germany and other EU countries and should be evaluated further.

The current risk assessment for plants defines a non-target plant as one that grows in the terrestrial non-target habitat (EC, 2002). With many field margins in our study regions (especially in RLP) not fulfilling the criteria as non-target habitat in Germany (<3 m wide), the plant community in these field margins is not protected from negative pesticide effects. The same is true for arthropods (insects and spiders), where the so called "off-field habitat" is represented by the non-target terrestrial habitat. Although studies indicate a lower species richness and density of organisms in narrow compared to wide margins (Bäckman and Tiainen, 2002; Link and Harrach, 1998), narrow elements can fulfill crucial habitat and corridor functions in intensively used agricultural landscapes nonetheless because of their widespread occurrence and the lack of other, high quality habitats. To enhance biodiversity in agro-ecosystems, narrow habitats should be protected from pesticide inputs, at least in intensified systems, because these landscape elements can represent, as shown in this study, the majority of the remaining semi-natural habitats. Furthermore, the proximity of crops and their pesticide use pattern should be taken into account when studying plant and animal communities in field margins in agricultural landscapes.

However, the aim of the present study was to quantify and characterize field margins especially concerning their width because RMM for pesticides depend on the field margin width in Germany. Nonetheless, other agricultural management operations, like the application of fertilizer and the mowing regime, affect the plant and insect communities of field margins as well (Feber *et al.*, 1996; Kleijn and Verbeek, 2000). To improve the quality of (narrow) field margins in intensively used agricultural landscapes, these factors should also be taken into account.

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4 The effects of agrochemicals on Lepidoptera, with a focus on moths, and their pollination service in field margin habitats

Paper 2

This chapter presents the author’s final version of the article

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Abstract – In agricultural landscapes, field margins are potential habitats for moths and butterflies (Lepidoptera). However, because of their proximity to agricultural sites, field margins can be affected by inputs of pesticides and fertilizers. In the present study, we assessed the use of field margins by caterpillars as habitat. Furthermore, the effects of realistic field margin input rates of various agrochemicals on moths, especially on their caterpillar stages, were studied in field, semi-field, and laboratory experiments. Our monitoring results indicate that, although caterpillars were found in field margins, their mean abundance was 35–60% lower compared to meadows. In a field experiment, the insecticide treatment (pyrethroid, lambda-cyhalothrin) significantly reduced the number of caterpillars and only 15% of the sampled caterpillars occurred in the insecticide-treated plots. Furthermore, the insecticide affected the community composition of the caterpillars, whereas the fertilizer treatment slightly increased the caterpillar abundance. In laboratory experiments, *Mamestra brassicae* caterpillars were shown to be very sensitive when exposed to insecticide-treated leaves (rate that kills 50% of the test caterpillars (LR50) after 48 h: 0.78% of the recommended field rate; this rate corresponds to the arable spray drift input in field margins at a distance of 3–4 m from the crop), and the caterpillars also appeared to avoid feeding on the treated leaves. In addition, in a semi-field study, 40% fewer eggs of *Hadena bicruris* moths were found on *Silene latifolia* plants sprayed with the insecticide compared to control plants and the flowers of insecticide-treated plants were less likely to be pollinated by moths. Overall, these studies illustrate that moths use field margins as habitats and that they can be affected by realistic input rates of agrochemicals. As caterpillars are important prey organisms and adult moths can act as pollinators, inputs of agrochemicals in field margins should be reduced to maintain biodiversity in agricultural landscapes.

4.1 Introduction

Agriculture is the most common form of land use in Europe (Stoate *et al.*, 2009). As a result, a large portion of European biodiversity can now be found in agricultural landscapes (Robinson and Sutherland, 2002). Modern agricultural landscapes are often subject to intensified use, which is characterized by, for example, increased field sizes, decreased crop diversity, a reduced availability of semi-natural habitats, and high inputs of agrochemicals (pesticides and fertilizers) in fields (Stoate *et al.*, 2001; Robinson and Sutherland, 2002). This intensified management of agricultural sites has negative effects on biodiversity, such as plants, birds, and invertebrates (Wilson *et al.*, 1999; Stoate *et al.*, 2001). The loss and degradation of semi-natural habitats in agricultural landscapes and the intensification of agricultural management are thought to be major reasons for declines in the abundances of moths (Fox, 2012). For instance, agricultural intensification has been shown to decrease species richness of moths and abundance of nationally declining moth species in the UK (Merckx *et al*., 2012).

Moths and butterflies belong to the Lepidoptera, a species-rich insect order. Although a large portion of research on Lepidoptera has focused on butterflies (New, 2004), the majority of Lepidoptera (approximately 90%; Shields, 1989) are classified as moths. Field margins are common semi-natural habitats (Marshall and Moonen, 2002) that are often vegetated with grasses and herbs. Because the large majority of caterpillars are herbivores, and a majority of adult moths (and butterflies) visit flowering plants, field margins are a potential habitat for Lepidoptera, especially in agriculture-intensive regions in which these elements represent a majority of semi-natural habitats (Hahn *et al.*, 2014b). Adult moths have been found to benefit from extended-width field margins in terms of the overall species richness (Merckx *et al*., 2012) and the abundance of certain species (Merckx *et al.*, 2009; Merckx *et al.*, 2010), possibly because of an increased host and nectar plant availability (e.g., the results of Pywell *et al.*, 2004, for butterflies). Furthermore, field margins can increase the connectivity of ‘stepping stone’ habitats for moths (e.g., solitary trees) which may mitigate the negative consequences of habitat fragmentation (Slade *et al*., 2013). However, field margins can receive substantial inputs from agrochemicals that are applied on adjacent agricultural sites via spray drift or direct overspray (Rautmann *et al*., 2001; de Jong *et al*., 2008; Otto *et al*., 2013; Schmitz *et al.*, 2013) and that might be detrimental to Lepidoptera (Sinha *et al.*, 1990; Davis *et al.*, 1991; Cilgi and Jepson, 1995; de Jong *et al*., 2008).

Herbicides and fertilizers may influence Lepidoptera via changes in host plant abundance, diversity (Longley and Sotherton, 1997; Fox, 2012), or quality (Hahn *et al.*, 2014a). Insecticides can directly target juvenile and adult Lepidoptera and cause lethal effects (Sinha *et al.*, 1990; Davis *et al.*, 1991; Cilgi and Jepson, 1995; Abivardi *et al.*, 1998). Furthermore, insecticides can also cause sublethal effects or act as a repellent to moths. These effects include, for example, avoidance of oviposition on sprayed surfaces by the adults (Kumar and Chapman, 1984; Gist and Pless, 1985; Abivardi *et al.*, 1998; Seljasen and Meadow, 2006) or antifeedant effects against caterpillars (Kumar and Chapman, 1984).

The negative effects of agrochemicals on Lepidoptera might affect other organisms as well. For example, adults contribute to the transport of pollen as they visit flowers (Clinebell *et al.*, 2004; Alarcon *et al.*, 2008; Devoto *et al.*, 2011) and hence can provide pollination services. In addition, both caterpillars and adults are important prey for various organisms such as birds (Wilson *et al.*, 1999) and bats (Vaughan, 1997).

We hypothesized that agrochemicals, especially insecticides, affect Lepidoptera in various ways. One of the most commonly used insecticide in winter wheat in Germany (Freier *et al*., 2008) is Karate Zeon (Syngenta; active ingredient: lambda-cyhalothrin), a pyrethroid with contact, stomach action and repellent properties. We assumed that this insecticide could reduce the number of caterpillars in field margins due to toxic and antifeedant effects. Furthermore, synthetic pyrethroids have been found to act as ovipositional repellent for a moth species (Gist and Press, 1985), and we presumed that such an effect would reduce the pollination service of a specialized moth pollinator (*Hadena bicruris*) whose females pollinate *Silene latifolia* flowers during their oviposition.

To assess if field margins are used as habitats by caterpillars and to determine whether moths and their pollination services are affected by agrochemical inputs in field margins, we conducted four studies: First, we surveyed the occurrence of caterpillars in actual field margins. Second, we analyzed the effects of realistic input rates of an insecticide, an herbicide, and fertilizer in field margins on caterpillars in a field experiment. Third, we applied realistic field margin insecticide rates on host plants and assessed the survival and feeding behavior of *Mamestra brassicae* caterpillars in laboratory experiments. Fourth, we evaluated the avoidance of insecticide-treated flowers by moths regarding pollination and oviposition in a semi-field experiment.

4.2 Methods

The methods section is divided into four chapters that describe the design and statistics of each of the four experiments. The aim of the first study (Section 4.2.1) was to assess whether caterpillars use field margins as habitats. It was assumed that agrochemical inputs would have a negative effect on caterpillar abundance, and we therefore also sampled meadows for comparison that received no agrochemical inputs. The subsequent experiments focused on the effects of agrochemicals on caterpillars (Section 4.2.2, field experiment; Section 4.2.3, laboratory experiments) and adult moths (Section 4.2.4, semi-field study).

4.2.1 Caterpillars in field margins

4.2.1.1 Study design and sampling methods

Caterpillars were surveyed in cereal field margins and meadows in the area surrounding Landau, Germany, using sweep nets (300 sweeps per site and transect length of approximately 180 m) on sunny to partly cloudy days when the vegetation was dry. Overall, 14 field margins and twelve meadows were sampled for caterpillars during an initial sampling phase in May (18 – 26 May 2011). In addition, caterpillar abundances were assessed in nine cereal field margins and eleven meadows during a second sampling period in June (9 – 17 June 2011). The surveyed meadows had a size of approximately 1-1.5 hectares. The field margins were between 1-2 m wide, which is a common margin width in the study area (Hahn *et al.*, 2014b), and were vegetated with grasses and herbs. In Germany, field margins less than 3 m in width can receive high inputs of pesticides from overspray and spray drift because farmers are not forced to maintain a certain distance from such narrow elements during pesticide applications (Schmitz *et al.*, 2013; Hahn *et al.*, 2014b).

If possible, the same field margins and meadows were surveyed for caterpillars in both sampling phases (i.e., = six field margins and seven meadows). However, if a study site was mown between the first and the second sampling period and, hence, the vegetation height was inadequate (< 30-40 cm) for appropriate sampling with sweep nets, another unmown site was chosen.

The sampled caterpillars were identified at the family level (Carter and Hargreaves, 1987; Porter, 1997; Rennwald and Rodeland, 2004; Bellmann, 2009). If a clear identification of a caterpillar was not possible, it was reared to an adult state.

In addition to caterpillars, the vegetation of the sampling sites was also assessed. The details of the identified plant species are presented in the Supplemental Data (Part 1).

4.2.1.2 Statistics

Data for caterpillars in field margins and in meadows were compared for each phase using the Primer (Version 6) statistical program and the PERMANOVA+ add-on (Anderson *et al.*, 2008). We conducted permutational analyses of variance for the analysis of caterpillar abundance (PerAnova, univariate data, resemblance matrices: Euclidean distance) and the caterpillar communities at family level (PerManova, multivariate data, resemblance matrices: Bray-Curtis distance). Each analysis was based on 999 permutations.

4.2.2 Effects of agrochemicals on caterpillars in a field experiment

4.2.2.1 Study design

Caterpillars were sampled during the course of a field experiment with the aim of identifying the individual and combined effects of repeated agrochemical applications (duration of the experiment: 2010-2012) on the flora (Schmitz *et al.*, 2013; Schmitz *et al.*, 2014a; Schmitz *et al.*, 2014b) and fauna of field margins. In the experiment, 64 plots (each 8 m × 8 m) were created within an extensively managed hay meadow located near Landau, Germany. The plots were assigned to one of seven treatments (either a single application of fertilizer (F), herbicide (H), or insecticide (I), or a combination of these treatments (F+I, H+I, F+H, F+H+I)), or the control (C). Each treatment and the control were replicated eight times within a randomized block design (see Schmitz *et al.*, 2013, for more details on the experimental design).

The applications of the agrochemicals and their application sequences mimicked the field management of winter wheat fields in the study area with their recommended agrochemical products. Both chosen pesticides were among the five most commonly used pesticides in winter wheat fields in Germany at the beginning of the study (Freier *et al*., 2008). The fertilizer and pesticide application rates used for the plots corresponded to the mean input rates for the first meter of a field margin directly adjacent to a field (25% of the in-field rate for fertilizer and 30% of the in-field rate for pesticides, see Schmitz *et al.*, 2013). The application of the agrochemicals was conducted as described below in each year of the experiment (2010-2012).

Fertilizer was applied twice per year in April. At first, a granular NPK (nitrate, phosphorus, potassium) fertilizer (14% N, Floral Düngemittel, application rate: 25 kg N/ha) was applied, and approximately two weeks later a calcium carbonate and ammonium nitrate fertilizer (27% N; Raiffeisen Markt, application rate: 25 kg N/ha) was used.

As herbicide, we applied Atlantis WG (sulfonylurea; recommended field rate 400 g/ha, actual application rate 120 g/ha, active ingredients [a.i.] 30 g/kg mesosulfuron-methyl, 6 g/kg iodosulfuron-methyl-natrium, 90 g/kg mefenpyr-diethyl (Safener), mode of action: inhibitors of plant cell division [e.g., acetolactate synthase], Bayer CropScience) once a year in April.

The applied insecticide, Karate Zeon (pyrethroid: recommended field rate 75 mL/ha, actual application rate, 22.5 mL/ha, a.i. lambda-cyhalothrin 7.5 g/ha; mode of action: non-systemic insecticide with contact and stomach action, repellent properties, Syngenta), was sprayed once per year at the end of May or at the beginning of June.

The pesticides were applied using a purpose-built and air-assisted experimental field sprayer on wheels (Schachtner Gerätetechnik) equipped with an 8-m spray boom and 15 flat-fan TeeJet nozzles (XR 11002-VS; Schachtner Gerätetechnik).

4.2.2.2 Sampling of caterpillars

Caterpillars were sampled in the second year of the field experiment at the end of May (30 May 2011; six days after the insecticide application) and at the end of June (27 June 2011; 34 days after the insecticide application) using sweep nets. On the sampling dates, the sky was sunny, and the vegetation was dry. We swept 80 times per plot in May and 100 times per plot in June (overall 5,120 and 6,400 sweeps, respectively).

An overview of the plant species in each treatment (assessed in June 2011) is given in the Supplemental Data (Part 2). Furthermore, the vegetation data are presented and discussed in detail in Schmitz *et al.* (2014).

4.2.2.3 Statistics

The three-factorial design of the study allowed for the consideration of the effects of the three treatment factors (fertilizer, herbicide, and insecticide) on the caterpillars. Each factor had two levels (0: not applied; 1: applied). The effects of the factors were assessed using the Primer (Version 6) program with the PERMANOVA+ add-on (Anderson *et al.*, 2008). We analyzed the effects of fertilizer, herbicide, and insecticide on caterpillar abundance (PerAnova, univariate data, resemblance matrices: Euclidean distance, 999 permutations) and on the caterpillar community at the family level (PerManova, multivariate data, resemblance matrices: Bray Curtis distance, 999 permutations) for each sampling phase.

4.2.3 Toxic and repellent effects of insecticide-treated host plants on *Mamestra brassicae* caterpillars

4.2.3.1 Study design

The aim of these experiments was to assess the toxic and repellent effects of plant material (leaves) treated with an insecticide against caterpillars of the cabbage moth *Mamestra brassicae* L.

The English plantain, *Plantago lanceolata* L., was used as the host plant for the caterpillars. Seeds were obtained from a commercial seed supplier (Appels Wilde Samen GmbH, Darmstadt, Germany). The plants were cultivated individually in 7x7 cm pots with universal potting compost (Compo Sana Qualitäts-Blumenerde, Compo, Münster, Germany) in a climate chamber (20°C, 16/8 h light/dark cycle) for approximately ten weeks prior to the start of the experimental treatment.

Eggs of *M. brassicae* were provided by the Laboratory of Entomology, Wageningen University and Research Centre, The Netherlands. After hatching, the caterpillars were housed in plastic containers (17×12×5.5 cm; lined with a layer of paper towels to absorb moisture) at room temperature (approximately 20°C). The caterpillars were fed untreated leaves of *P. lanceolata* until they were 14 days old.

The insecticide (Karate Zeon, see Section 4.2.2) was applied by dipping the aboveground parts (leaves) of the potted plants into a beaker filled with the desired insecticide concentration for approximately ten seconds. The plants were treated with the insecticide at 4%, 2%, 1%, 0.5%, or 0.25% of the recommended field rate (= 75 ml Karate Zeon/ha, water volume 400 L/ha) for the toxicity test. To test for repellent effects on caterpillars (repellence test), we treated plants with 1% of the recommended field application rate. Control plants were dipped in water for both experiments. The plants were left to dry and subsequently stored in the climate chamber.

Toxicity test: The toxicity test was started two hours after the insecticide or water treatment of the plants (when the plant surfaces had dried). For each replicate, two fresh leaves of either a treated or a control plant and three *M. brassicae* caterpillars (14-days old) were carefully introduced into a transparent plastic container (diameter 10 cm). For each insecticide rate and the control, the test was replicated five times. The test vessels were stored in a climate chamber (20°C, 16/8 h light/dark cycle), and fresh leaves (from the treated or control test plants, respectively) were provided each day. Mortality was assessed at 24 h, 48 h, 72 h, 96 h, 120 h, and 144 h after the test was started.

Repellence test: The test of the repellence effects on the feeding of *M. brassicae* caterpillars was started two hours after the insecticide or water application to the plants. Twenty 15-day-old *M. brassicae* caterpillars were individually transferred into 20 transparent plastic containers (diameter 10 cm), each of which contained one *P. lanceolata* leaf treated with insecticide (1% of the recommended field rate) and one leaf treated with water (control). The caterpillars were able to choose the leaf on which to feed. The leaves were assessed for traces of herbivory at 24 h, 48 h, 72 h, 96 h, 120 h, and 144 h after the start of the test.

4.2.3.2 Statistics

The LR50-values (LR50: lethal rate 50, i.e., the rate that kills 50% of the individuals) at 24 h, 48 h, 72 h, 96 h, 120 h, and 144 h of exposure were calculated using the package ‘drc’ (Ritz and Streibig, 2005) in R (Version 3.1.0, R Development Core Team, 2014).

4.2.4 Effects of an insecticide on moth pollination and egg-laying behavior

4.2.4.1 Study design

We studied the indirect effects of an insecticide (Karate Zeon, see Section 4.2.2) on adult moths and the pollination services provided by these moths.

As a test plant species, we used the White Campion (*Silene latifolia* subsp. *alba* (Mill.) Greuter & Burdet). This species is commonly found in disturbed or cultivated habitats (Jürgens, 1996), including field margins. *Silene latifolia* is specialized for nocturnal moth pollination, and a main pollinator is the moth *Hadena bicruris* Hufn. (Noctuidae), whose caterpillars feed on the developing seeds (pollinating seed predator) (Kephart *et al.*, 2006). *Silene latifolia* is a dioecious plant species; hence, self-pollination cannot occur because the male and female flowers are developed on different plant individuals. The test plants were grown from seeds (provided by Appels Wilde Samen GmbH, Darmstadt, Germany) and cultivated individually in 10-cm pots containing universal potting compost (Compo Sana Qualitäts-Blumenerde, Compo, Münster, Germany), in a climate chamber (20°C, 16/8 h light/dark cycle). When the roots of the plants penetrated the pots, each plant was potted in a 2-L plant container (diameter: 16 cm) and stored outdoors until flowering started. Male and female plants were then identified.

In the pollination experiment, we used twelve female and six male *S. latifolia* plants. The female test plants were divided into two groups and sprayed either with 30% of the field application rate of the insecticide Karate Zeon (six plants, 36 unpollinated flowers) or with water (six plants, 34 unpollinated flowers) using a hand-operated sprayer (Blumensprüher OASE, EMSA, Emsdetten, Germany). After the spraying, the plants were stored indoors for approximately 60 minutes until sunset. The six male plants (each with at least 20 flowers) were used as pollen donors and remained unsprayed. The test plants were exposed to natural pollination during one night (4 – 5 September 2012) in a semi-field design (Figure 4-1). The next morning, each female flower was carefully wrapped in gauze to avoid any contact with further pollinators or seed predators. Nine days later, the seed numbers of the flowers were compared between treated and untreated plants. Furthermore, we examined the ovaries of the flowers to search for eggs or caterpillars of the specialized moth pollinator (*H. bicruris*) to assess if the flowers had been used for oviposition.

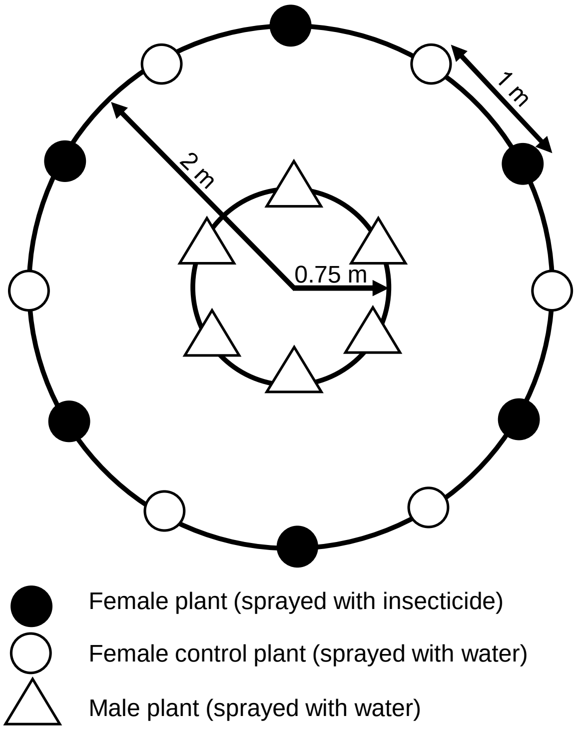

Figure 4-1 Design of the pollination experiment with *Silene latifolia* plants. There were 36 and 34 unpollinated female flowers on the insecticide-treated and control plants, respectively. Approximately 60 min after insecticide application, the flowers were exposed to natural pollination for one night.

4.2.4.2 Statistics

The data were analyzed using Primer (Version 6) software with the PERMANOVA+ add-on (Anderson *et al.*, 2008). The treatment (insecticide or control) was included as a fixed factor and the plant individual (nested in the treatment) as a random factor. The analyses focused on the number of pollinated flowers

(PerAnova, univariate data, resemblance matrices: Euclidean distance, 999 permutations) and on the numbers of seeds and *Hadena* offspring (eggs or caterpillars) per flower (PerManova, multivariate data, resemblance matrices: Bray Curtis distance, 999 permutations).

4.3 Results

4.3.1 Caterpillars in field margins

Overall, in the cereal field margins, 68 (4.9 ± 0.9, mean ± SE per site) and 105 (11.7 ± 1.6) caterpillars were recorded during the study phases in May and June, respectively, while in the meadows 139 (11.6 ± 2.6) and 199 (18.1 ± 3.6) caterpillars, respectively, were sampled. The caterpillars of the field margins and meadows could be classified into nine and seven families, respectively; Noctuidae and Geometridae were the most abundant groups in both habitats (Figure 4-2).

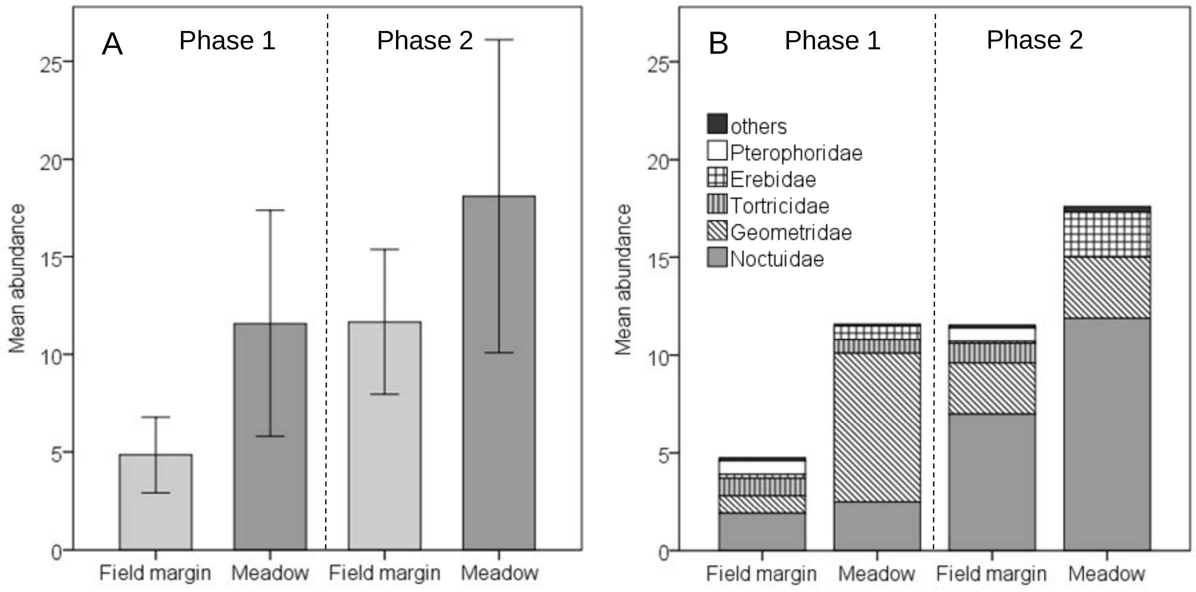

Figure 4-2 Overall mean caterpillar abundance ± SE (A) and mean caterpillar abundance per family (B) in the sampled field margins (N_{phase1}: 14, N_{phase2}: 9) and meadows (N_{phase1}: 12, N_{phase2}: 11). Families with very low caterpillar numbers were pooled (others: Crambidae, Hesperiidae, Lycaenidae, Nymphalidae, and Pieridae).

Overall, the caterpillar number was smaller in the field margins compared with the meadows, significantly in phase 1 (PerAnova; p = 0.018) but not in phase 2 (PerAnova; p = 0.141). The community composition of the lepidopteran families differed significantly between the two habitats for both phases (PerManova, phase 1: p = 0.002; phase 2: p = 0.011) (Figure 4-2).

In general, fewer species of flowering plants were present in field margins compared to meadows (phase 1: field margins: 8.6 ± 0.9; meadows: 11.5 ± 1.0; phase 2: field margins: 10.2 ± 0.9; meadows: 13.1 ± 1.2).

4.3.2 Effects of agrochemicals on caterpillars in a field experiment

On the first and the second sampling dates, 76 and 62 caterpillars were counted, respectively. Overall, the plots that had received an insecticide treatment were characterized by low numbers of caterpillars (Figure 4-3).

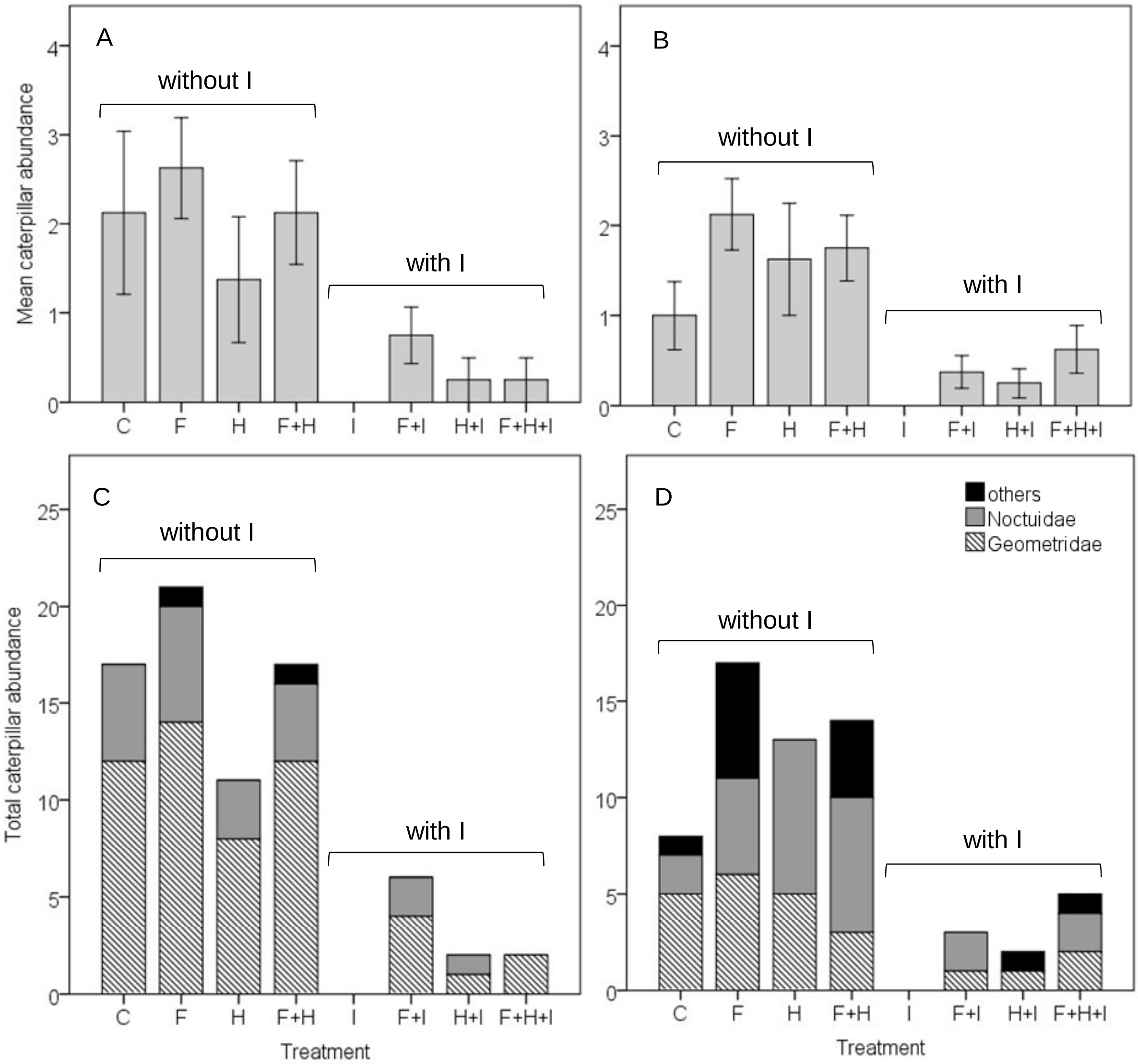

Figure 4-3 Mean caterpillar number ± SE per plot and treatment (A, B) in the field experiment (treatments: C: control, F: fertilizer, H: herbicide, I: insecticide, F+H, F+I, H+I, and F+H+I; N = 8 replicates per treatment) and total number of caterpillars per family per treatment (C, D). (A, C) represent sampling date 1 (= 6 days after insecticide treatment) and (B, D) represent sampling date 2 (= 34 days after insecticide treatment). Families with low caterpillar numbers were pooled (others; (C): Tortricidae; (D): Erebidae, Lycaenidae, Nymphalidae, Pterophoridae, and Tortricidae).

The results of the PerAnovas confirmed that the insecticide treatment reduced caterpillar abundance significantly, both at six and at 34 days after application (PerAnova; sampling 1: $p_{insecticide}$ = 0.001, sampling 2: $p_{insecticide}$ = 0.001). Herbicide treatments did not result in any significant effect on caterpillar abundance at either sampling date (PerAnova; sampling 1: $p_{herbicide} = 0.322$, sampling 2: $p_{herbicide} = 0.437$). The fertilizer addition slightly increased the caterpillar abundance for the second sampling date but showed no effect during the first sampling (PerAnova; sampling 1: $p_{fertilizer} = 0.171$, sampling 2: $p_{fertilizer} = 0.039$).

Regarding the composition of the caterpillar families, the insecticide treatment caused significant effects (PerManova; sampling 1: $p_{insecticide} = 0.001$, sampling 2: $p_{insecticide} = 0.001$) due to the strongly reduced caterpillar numbers in the families Geometridae and Noctuidae (Figure 4-3). Furthermore, the fertilizer (F) treatment showed an effect on the caterpillar community in the first sampling (PerManova; sampling 1: $p_{fertilizer} = 0.022$, sampling 2: $p_{fertilizer} = 0.257$) which could be attributed to higher numbers of Geometridae (treatments without F (N = 32): 0.66 ± 0.26; treatments with F (N = 32): 1.00 ± 0.20 caterpillars per plot; mean ± SE) and Noctuidae (without F (N = 32): 0.28 ± 0.10; with F (N = 32): 0.38 ± 0.13 caterpillars per plot). The herbicide treatment had no significant effect on the composition of the caterpillar community (PerManova; sampling 1: $p_{herbicide} = 0.453$, sampling 2: $p_{herbicide} = 0.647$).

4.3.3 Toxic and repellent effects of insecticide-treated host plants on *Mamestra brassicae* caterpillars

From the toxicity test, the results demonstrate that the insecticide affected *M. brassicae* caterpillars at low application rates. For example, the LR50 value after 48 h was 0.78% of the field rate (Confidence Interval (CI): 0.58 - 0.99%).

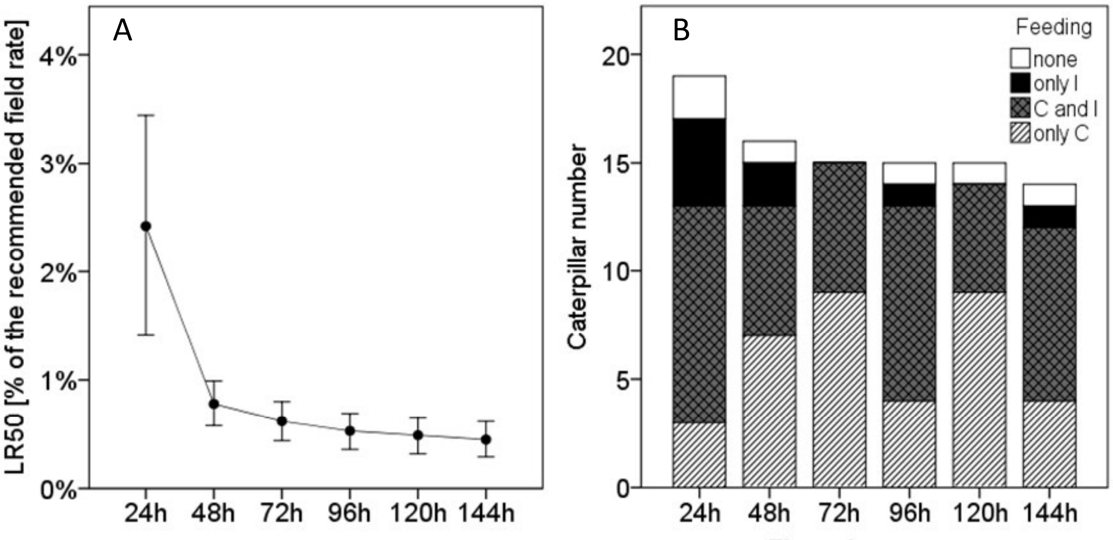

Figure 4-4 (A) LR50 values (black dots) and confidence intervals (bars) of 14-day-old *Mamestra brassicae* caterpillars fed with insecticide-treated leaves (Karate Zeon, pyrethroid) for 24 h to 144 h. N = 5 replicates per treatment, with 3 caterpillars per replicate. (B) Food choices of 15-day-old caterpillars at 24 h to 144 h after their introduction into test vessels. N = 20, with one caterpillar per replicate. ‘only C’: caterpillars fed only untreated control leaves; ‘only I’: caterpillars fed only leaves treated with 1% of the recommended field rate of an insecticide (Karate Zeon); ‘C and I’: caterpillars fed untreated and insecticide treated leaves; ‘none’: no feeding. Dead caterpillars are not included.

The LR50 values decreased with increasing time to 0.45% (CI: 0.29 – 0.62%) after 144 h (Figure 4-4A). All caterpillars in the control group survived (mortality $_{\text{control}}$: 0%).

In the feeding behavior experiment (repellence test), the caterpillars only occasionally fed solely on insecticide-treated leaves. The caterpillars primarily fed either on the control leaves or their diet consisted of a mixture of both treated and untreated leaves (Figure 4-4B).

4.3.4 Effects of an insecticide on moth pollination and egg-laying behavior

The treatment with the insecticide resulted in a significant reduction in the number of pollinated flowers per *S. latifolia* plant (PerAnova, p = 0.004). Approximately 30% of the insecticide-treated flowers were not pollinated and, hence, developed no seeds, whereas all of the control flowers produced seeds (Table 4-1). In addition, a multivariate analysis that included the number of seeds per flower and the number of *Hadena* offspring indicated a significant difference between the insecticide treatment and the control (PerManova, p = 0.005). *Hadena bicruris* females only oviposited single eggs on the flowers, and overall, the number of *Hadena*-offspring (eggs or caterpillars) was reduced by nearly 40% on insecticide-treated plants compared with control plants (control: 18; insecticide: 11; Table 4-1). We recorded approximately 30% more seeds in the pollinated flowers of insecticide-treated plants (control: 206 seeds; insecticide: 269; Table 4-1).

Table 4-1 Results of the pollination and oviposition experiment with *Silene latifolia* plants.

	Control[a]	Insecticide[b]
Flowers		
Overall number of flowers	34	36
Pollinated flowers	34	26
Pollinated flowers per plant ([%]; mean ± SE)	100 ± 0	72 ± 6
Seeds		
Seeds per flower (mean ± SE)	206 ± 25	194 ± 28
Seeds per pollinated flower (mean ± SE)	206 ± 25	269 ± 27
Seeds per plant (mean ± SE)	1243 ± 267[c]	1164 ± 212
***Hadena* eggs and caterpillars**		
Overall number of *Hadena* offspring	18	11
Hadena offspring per flower (mean ± SE)	0.5 ± 0.1	0.3 ± 0.1
Hadena offspring per plant (mean ± SE)	3.1 ± 0.7[c]	1.8 ± 0.5

[a] Control: 5 plants with 6 flowers each and 1 plant with 4 flowers (= 34 flowers)

[b] Insecticide: 6 plants with 6 flowers each (= 36 flowers)

[c] The calculations of the numbers of seeds and *Hadena* offspring per plant are based on 6 flowers per plant. In the case of the one control plant that held 4 flowers, the numbers (911 seeds and 1 *Hadena* egg per 4 flowers) were increased by 50% (1,367 seeds and 1.5 *Hadena* eggs, respectively) to be comparable to the other plants with 6 flowers.

4.4 Discussion

4.4.1 Caterpillars in field margins

Caterpillars depend on the availability of host plants for their development, whereas many adult Lepidoptera feed on nectar. Field margins are common elements in agricultural landscapes and provide habitats for various plant species (Joenje and Kleijn, 1994; Hamre and Austad, 1999; Tarmi *et al.*, 2002). Hence, field margins represent potential habitats for adult and juvenile Lepidoptera (e.g., Feber *et al.*, 1999), and wider field margins have the potential to increase the abundance and species richness of adult moths (Merckx *et al*., 2009; Merckx *et al*., 2012). Though the occurrences of adult butterflies and moths in field margin habitats have been recorded in various studies (e.g., Boutin *et al.*, 2011; Feber *et al.*, 1996; Dover, 1999; Field *et al.*, 2005, 2007; Kuussaari *et al.*, 2007; Merckx *et al.*, 2009; Merckx *et al.*, 2010; Merckx *et al.*, 2012), less information is available for their caterpillars (e.g., Feber *et al.*, 1999).

In our first experiment, we sampled caterpillars in cereal field margins to determine whether these elements are used as habitats for the development of caterpillars. Overall, we found caterpillars from nine families (Figure 4-2). However, as field margins can be strongly affected by the management of the adjoining agricultural site, which we hypothesized could influence the occurrence of caterpillars, we also sampled caterpillars in meadows, which represent a less disturbed semi-natural habitat element. Compared with the meadows, the field margins harbored a smaller number of caterpillars (Figure 4-2). There are three factors that could contribute to this observation. First, the abundance of caterpillars could be affected by differences in habitat size. Meadows provide a greater patch size compared with field margins, and certain studies have found a positive correlation between patch size and population density for insects (Connor *et al.*, 2000, Krauss et al. 2003). Nonetheless, connections between density and area are probably species specific; they depend on migration characteristics (e.g., Bowman et al. 2002, Hambäck & Englund 2005), and there seem to be differences between specialists and generalists (Krauss et al. 2003). Second, a linear shape of a habitat can be associated with a reduced number of individuals (Ewers and Didham, 2007) because linear elements (e.g., field margins) have a higher ratio of edge to interior and, hence, pressure from edge-related stressors (e.g., predation or parasitism, see Paton, 1994) might be more important than in non-linear habitats (e.g., meadows). Third, field margins are exposed to inputs of agrochemicals that might affect caterpillar abundances either directly or indirectly (Feber *et al.*, 1996; Longley and Sotherton, 1997). Possible indirect effects include changes in the abundance, diversity, or quality of host plants; for instance, we found fewer flowering plant species in field margins compared to meadows.

4.4.2 Effects of agrochemicals

To assess the effects of agrochemicals (fertilizer, herbicide, and insecticide) on caterpillars, their abundance and community composition were studied in field experiment plots, which received single or combined applications of these three agrochemicals (see Section 4.2.2).

4.4.2.1 Fertilizer

The application of fertilizer tended to increase the abundance of caterpillars in the plots (Figure 4-3). Studies on the effects of an increase in nitrogen levels on the abundance and development of herbivores, including Lepidoptera, found positive (Wheeler and Halpern, 1999; Haddad *et al.*, 2000; Butler *et al.*, 2012) and negative effects (Fischer and Fiedler, 2000; Kula *et al.*, 2014). Such differences between species may depend on their adaption to increased nitrogen levels in host plants (Kula *et al.*, 2014) or to changes in microclimate caused by advanced plant growth (WallisDeVries and van Swaay, 2006). Possible explanations for the higher caterpillar numbers in the fertilized plots could be (1) that the additional supply of nitrogen increased the host plant quality for certain species (Haddad *et al.*, 2000) or (2) that the fertilizer inputs altered the composition of plant communities (Schmitz *et al.*, 2014a), thereby promoting the occurrence of certain plant species (Boatman, 1994; Inouye and Tilman, 1995; Schmitz *et al.*, 2014a) that might be beneficial to the herbivores that rely on them. However, the responses of plant species to fertilizer inputs also vary, and a number of smaller species tend to be overgrown by grasses (Kleijn and Snoeijing, 1997; Schmitz *et al.*, 2014a). When evaluating the effects of fertilizer inputs over several years, fertilizer was found to reduce plant species richness (Kleijn and Snoeijing, 1997; Schmitz *et al.*, 2014a) and, hence, fertilizer inputs may decrease the abundance and diversity of caterpillars and other herbivores as well. We assessed the effects of fertilizer on caterpillar abundance and community composition in the second year of the field experiment in which the plant community composition had not been altered in response to the fertilizer treatments (Schmitz *et al.*, 2014a). However, a year later (in 2012), the plant community of a plot receiving a fertilizer treatment could be clearly distinguished from that of a control plot (see the results for the community composition analysis in Schmitz *et al.*, 2014a), which could possibly also lead to changes in the occurrences and abundances of caterpillars.

4.4.2.2 Herbicide

In addition to fertilizers, plants can also be affected by herbicides (Kleijn and Snoeijing, 1997; Schmitz *et al.*, 2014a). These effects include not only lethal effects but also sublethal effects, such as reductions in flowering and seed production (Schmitz *et al.*, 2014b). As a result, herbicides can change the density of individual plant species as well as the composition of the plant community and, furthermore, the resources that the plants provide for herbivores and pollinators (Schmitz *et al.*, 2013; 2014a; 2014b). Although lethal effects directly diminish the availability of host plants, decreased flowering might reduce the nectar resources for adult Lepidoptera. A decreased seed number could affect not only lepidopteran species, which feed on seeds during their development (e.g., *H. bicruris*), but also diminish the abundance of plant species in the future (Schmitz *et al.*, 2014b) and thereby negatively affect the Lepidoptera that rely on these species as caterpillar hosts. Moreover, sublethal herbicide application rates might reduce the quality of host plants and cause higher mortality rates or prolonged development times for herbivores (Kjær and Elmegaard, 1996; Hahn *et al.*, 2014a). Nonetheless, there were no significant effects of the herbicide applications on caterpillar abundance detected in the plots of the field experiment. One reason might be that herbicide effects on the host plant quality (Hahn *et al.*, 2014a) and plant resources appear to be rather species-specific, and their identification would most likely require another sampling method that would allow the assessment of individual host plant species with their associated caterpillars. However, although individual plant species displayed herbicide effects even during the first year of the field experiment, changes in the plant community composition were first apparent in the third year (Schmitz *et al.*, 2014a). Accordingly, effects on caterpillars might possibly also be detected at this time.

4.4.2.3 Insecticide

The most marked effects on caterpillar abundance and community structure in the field experiment were caused by the insecticide. In plots receiving an insecticide treatment, the abundance of caterpillars was extremely low compared with plots receiving no insecticide application (Figure 4-3). Significant reductions in caterpillar numbers were even recorded during the second sampling period, nearly five weeks after the insecticide application. There are two possible explanations. First, the insecticide used, a pyrethroid, might be directly toxic to the caterpillars at lower concentrations than the recommended field rate. To obtain further insight into this topic, we assessed the effects of leaves treated with the same insecticide used in the field experiment (Karate Zeon) on the survival of 14-day-old *M. brassicae* caterpillars. The caterpillars exhibited a high mortality rate even at low insecticide rates. The LR50 value (48 h) for *M. brassicae* caterpillars was approximately 0.78% (= 0.059 g a.i. ha^{-1}) of the recommended field rate. This amount of pesticide input would occur at a distance of 3-4 m from the applied agricultural field in an arable spray drift scenario (Rautmann *et al.*, 2001). Other studies have also confirmed that caterpillars can be highly sensitive to insecticides. For example, Cilgi *et al.* (1995) detected toxic effects of deltamethrin deposits on cabbage leaves for *Pieris brassicae* caterpillars at rates of 0.19% of the field application rate (= 0.012 g a.i. ha^{-1}). Pyrethroids can also have ovicidal activities against lepidopteran eggs (Tysowsky and Gallo, 1977; Gist and Pless, 1985). In the field experiment, the insecticide was applied at 30% of the recommended field rate. In view of the low LR50 values for *M. brassicae* caterpillars in the laboratory assessment, the lepidopteran offspring (eggs and caterpillars) in the insecticide-sprayed plots might have died from contact with the sprayed plant surfaces, but more information on the toxic effects on other caterpillar species would be necessary to prove this theory.

Second, certain pesticides, including pyrethroids, are known to repel caterpillars and adult moths (Kumar and Chapman, 1984; Gist and Pless, 1985; Blair, 1991; Abivardi *et al.*, 1998). To test for such effects on caterpillars, we observed the feeding behavior of *M. brassicae* caterpillars when they were forced to choose between leaves treated with 1% of the recommended field rate of a pyrethroid insecticide and untreated control leaves. The caterpillars in the feeding experiment did not completely avoid the insecticide-treated leaves, but they appeared to prefer insecticide-free leaves (Figure 4-4B), which indicates minor antifeedant effects. In cases in which the caterpillars had fed on both leaves, it appeared that more plant material had been consumed from the untreated leaves, but this was not quantified during the experiment. However, the addition of untreated leaves in the test systems increased the survival of the *M. brassicae* caterpillars. In the toxicity test, the mortality in the 1% treatment was approximately 75% after 48 h, whereas only 25% of the caterpillars died after the same amount of time in the feeding experiment.

In addition to the effects on caterpillars, we also included experiments that assessed the effects of this insecticide on adult moths. For female Lepidoptera, the choice of an oviposition site is a particularly crucial event because caterpillars are rather immobile and thus depend on a suitable host plant (Renwick and Chew, 1994). Therefore, females typically assess both the physical and chemical characteristics of a plant prior to oviposition (Renwick and Chew, 1994). Certain lepidopteran species have been observed to avoid oviposition on insecticide-treated surfaces (Kumar and Chapman, 1984; Gist and Pless, 1985; Seljasen and Meadow, 2006). Thus, in the field experiment, the reduced caterpillar numbers in the insecticide-treated plots might also result from reduced oviposition by the adult females. To test this hypothesis, we assessed the egg deposition of moths (*H. bicruris*) in a semi-field experiment using *S. latifolia* plants (see 2.4). There were approximately 40% fewer *H. bicruris* eggs on the insecticide-treated flowers, indicating that *Hadena* moths avoided oviposition on insecticide-treated flowers. Hence, the low caterpillar numbers in the insecticide-treated plots of the field experiment might result not only from the toxic effects of the insecticide but also from the repellent effects on the adults.

4.4.3 Insecticide effects on the pollination of *Silene latifolia*

In addition to the lethal or sublethal effects on moths and their offspring, insecticides can also affect pollination and the seed number of *S. latifolia* flowers. Overall, flowers of *S. latifolia* sprayed with insecticide were less likely to be pollinated compared with flowers of control plants. Pollination is an important service in ecosystems, and approximately 87% of angiosperm plant species rely on animal pollination (Ollerton *et al.*, 2011). Little information is available concerning the role of moths as pollinators in ecosystems (Clinebell *et al.*, 2004; Alarcon *et al.*, 2008; Devoto *et al.*, 2011), although moths have been observed to carry pollen of various plant species. However, if deterrent effects of insecticides reduce the probability that flowers will be pollinated, this could negatively affect the biodiversity of agro-ecosystems, but more data are necessary to confirm this hypothesis.

We recorded approximately 30% more seeds in the pollinated flowers of the insecticide-treated plants than in the control (Table 4-1). This increase might be caused by the longer foraging time of the visiting moths on the sprayed flowers (see Labouche and Bernasconi, 2010), as a reduced number of flower visitors might result in an increased availability of nectar at each flower. The higher seed number in the pollinated insecticide flowers compensated for the reduced overall number of pollinated flowers (Table 4-1, see seeds per flower and seeds per pollinated flower) and, hence, we would not expect negative consequences for *S. latifolia* populations in the field if female plants were sprayed with the applied insecticide (Table 4-1, seeds per plant). Indeed, in the case of *S. latifolia*, the reduced oviposition of *H. bicruris* and the associated reduction in seed predation by the caterpillars might even have beneficial effects on the reproduction of the plant species. However, moths exhibit strong temporal fluctuations in their abundance and community composition (Devoto *et al.*, 2011), and long-term observations and the consideration of other plant species are thus necessary to gain further insight into this topic.

4.5 Conclusion

Field margins are an important habitat for moths in agricultural landscapes and are used as a developmental habitat for caterpillars, but field margins are also exposed to inputs of agrochemicals. Overall, our experiments illustrate that moths are affected by low and realistic rates of agrochemicals in various ways. Insecticides can have particularly strong negative effects on Lepidoptera, acting lethally on the offspring or as repellents to deter oviposition by adult females. Herbicides and fertilizers might affect the availability and quality of host plants.

Caterpillars are an important food source for birds, shrews, and various invertebrates. Hence, negative effects on their abundances most likely influence other species. Furthermore, a reduction in the pollination service provided by adult moths might also have an impact on plant species. For this reason, field margins should be protected from any input of agrochemicals.

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4.7 Supplemental Data

Part 1

Table 4-2 Herbs assessed on the sampling sites (field margins or meadows) in phase 1 (18.-26. May 2011). x: plant occurred on the site. Grasses were not identified, because some sites had been mown.

Phase 1	Field margins														Meadows											
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	1	2	3	4	5	6	7	8	9	10	11	12
Achillea millefolium agg.	x				x		x								x	x			x	x		x				
Anthriscus sylvestris																			x			x				
Bellis perennis																					x	x				
Capsella bursa-pastoris	x	x		x	x																					
Centaurea cyanus							x																		x	
Cirsium arvense	x	x	x	x		x		x	x	x	x	x	x	x	x		x	x			x	x	x	x	x	x
Convolvulus arvensis	x	x	x	x	x	x	x	x	x	x	x	x	x										x			
Crepis biennis															x					x						
Daucus carota											x															
Equisetum arvense	x								x				x		x		x	x								
Galium mollugo agg.		x		x			x				x				x		x	x	x	x	x	x	x	x	x	x
Galium verum																	x	x	x							
Geranium molle									x																	
Heracleum sphondylium													x												x	
Hypericum perforatum																									x	x
Hypochaeris radicata		x													x					x						
Knautia arvensis																					x	x	x			
Lathyrus aphaca															x											
Lathyrus pratensis	x																									
Lathyrus tuberosus							x		x																	
Leucanthemum vulgare agg.																x	x	x	x	x	x	x	x		x	
Lotus corniculatus							x										x	x			x	x	x	x	x	
Matricaria discoidea	x	x	x	x	x						x															
Matricaria recutita		x		x						x																
Medicago lupulina																					x	x				
Medicago sativa															x	x						x				
Melilotus officinalis											x															
Onobrychis viciifolia							x														x	x	x			
Papaver rhoeas					x	x			x																	
Plantago lanceolata					x		x				x				x	x	x	x		x	x	x		x		
Plantago major	x	x	x	x			x				x						x	x								
Polygonum aviculare	x	x	x	x	x	x	x	x	x	x	x	x	x	x												
Potentilla anserina																			x							x
Potentilla reptans													x													
Ranunculus acris																	x	x	x			x			x	x
Ranunculus repens																									x	
Rhinanthus alectorolophus															x	x										
Rosa corymbifera												x												x		
Rubus fruticosus agg.											x		x	x										x	x	
Rumex crispus					x								x	x					x	x		x		x	x	
Salvia pratensis																					x	x	x			
Securigera varia																						x	x	x		
Silene vulgaris											x										x	x	x			
Sisymbrium officinale		x	x	x																						
Sonchus oleraceus		x		x	x	x			x																	
Stellaria graminea																									x	x
Symphytum officinale														x												
Taraxacum sect. *Ruderalia*	x	x	x		x	x	x		x						x	x	x	x	x	x		x				
Tragopogon pratensis															x				x				x			
Trifolium pratense		x					x								x	x				x		x	x			
Urtica dioica						x							x	x			x	x							x	
Veronica filiformis		x							x	x		x					x	x								x
Vicia angustifolia									x																	
Vicia cracca									x						x	x	x	x				x				
Summarized species number	10	14	7	10	10	7	12	3	12	5	11	5	9	6	14	8	13	13	10	9	11	20	12	8	13	7
mean ± SE	8.6 ± 0.9														11.5 ± 1.0											

Table 4-3 Herbs assessed on the sampling sites (field margins or meadows) in phase 2 (9.-17. June 2011). x: plant species occurred on the site. Grasses were not identified, because some sites had been mown.

Phase 2	Field margins									Meadows										
	2	4	5	9	11	14	15	16	17	1	2	5	7	8	9	11	13	14	15	16
Achillea millefolium agg.	x				x		x	x	x	x	x			x	x		x	x	x	x
Agrimonia eupatoria																		x		
Anthriscus sylvestris														x						
Bellis perennis																x				
Capsella bursa-pastoris	x	x		x	x															
Centaurea cyanus								x			x	x	x	x	x	x	x	x		
Cirsium arvense	x	x	x	x		x			x	x		x	x			x		x		x
Convolvulus arvensis	x	x	x	x	x	x	x	x	x									x	x	x
Crepis biennis										x					x					x
Daucus carota											x							x		
Equisetum arvense	x							x	x	x		x	x					x		x
Galium mollugo agg.		x		x				x	x	x		x	x	x	x	x	x	x	x	x
Galium verum												x	x	x			x			
Geranium molle																				x
Heracleum sphondylium																				x
Hypericum perforatum						x		x										x		
Hypochaeris radicata		x								x					x					
Knautia arvensis																x				
Lathyrus aphaca										x										
Lathyrus pratensis	x																	x		
Lathyrus tuberosus							x													x
Linaria vulgaris							x													
Lotus corniculatus								x				x	x			x	x	x		
Matricaria discoidea	x	x	x	x	x															
Matricaria recutita		x		x		x	x	x										x		
Medicago lupulina							x									x				
Medicago sativa										x	x									
Onobrychis viciifolia																x				
Papaver rhoeas					x	x														
Plantago lanceolata					x		x	x		x	x	x	x		x	x	x	x	x	x
Plantago major	x	x	x	x				x	x			x	x							x
Polygonum aviculare								x	x											
Potentilla anserina														x			x		x	
Potentilla reptans									x										x	
Ranunculus acris								x	x			x	x	x			x	x	x	
Ranunculus repens									x											x
Rhinanthus alectorolophus										x										
Rubus fruticosus agg.								x									x	x		x
Rumex crispus					x			x						x	x		x	x	x	x
Salvia pratensis																x				
Securigera varia							x													
Silene vulgaris																x				
Sisymbrium officinale		x	x	x																
Sonchus oleraceus		x		x	x	x														x
Symphytum officinale																				x
Taraxacum sect. *Ruderalia*	x	x	x		x	x	x	x	x	x	x	x	x	x	x			x	x	x
Tragopogon pratensis									x	x				x						
Trifolium pratense		x								x	x				x		x	x	x	x
Trifolium repens																			x	x
Urtica dioica						x			x			x	x						x	x
Veronica filiformis		x				x						x	x							
Vicia cracca										x	x	x	x				x	x	x	
Vicia hirsuta																		x		
Vicia sativa agg.																			x	
Summarized species number	9	13	6	9	9	9	9	15	13	14	8	13	13	10	9	11	12	20	14	20
mean ± SE	10.2 ± 0.9									13.1 ± 1.2										

Part 2

Table 4-4 Plant species assessed in the plots of the field experiment in June 2011*. x: plant species occurred within the plots. Treatments: C: Control, F: Fertilizer, H: Herbicide, I: Insecticide, F+H, F+I, H+I, F+H+I. N = 8 plots per treatment.

	C	**F**	**H**	**I**	**F+H**	**F+I**	**H+I**	**F+H+I**
Achillea millefolium agg.	x	x	x	x	x	x	x	x
Ajuga reptans	x	x	x	x	x	x	x	x
Alchemilla vulgaris agg.		x			x		x	
Calystegia sepium	x	x	x	x	x	x	x	x
Cardamine pratensis				x				
Cerastium fontanum		x					x	
Cirsum spec.	x	x	x	x	x	x	x	x
Crepis biennis				x				
Equisetum arvense					x		x	x
Galium mollugo agg.	x	x	x	x	x	x	x	x
Glechoma hederacea	x	x	x	x	x	x	x	x
Heracleum sphondylium	x	x	x	x	x	x	x	x
Hypericum perforatum	x	x	x	x	x	x	x	x
Hypochaeris radicata			x					
Lathyrus pratensis	x	x	x	x	x	x	x	x
Leucanthemum vulgare agg.	x	x	x	x	x	x	x	
Linaria vulgaris			x	x	x	x	x	x
Lotus corniculatus	x	x	x	x	x	x	x	x
Lychnis flos-cuculi	x	x	x			x	x	
Lythrum salicaria		x						
Plantago lanceolata	x	x	x	x	x	x	x	x
Prunella vulgaris	x		x			x		x
Ranunculus acris	x	x	x	x	x	x	x	x
Ranunculus lanuginosus			x					x
Ranunculus repens	x	x	x	x	x	x	x	x
Rhinanthus alectorolophus	x	x		x		x		
Rosa arvensis			x		x	x		
Rubus fruticosus agg.	x	x		x		x		
Rumex acetosa	x	x	x	x	x	x	x	x
Silene nutans	x							
Stellaria graminea	x	x	x	x	x	x	x	x
Symphytum officinale	x	x	x	x	x	x	x	x
Taraxacum sect. *Ruderalia*			x				x	
Tragopogon pratensis	x							
Trifolium pratense	x			x		x	x	x
Trifolium repens	x			x	x			
Urtica dioica		x	x		x	x		
Valeriana officinalis				x				
Veronica chamaedrys	x	x	x	x	x	x	x	x
Vicia hirsuta	x	x	x		x	x	x	
Vicia sepium	x	x	x	x	x	x	x	x
Summerized species number per treatment	28	27	28	27	26	28	27	23
Mean species number ± SE per plot and treatment	17.9 ± 0.7	15.9 ± 0.4	15.6 ± 0.6	18.0 ± 1.1	15.8 ± 0.9	15.9 ± 0.7	17.0 ± 0.9	15.3 ± 0.5

* Details on the vegetation characteristics are also presented in Schmitz *et al*. (2014): Agrochemicals in field margins – An experimental field study to assess the impacts of pesticides and fertilizers on a natural plant community. Agric. Ecosyst. Environ. 193, 60-69

5 Effects of herbicide-treated host plants on the development of *Mamestra brassicae* L. caterpillars

Paper 3

This chapter presents the author's final version of the article

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Abstract – Herbicides are widely used pesticides that affect plants by changing their chemistry. In doing so, herbicides might also influence the quality of plants as food for herbivores. To study the effects of herbicides on host plant quality, 3 plant species (*Plantago lanceolata* L., *P. major* L., and *Ranunculus acris* L.) were treated with sublethal rates of either a sulfonylurea (Atlantis WG, Bayer CropScience) or a glyphosate (Roundup LB Plus, Monsanto) herbicide, and the development of caterpillars of the cabbage moth *Mamestra brassicae* L. that fed on these plants was observed. Of the 6 tested plant–herbicide combinations, 1 combination (*R. acris* + sulfonylurea herbicide) resulted in significantly lower caterpillar weight, increased time to pupation, and increased overall development time compared with larvae that were fed unsprayed plants. These results might be caused by a lower nutritional value of these host plants or increased concentrations of secondary metabolites that are involved in plant defense. The results of the present and other studies suggest potential risks to herbivores that feed on host plants treated with sublethal rates of herbicides. However, as the effects of herbicides on host plant quality appear to be species-specific and as there are numerous plant–herbicide–herbivore relationships in agricultural landscapes, a general reduction in herbicide contamination of non-target habitats (e.g., field margins) might mitigate the negative effects of herbicides on host plant quality.

5.1 Introduction

As primary producers, plants are an essential component of terrestrial ecosystems. However, as modern agricultural production is aimed at optimizing crop yield, non-crop plant species in croplands are often controlled by herbicides, to limit competition with crops for resources (Freemark and Boutin, 1995) or to inhibit the occurrence of pest organisms (Norris and Kogan, 2005). Herbicides are the most frequently used class of pesticides worldwide (Cooper and Dobson, 2007).

The widespread use of herbicides has been associated with negative effects on wildlife in treated fields and, as a result of herbicide spray drift, in adjacent non-crop habitats such as field margins (Freemark and Boutin, 1995; Wilson *et al.*, 1999). For example, the abundance and diversity of plants can be reduced through herbicide treatments (Freemark and Boutin, 1995; Stoate *et al.*, 2001). In addition, as each plant species interacts with numerous other species (Nentwig, 2000), for example, acting as a food source (to pollinators and herbivores), herbicides can also influence species at higher trophic levels (Freemark and Boutin, 1995; Wilson *et al.*, 1999). The abundance of herbivores may decrease if their host plants are lethally affected by an herbicide (see Longley and Sotherton, 1997, for such effects on butterflies).

Sublethal effects of herbicides on plants might also negatively influence herbivores. Herbicides affect biochemical processes in plants (Freemark and Boutin, 1995), such as electron transport and amino acid synthesis. For example, glyphosate inhibits an enzyme of the shikimate pathway (Duke and Powles, 2008), and sulfonylurea herbicides inhibit acetolactate synthase (Drobny *et al.*, 2012). Both enzymes are necessary for the synthesis of some amino acids in plants. As amino acids and proteins are crucial to the development of herbivores (and other organisms), herbicide-treated plants may not meet the dietary requirements of herbivores. In addition, herbicides cause stress in plants and can induce genes involved in plant defense (Pasquer *et al.*, 2006). Many plants can synthesize secondary metabolites, such as glucosinolates, as defense mechanisms that may deter or be toxic to herbivores (Ahuja *et al.*, 2010; Kjær *et al.*, 2001). Accordingly, some plant secondary metabolites, such as pyrethrum, are also used as insecticides (Glynne-Jones, 2001).

Therefore, even if a plant is not killed by an herbicide, it might nonetheless become unsuitable or less nutritious to herbivores. The few studies that focus on the effects of herbicides on host plant quality have yielded mixed results. The observed responses include no effects (Kjær and Heimbach, 2001), increased numbers of aphids (*Rhopalosiphum maidis* [Fitch], Hemiptera) and heavier corn borer pupae (*Ostrinia nubilalis* [Hübner], Lepidoptera) on herbicide-treated maize plants (Oka and Pimentel, 1976), reduced longevity of caterpillars of the soybean looper (*Pseudoplusia includens* [Walker], Lepidoptera) on soybean plants (Agnello *et al.*, 1986a), and extended development times and reduced female egg numbers of the green dock beetle (*Gastrophysa viridula* Degeer, Coleoptera) on the broad-leaved dock *Rumex obtusifolius* L. (Speight and Whittaker, 1987). In an extensive study, Kjær and Elmegaard (1996) treated black bindweed (*Polygonum convolvulus* L.) plants with sublethal rates of chlorsulfuron and then introduced larvae of the leaf-eating beetle *Gastrophysa polygoni* L. (Coleoptera). The larvae showed up to 80% mortality on those plants receiving the highest herbicide dosage and highest number of larvae. Although the herbicide was not directly toxic to the larvae, the authors argue that the pesticide might enhance an herbivore-induced plant response (Kjær and Elmegaard, 1996). In general, aphids and other species living in meristematic tissues appear to respond positively to herbicide-treated plants, whereas foliar feeders (and other feeding guilds) tend to be negatively affected (Kjær *et al.*, 2001).

The Lepidoptera, a species-rich insect order, are sensitive to pesticides (Dover *et al.*, 1990; Longley and Sotherton, 1997), and some species also appear to be affected by herbicide-treated host plants (Agnello *et al.*, 1986a; Agnello *et al.*, 1986b; Oka and Pimentel, 1976). In the present study, 3 host plants of the foliar-feeding cabbage moth *Mamestra brassicae* L. (Lepidoptera) were treated with sublethal rates of 2 herbicides, and the development of *M. brassicae* caterpillars into adult moths was observed.

5.2 Methods

Moths

The moth *M. brassicae* L. (Lepidoptera, Noctuidae) is widely distributed throughout Europe and Asia (Ahuja *et al.*, 2010). The moth eggs used in the present study were provided by the Laboratory of Entomology, Wageningen University and Research Center, The Netherlands. *Mamestra brassicae* caterpillars are polyphagous and feed on various herbs (see examples in Ebert, 1998; Rojas *et al.*, 2000, 2001), such as dandelion *Taraxacum officinale* agg. Wiggers, which was accepted as a food plant by *M. brassicae* caterpillars during their development. In the present study, caterpillars were fed freshly sampled, untreated leaves of *T. officinale* until 4 d of age. During this time, the caterpillars were housed at room temperature (~20 °C).

Plants

Three host plant species of *M. brassicae*, English plantain *Plantago lanceolata* L., greater plantain *Plantago major* L., and common buttercup *Ranunculus acris* L., were cultured from seeds provided by a commercial seed supplier (Appels Wilde Samen). As *R. acris* has a relatively low germination rate compared with the 2 *Plantago* species, its germination was triggered by placing the seeds in a 0.1% solution of the plant hormone gibberellic acid (GA3) for 24 h at 4 °C before sowing.

Seeds of the test species were sown in plastic containers (13-cm diameter) containing a 3-mm- to 4-mm-thick layer of cotton wool soaked with water and a layer of moist filter paper. The containers were covered with plastic wrap to prevent evaporation and stored in a climate chamber (25 °C, 12:12-h, light:dark cycle). After germination, the seedlings were planted in multipot plates (pot diameter 3 cm) filled with potting compost (Compo Sana Anzucht- und Kräutererde, Compo). When the roots of the plants penetrated the pots, each seedling was transferred to separate 10-cm pots containing universal potting compost (Compo Sana Qualitäts-Blumenerde, Compo). The plants were then returned to the climate chamber (25 °C, 80% humidity, 16:8-h, light:dark cycle) for approximately 8 wk and fertilized once a week with NPK-fertilizer (Gartenkrone Universal Dünger flüssig NPK 7+3+5, green partners international) at the recommended dosage (25 mL fertilizer/8 L water; product information Gartenkrone Universal Dünger). On the day of caterpillar hatching, plants of each test species were randomly divided into 3 groups: unsprayed (for the control treatment), sprayed with the herbicide Roundup LB Plus (Monsanto), or sprayed with the herbicide Atlantis WG (Bayer CropScience). To avoid contact between plants and herbivores before the start of the experiment, the plants were maintained indoors, and the herbicide was applied in a laboratory fume hood.

Each plant had approximately 10 to 16 (*P. lanceolata*), 6 to 9 (*P. major*), or 7 to 10 leaves (*R. acris*) at the beginning of the experiment (see Supplemental Data: Part A for representative photos).

Herbicides and the testing process

We tested the effects of 2 herbicides: Roundup LB Plus (glyphosate; recommended application rate 5000 mL/ha, active ingredient 360 g/L glyphosate) and Atlantis WG (sulfonylurea; recommended application rate 400 g/ha, active ingredient 30 g/kg mesosulfuron-methyl, 6 g/kg iodosulfuron-methyl-natrium, 90 g/kg mefenpyr-diethyl [safener]). We aimed to avoid lethal effects of the herbicides on the test plant species (at least over the 14 d following treatment), but the herbicide treatments were expected to cause slight sublethal herbicide effects, such as chlorosis or reduced growth. Therefore, we used application rates of 10% of the recommended field rate for Atlantis WG and 3% of the recommended field rate for Roundup LB Plus (for results of previous dose–response tests; see Supplemental Data: Part B).

A custom-made, air-assisted experimental field sprayer (Schachtner Gerätetechnik) was used to spray the herbicide onto the test plants. The sprayer was equipped with a spray arm with 4 110° flat-fan nozzles (TeeJet XR 11002-VS, Schachtner Gerätetechnik). The spray-arm was positioned in a laboratory fume hood approximately 50 cm above the potted plants. In accordance with the label recommendations of both herbicides, we used a spray volume of 400 L/ha for the application (operation pressure 3.5 bar). We also visually confirmed the homogeneous deposition of the spray over the plant surfaces. For calibration, pots (7 cm × 7 cm, 49 cm^2, not filled with soil) were sprayed with water and weighed to confirm that an adequate volume of water was applied. After herbicide application, the plants were left to dry before being transferred back into the climate chamber.

The number of replicates per group was 23 plants for *P. major* (n_{total} = 69 plants), 20 plants for *P. lanceolata* (n_{total} = 60 plants), and 22 plants for *R. acris* (n_{total} = 66 plants).

Four days after the caterpillar hatching and the herbicide application, acrylic glass cylinders were placed on the plant pots, and 1 caterpillar was transferred to each plant by using a fine hair pencil (Figure 5-1). We only used motile caterpillars of typical size (indicating typical feeding behavior). As young caterpillars can be sensitive to handling, they were not weighed at the beginning of the test. After caterpillar transfer, the upper portion of each test system was carefully closed off with gauze and a rubber band.

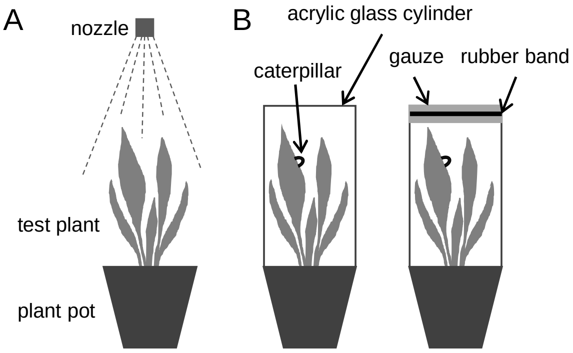

Figure 5-1 Caterpillar test system. In a first step (A), the plants were sprayed with herbicide at the day the caterpillars hatched. Four days later (B), an acrylic glass cylinder was placed and fixed on each plant pot, and a caterpillar was carefully introduced in the system. The cylinder was then closed off with gauze and a rubber band.

Data collection

Caterpillars were weighed using an electronic precision balance (Mettler AT261 DeltaRange) after complete consumption of the first replicate of the test plant species. If a control plant was consumed first, caterpillars from the control and both herbicide treatments were weighed. They were then individually maintained in plastic boxes (10 cm × 7 cm × 5 cm) and fed untreated, fresh *T. officinale* leaves until pupation.

If a plant of either herbicide treatment (Roundup LB Plus or Atlantis WG) was consumed first, only caterpillars of that herbicide treatment and the control treatment were weighed. Thereafter, the caterpillars of the herbicide treatment were transferred to plastic boxes and fed *T. officinale* leaves, whereas the control caterpillars were returned to their host plants. After complete consumption of plants of the remaining herbicide treatment or the control treatment, the caterpillars of both treatments were weighed (yielding weights of control caterpillars at 2 different ages), individually transferred to plastic boxes, and fed *T. officinale* leaves.

This approach ensured that the caterpillars could remain as long as possible on their test plants. However, as a result, the caterpillars of the herbicide treatment that had been removed from their food plants several days before the caterpillar controls were only compared with the control in terms of caterpillar weight.

Day of pupation, pupal weight, and day of eclosion were also recorded. Mortality was monitored throughout the experiment. Caterpillars were considered dead if they did not complete development (e.g., failed to pupate or died during hatching as imago). Caterpillars were also classified as dead if they could not be found within the confined test systems (Figure 5-1B) after 9 d to 17 d (weighing of the caterpillars) and if the plants showed minimal to no evidence of herbivory. Because of their small size, the bodies of dead caterpillars could not be found once they dropped onto the soil, particularly at the younger development stages.

Statistical analysis

Statistical analyses were performed using the program PAST (Version 1.95) (Hammer *et al.*, 2001). Most data were not normally distributed; in such cases, nonparametrical statistical tests were conducted. Mann–Whitney tests were used to compare between 2 treatments (control and an herbicide treatment). The Kruskal–Wallis test was used to test for differences among all 3 treatments (herbicide treatments and the control treatment). If the Kruskal–Wallis test yielded a p value < 0.05, Mann–Whitney tests pairwise comparisons with Bonferroni correction were conducted as post hoc tests.

5.3 Results

In the present study, 6 plant–herbicide combinations were tested (3 plant species × 2 herbicides). The weights of *M. brassicae* caterpillars reared on 5 of these combinations (*P. lanceolata*: both herbicides; *P. major*: both herbicides; *R. acris*: Roundup LB Plus) did not differ significantly from those of caterpillars feeding on untreated plants. The caterpillars from 2 of these treatments (*P. lanceolata*: Roundup LB Plus; *P. major*: Roundup LB Plus) were removed from their plants before those of the control treatments; therefore, the data from these 2 treatments were not further analyzed statistically. The remaining 3 combinations (*P. lanceolata*: Atlantis WG; *P. major*: Atlantis WG; *R. acris*: Roundup LB Plus) showed no differences in time to pupation, pupal weight, time from pupation to eclosion, or overall development time (Table 5-1).

However, caterpillars reared on *R. acris* treated with the herbicide Atlantis WG showed significantly lower weights (Kruskal–Wallis test with Mann–Whitney test post hoc, *R. acris*: $p_{\text{(control-Atlantis)}} < 0.001$) and were smaller than controls (Figure 5-2). They also exhibited a longer time to pupation (Kruskal–Wallis test with Mann–Whitney test posthoc, *R. acris*: $p_{\text{(control-Atlantis)}} = 0.003$) and a longer overall development time (Kruskal–Wallis test with Mann–Whitney test posthoc, *R. acris*: $p_{\text{(control-Atlantis)}} = 0.031$) than caterpillars fed untreated *R. acris* plants. Moreover, they exhibited higher mortality during development, particularly during the caterpillar phase. Six of 22 caterpillars (~ 30%) died within 17 d on the Atlantis WG-treated *R. acris* plants, whereas only 1 (less than 5%) died on the control plants during the same period (Table 5-1).

Table 5-1 Overview on *Mamestra brassicae* development in different treatments[a].

		Control[b]		Roundup[c]	Atlantis WG[d]
Ranunculus acris (*N* per group = 22)					
Caterpillars	age when caterpillars were weighted	21 days		21 days	21 days
	number of caterpillars alive	21		19	16
	weight (mean ± SE [mg])	153.1 ± 24.9		168.7 ± 31.5	41.5 ± 13.2***
Pupae	number of pupated caterpillars	21		19	15
	pupation age (mean ± SE [days])	35.2 ± 0.7		34.5 ± 0.8	41.3 ± 1.4**
	pupation weight (mean ± SE [mg])	431.4 ± 10.3		397.2 ± 11.1	422.0 ± 12.2
Eclosion	number of hatched moths	21		18	13
	time span as pupa (mean ± SE [days])	23.2 ± 0.4		22.8 ± 0.4	23.0 ± 0.3
overall development time (mean ± SE [days])		58,4 ± 0,8		57.1 ± 1.0	64.1 ± 1.7*
Plantago lanceolata (*N* per group = 20)					
Caterpillars	age when caterpillars were weighted	13 days[e]	20 days[e]	13 days	20 days
	number of caterpillars alive	19	19	19	18
	weight (mean ± SE [mg])	25.7 ± 4.6	253.4 ± 50.4	33.4 ± 5.4	308.6 ± 59.4
Pupae	number of pupated caterpillars	18		18[f]	17
	pupation age (mean ± SE [days])	33.7 ± 1.4		29.8 ± 1.1[f]	33.1 ± 2.0
	pupation weight (mean ± SE [mg])	412.3 ± 11.5		389.3 ± 11.2[f]	412.5 ± 12.9
Eclosion	number of hatched moths	16		18[f]	17
	time span as pupa (mean ± SE [days])	21.9 ± 0.4		21.0 ± 0.3[f]	22.6 ± 0.5
overall development time (mean ± SE [days])		55.9 ± 1.7		50.8 ± 1.3[f]	55.7 ± 2.4
Plantago major (*N* per group = 23)					
Caterpillars	age when caterpillars were weighted	15 days[e]	20 days[e]	15 days	20 days
	number of caterpillars alive	23	23	20	19
	weight (mean ± SE [mg])	65.4 ± 11.5	305.0 ± 44.1	61.8 ± 15.0	310.1 ± 39.1
Pupae	number of pupated caterpillars	22		19[f]	17
	pupation age (mean ± SE [days])	31.9 ± 1.1		33.2 ± 1.9[f]	32.1 ± 1.0
	pupation weight (mean ± SE [mg])	409.7 ± 8.9		408.7 ± 11.1[f]	430.7 ± 13.3
Eclosion	number of hatched moths	22		17[f]	15
	time span as pupa (mean ± SE [days])	22.2 ± 0.4		23.5 ± 1.4[f]	23.1 ± 0.6
overall development time (mean ± SE [days])		54.1 ± 1.2		56.9 ± 2.0[f]	55.1 ± 1.3

[a] Significant differences to the control are marked in grey (Kruskal-Wallis test with Mann-Whitney posthoc test, Bonferroni corrected) ***: $p < 0.001$, **: $p < 0.01$, *: $p < 0.05$.

[b] Control: Caterpillars were fed untreated *Ranunculus acris*, *Plantago lanceolata*, or *P. major* plants. After they had been removed from their host plants, they were fed untreated *Taraxacum officinale* leaves.

[c] Roundup: Caterpillars were fed test plants treated with Roundup LB Plus (3% of the field rate). After they had been removed from their host plants, they were fed untreated *T. officinale* leaves.

[d] Atlantis WG: Caterpillars were fed test plants treated with Atlantis WG (10% of the field rate). After they had been removed from their host plants, they were fed untreated *T. officinale* leaves.

[e] Caterpillars of control plants were weighted in parallel with caterpillars of herbicide treated plants. If plants of both herbicide treatments were completely consumed at different times, control caterpillars were returned to their appropriate host plants after the first weighing until plants of the second herbicide treatment (or the control) were also consumed. This approach resulted in two values for the control caterpillars (at different ages) feeding on *Plantago* plants.

[f] This endpoints could not be compared along with caterpillars of the control because caterpillars of the Roundup LB Plus treatment were fed *T. officinale* leaves earlier than the caterpillars of the control (see e).

Figure 5-2 Sizes of 21-d-old *Mamestra brassicae* caterpillars after feeding on untreated *Ranunculus acris* plants (n = 22) and *R. acris* plants sprayed with the sulfonylurea herbicide (Atlantis WG, 10% of the recommended application rate, n = 22) for 17 d.

5.4 Discussion

The present study evaluated the effects of 2 herbicides on the quality of 3 different host plants as food resources for a moth species (*M. brassicae*). Even without herbicide treatment, there were slight differences among the 3 host plant treatments, including overall development time (54 d for caterpillars feeding on *P. major*/*T. officinale* to 58 d for *R. acris*/*T. officinale*). These differences might indicate different suitabilities of the test plant species for *M. brassicae* (see also Metspalu *et al.*, 2013), possibly because of differing nutritional content or chemical defense mechanisms. These differences in development times were confirmed in subsequent feeding tests with the 3 test plant species (see Supplemental Data, Part C). Regardless of whether *R. acris* tends to extend the development time of *M. brassicae* relative to the *Plantago* species, the mortality of caterpillars feeding on untreated *R. acris* plants was low (Table 5-1).

Five of the 6 plant–herbicide combinations had no effects on the variables measured in *M. brassicae* caterpillars (Table 5-1). These findings are in accordance with those of Kjær and Heimbach (2001), who found no effects of herbicide-treated host plants on 3 different insect species, including the caterpillars of a butterfly species.

However, the development time of caterpillars feeding on *R. acris* treated with the sulfonylurea herbicide was significantly longer (by 10%; an average of 6 d) than that of caterpillars feeding on untreated *R. acris* plants. Mortality in the former group was approximately 40% by the end of the present study (mortality in the control group: < 5%). This enhanced mortality could not have been the result of a direct toxic effect of the sulfonylurea herbicide because those caterpillars feeding on *P. lanceolata* plants treated with the same herbicide did not show increased mortality (Table 5-1, *P. lanceolata*: No. of caterpillars alive). Kjær and Elmegaard (1996) similarly found that the survival of leaf-eating beetles

(*Gastrophysa polygoni*) on herbicide-treated host plants (*Polygonum convolvulus*) was reduced, although the herbicide was not toxic to the herbivore.

Caterpillars feeding on *R. acris* plants treated with the sulfonylurea herbicide were smaller and weighed less than those reared on untreated plants (Table 5-1, Figure 5-2). There are 3 possible mechanisms underlying this result. First, the plant's nutrient content may have been altered by application of the herbicide. Sulfonylurea herbicides inhibit the enzyme acetolactate synthase, thereby blocking the synthesis of amino acids (leucine, valine, and isoleucine) and affecting protein synthesis (Drobny *et al.*, 2012). Leucine, valine, and isoleucine are essential amino acids for animals including insects (O'Brien *et al.*, 2005); therefore, a lack of these amino acids could be detrimental to the development of *M. brassicae* caterpillars. Second, the herbicide treatment might increase the expression of plant defense mechanisms. Sulfonylurea herbicides have been observed to trigger the expression of defense-related genes in wheat plants in laboratory tests and in the field (Pasquer *et al.*, 2006). Kjær *et al.* (2001) found higher amounts of secondary plant metabolites likely associated with plant defense (phenolic compounds) in the leaves of plants treated with a sulfonylurea herbicide. Plant secondary metabolites can negatively affect herbivores via toxic or repellent effects. Plant tissues of *R. acris* contain ranunculin, a substance that can be transformed into the toxin protoanemonin, which is known to negatively affect livestock as well as several insect species (Sedivy *et al.*, 2012). Third, this effect might be further intensified, as sulfonylurea herbicides inhibit the transport of assimilates and can increase the concentrations of chemicals produced in leaves (Bestman *et al.*, 1990). Therefore, there might be higher concentrations of ranunculin and other secondary metabolites in the leaves of herbicide-treated plants, which could contribute to higher mortality and slower development of caterpillars.

Caterpillars are preyed on by a number of organisms including birds, shrews, and various invertebrates (Fox *et al.*, 2006; Wilson *et al.*, 1999). If herbicides prolong caterpillar development time, it may increase their risk of predation. However, the results of studies often differ between controlled laboratory and uncontrolled field conditions (Kjær *et al.*, 2001), and it is therefore also necessary to test for effects in the field, such as changes in caterpillar development time. Nonetheless, the results of the present study and other laboratory studies (Kjær and Elmegaard, 1996) indicate potential risks of herbicides to herbivores. To date, these effects have been studied little, possibly because the responses are specific to the herbivores, host plants, and herbicides in question and vary with environmental conditions (Kjær *et al.*, 2001). For example, in Germany, there are approximately 3500 Lepidoptera species (Karsholt and Razowski, 1996), 4200 flowering plant and fern species (Wisskirchen and Haeupler, 1998), and more than 580 registered herbicide products (BVL, 2014). This situation yields a vast number of possible combinations, making it difficult to estimate the overall risks of 1 or more herbicides to herbivorous insects. Therefore, it might be important to protect non-target habitats, such as field margins, to minimize the potential risks to herbivorous insects and wildlife. This may be particularly prudent considering that the herbicide rates applied in the present and other studies (Kjær and Elmegaard, 1996; Kjær and

Heimbach, 2001) are within the magnitudes of realistic herbicide input rates in field margins. Next to an arable field, the pesticide inputs as a result of spray drift are approximately 3% of the applied field rate at a distance of 1 m from the field edge (Rautmann *et al.*, 2001). In addition, parts of field margins can be oversprayed, leading to higher input rates. For example, within the first meter of a field margin bordering a cereal field, the mean pesticide input can exceed 30% of the field rate (see Schmitz *et al.*, 2013, for more details and a figure). Kjær and Elmegaard (1996) found that the spraying of *Polygonum convolvulus* plants with 33% (= 1.32g active ingredient/ha) of the recommended field rate of a chlorsulfuron herbicide reduced the survival of leaf-eating *Gastrophysa polygoni* beetles.

In Germany, field margins can be narrow (often 1 m–2 m, Hahn *et al.*, 2014); therefore, a high proportion of available field margin habitats likely receive pesticide inputs and at least some of the inhabiting plant species are likely sublethally affected. In contrast to our experiment, in which caterpillars were fed untreated *T. officinale* leaves after consuming herbicide-treated test plants, caterpillars in field margins cannot switch to uncontaminated food, which might amplify the potential negative effects. As field margins are a major, semi-natural habitat type in agricultural landscapes and are inhabited by many herbivorous insects, further research is needed on the combinations of plants and herbivorous insects found in these habitats.

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5.6 Supplemental Data

Part A: Plants used in the caterpillar test

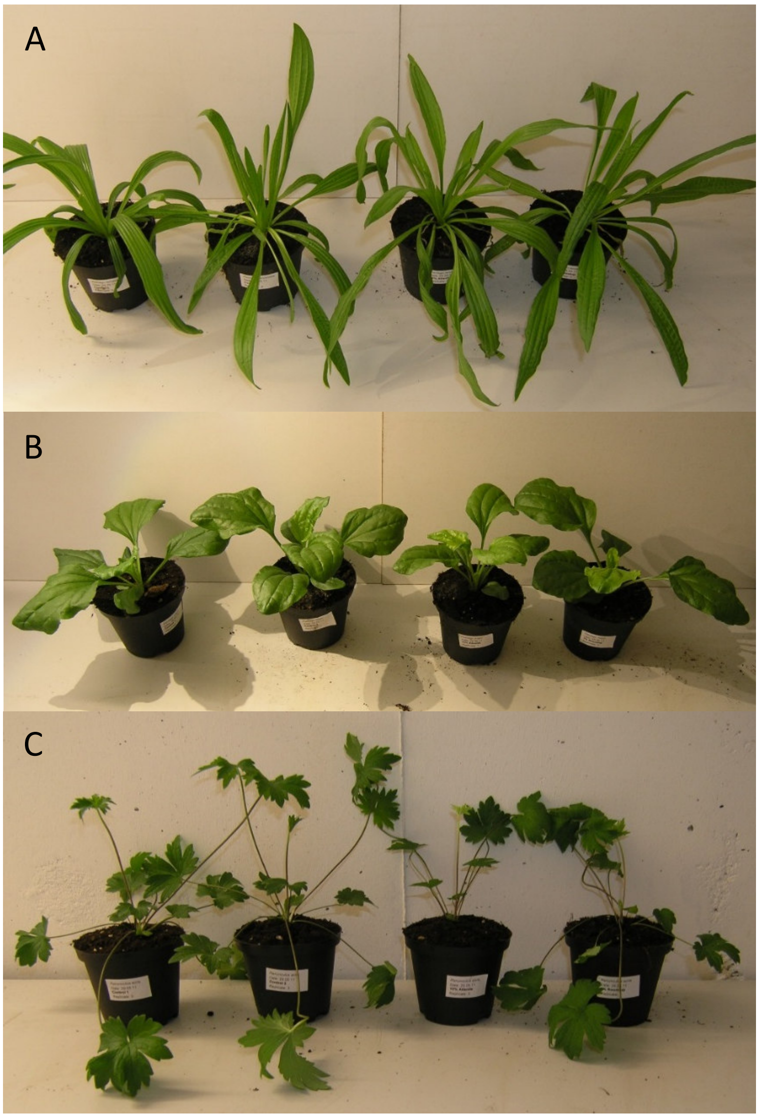


Figure 5-3 Representative *Plantago lanceolata* (A), *P. major* (B), and *Ranunculus acris* (C) plants one day before their herbicide application.

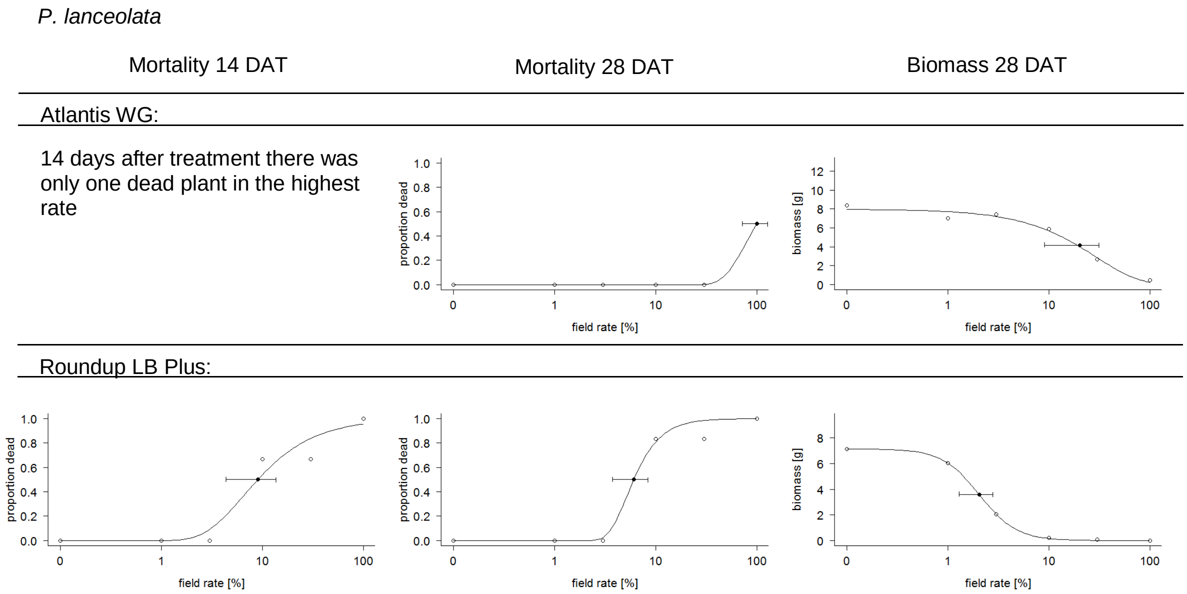
Part B: Previous dose-response-tests

Test design:

We conducted dose-response tests for the plant species *Plantago lanceolata*, *P. major*, and *Ranunculus acris* to decide which rates of the 2 herbicides (Atlantis WG, Roundup LB Plus) should be used in the main test. The test plants should not be lethally effected by the herbicide treatment (at least over the 14 days following treatment), but the herbicide treatments were expected to cause slight sublethal herbicide effects, such as reduced plant biomass, reduced growth or chlorosis. We measured several endpoints (e.g., mortality, biomass, number of leaves, plant length) and some of them are presented in the following figures. Calculations and figures were made using R (Version 3.1.0, R Core Team 2014).

Results:

Overall, mortality for all test plant species was higher in the Roundup LB Plus treatments than in the Atlantis WG treatments (Figures 5-4 to 5-6). In most cases, biomass tended to be a more sensitive endpoint than mortality.



14 days after treatment there was only one dead plant in the highest rate

Figure 5-4 Some results of the dose-response experiments with the plant *Plantago lanceolata*. At the test beginning, the plants had 5-10 leaves. The figures show mortality 14 and 28 days after treatment (DAT), and biomass 28 DAT for the herbicides Atlantis WG and Roundup LB Plus. Application rates: 1%, 3%, 10%, 30%, and 100% of the recommended field rates (application volume 400 L/ha). Replicates per herbicide and application rate: 6 plants. White dots: mean mortality or mean biomass per application rate; black dots: LR50 values (mortality 14 and 28 DAT) or EC50 values (biomass 28 DAT) with 95% confidence intervals.

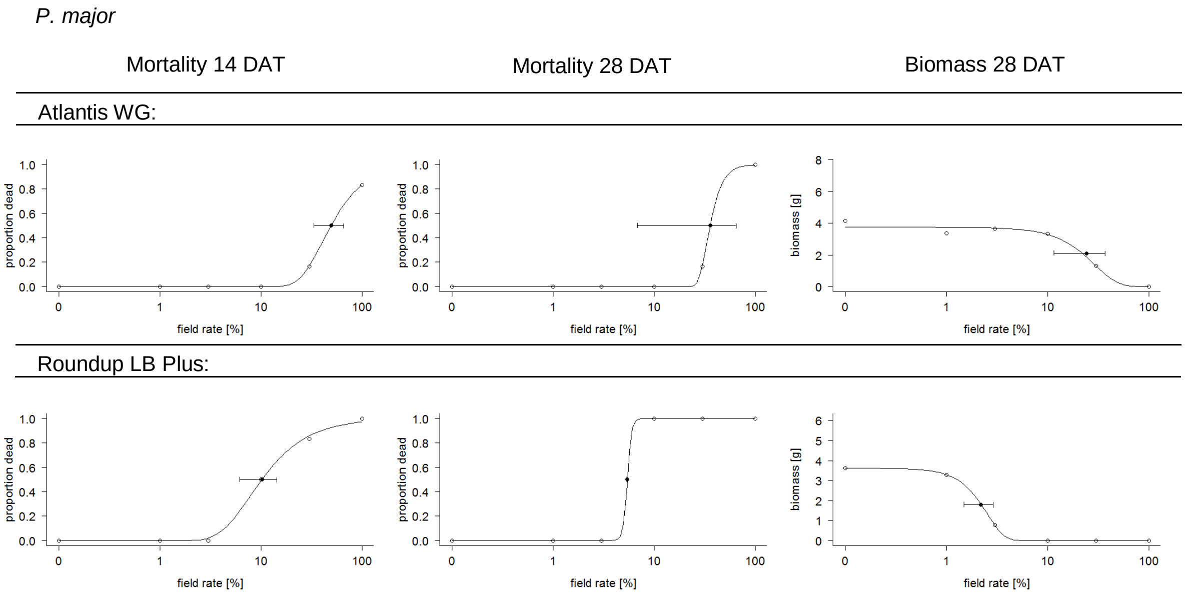
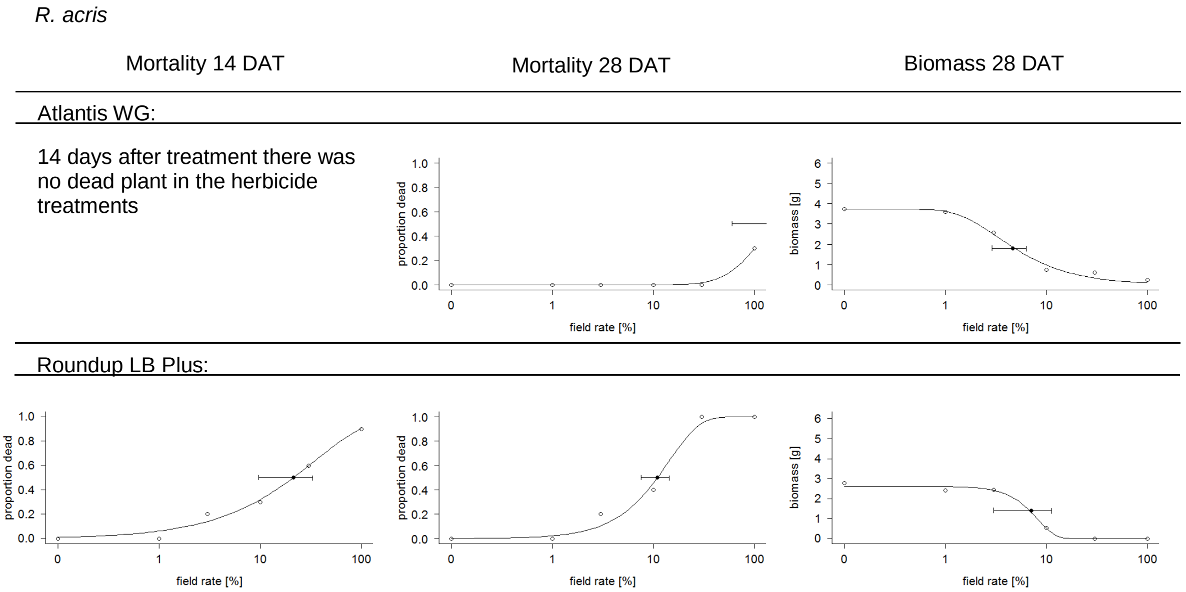


Figure 5-5 Some results of the dose-response experiments with the plant *Plantago major*. At the test beginning, the plants had 3-5 leaves. Further information is provided in the description of Figure 5-4.



14 days after treatment there was no dead plant in the herbicide treatments

Figure 5-6 Some results of the dose-response experiments with the plant *Ranunculus acris*. At the test beginning, the plants had 4-7 leaves. Further information is provided in the description of Figure 5-4.

Part C: Development times of *Mamestra brassicae* (L.) feeding on different (herbicide-free) plant species

Test design:

Mamestra brassicae caterpillars (4 days old) were carefully placed on 3 untreated host plant species (*Plantago lanceolata* (*N* = 20), *P. major* (*N* = 23), and *Ranunculus acris* (*N* = 22); one caterpillar per plant). The test design was the same as described in the Methods section of the main document, with one exception: After the caterpillars had completely consumed their plants and had been transferred in plastic boxes, they were fed exclusively with untreated leaves of their previous test plant species until they pupate. The overall development time until the adult eclosion was noted.

Results:

Caterpillars feeding on *R. acris* had a significantly higher development time as caterpillars feeding on *P. lanceolata* and *P. major* (Figure 5-7).

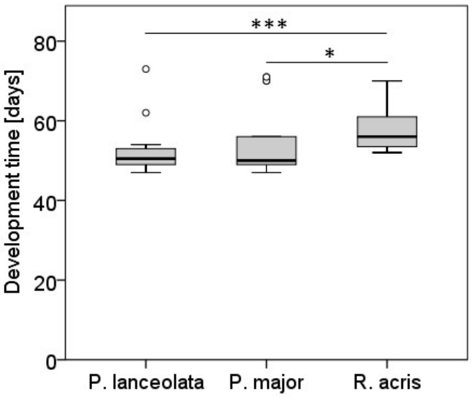


Figure 5-7 Development time of *Mamestra brassicae* from hatching to adult eclosion by feeding on different host plants: *Plantago lanceolata* (development time = 52 ± 6 days; mean ± SD; *N* = 18), *P. major* (54 ± 9 days; *N* = 18), and *Ranunculus acris* (58 ± 5 days; *N* = 20). Dots represent outliers. *** $p < 0.001$, * $p < 0.05$; Kruskal-Wallis test with Mann-Whitney pairwise comparisons as posthoc tests (results Bonferroni corrected).

6 The secret pollinators - an overview of moth pollination with a focus on Europe and North America

Paper 4

This chapter presents the author’s final version of the manuscript

Hahn, M. & Brühl, C.A. (subm.): The secret pollinators – an overview of moth pollination with a focus on Europe and North America.

Abstract – Pollination is a crucial plant-animal interaction in ecosystems. Moths (Lepidoptera) are a widespread and species-rich group of flower visitors. In this article, information on moth pollination, particularly for Europe and North America, is summarized. Plant and moth species connected via pollination interactions were identified from the literature, and information on the relevance of moth pollination in various ecosystems, including agro-ecosystems, was compiled. Overall, 227 pollination interactions between moths and flowers were found, including certain specialized relationships of plants with pollinating seed predators. Most of the interactions could be attributed to the moth families Noctuidae (90 interactions, 56 species) and Sphingidae (85 interactions, 32 species), and to the plant families Orchidaceae (109 interactions, 22 species) and Caryophyllaceae (59 interactions, 16 species). Limited information was available on the role of moth pollination in natural ecosystems (6 studies). In temperate agro-ecosystems, moths are most likely not essential to the pollination of crops; however, they can contribute to the pollination of non-crop plants, which is crucial to maintaining biodiversity in agro-ecosystems. In general, the role of moths as pollinators appears to be underestimated because only a few studies on moth pollination are available, and long-term research focusing on ecosystems is necessary to address temporal fluctuations in their abundance and community composition.

6.1 Introduction

Flower pollination is an essential aspect of reproduction for a number of plant species, and it often relies on animal pollinators (Kearns *et al*., 1998; Potts *et al*., 2010; Willmer, 2011; Abrol, 2012). Frequently, there is a mutualistic relationship between a plant and its pollinators, with plants providing pollinators with resources, such as food in the form of nectar and/or pollen, and pollinators transporting pollen grains from stamens to stigmas (Kevan and Baker, 1983; Kevan, 1999, and references therein). Approximately 87% of the angiosperm plant species (Ollerton *et al*., 2011) are dependent on animal pollination, with insects providing a major part of this service (Kearns *et al*., 1998). Declines in pollinators (e.g., Biesmeijer *et al*., 2006) have alarmed scientists and raised questions regarding the stability of ecosystem functions as well as food security (e.g., Allen-Wardell *et al*., 1998; Kluser and Pedizzi, 2007; Potts *et al*., 2010; however, see also Ghazoul, 2005). Furthermore, these declines have raised awareness that species other than honey bees (*Apis mellifera*), which are considered as main pollinators within many agricultural systems (Kearns *et al*., 1998), may also play an important role in the pollination of crops and wild plants (Buchmann and Nabhan, 1997; Allen-Wardell *et al*., 1998; Abrol, 2012) and that a high diversity of pollinators can buffer the effects of environmental changes regarding pollination service (Brittain *et al*., 2013).

Butterflies and moths belong to the species-rich order Lepidoptera. Overall, approximately 180,000 Lepidoptera species are currently described (Hamm and Wittmann, 2009), and they account for approximately 10% of all known insect species (Willmer, 2011). Lepidoptera have been recognized as one of the most common group of flower visitors (Knuth, 1898, in Willmer, 2011). Many lepidopteran adults either depend on nectar or benefit from its intake (increased longevity or reproduction, Cahenzli and Erhardt, 2013; Mevi-Schütz and Erhardt, 2005; von Arx *et al*., 2013); however, not all lepidopteran flower visitors are pollinators. Although it is known that several Lepidoptera species touch stamens and can transfer pollen (e.g., Courtney *et al*., 1982), limited investigations have been performed to determine their function as pollinators. Available research on this topic has predominantly addressed butterflies (e.g., Levin and Berube, 1972; Coates, 1977; Jennersten, 1984; Murphy, 1984; Subba Reddi and Meera Bai, 1984; Balasubramanian, 1990; Bloch *et al*., 2006), although butterflies account for approximately 10% of Lepidoptera (Shields, 1989). The majority of Lepidoptera can be classified as moths with predominantly crepuscular or nocturnal lifestyles. Nonetheless, butterflies have traditionally attracted the most attention from collectors and hobbyists (New, 2004), and a number of moth species are considered less attractive to collectors and more difficult to observe because of their small size and nocturnal activities; thus, their pollination service has rarely been studied.

Nevertheless, moths are mentioned to play a role in pollination services in ecosystems (e.g., Fox *et al*. 2012, Merckx *et al*. 2012), but to our knowledge, there is no overview of this topic available until now. For this reason, we have identified plant and moth species connected via pollination interactions from the literature, including the special case of pollinating seed predators, with a focus especially on moth pollination in Europe and North America. Furthermore, we have provided information on the relevance of moth pollination in natural and agricultural ecosystems.

6.2 Moth pollination

An extensive literature search using the literature database ISI Web of Knowledge has been performed to study the occurrence and relevance of moth pollination in Europe and North America. The search terms [(pollination OR pollinator*) AND (moth* OR Lepidoptera) NOT (Australia* OR Africa* OR Tropic*)] resulted in 2,838 hits, which were carefully screened by reading the title and abstract. In addition, various terms were searched via Google Scholar (e.g., "moth pollination agriculture", "moth pollination Europe"). The references of interesting papers were also searched for further articles on moth pollination. Overall, more than 300 articles and books focused on moth pollination and associated themes were found.

To obtain an overview of moth pollinators and pollinated plant species in Europe and North America, we searched the available literature for pollination interactions, mostly at the species level (moth species, plant species). Studies focusing on moth pollination without listing the interacting species were not included.

The following section is divided into two parts: (1) the identification of moth-flower interactions on a species basis with moths acting as pollinators and (2) the role of moths as pollinators in ecosystems.

6.2.1 Moth pollinators and pollinated plant species

Moths are common flower visitors, and hundreds of interactions between moths and plant species have been identified (e.g., Ebert, 1994). However, flower visitors may not necessarily provide a pollination service (Subba Reddi and Meera Bai, 1984; Venables and Barrows, 1985; Pettersson, 1991; Kevan, 1999). Therefore, this review only considers studies, in which a moth-flower interaction resulted in a pollen load on the moth body, a deposition of pollen during a flower visit, or the production of seeds after a flower visit. Hence, a number of studies on moth pollination were not included (some information from, e.g., Grant, 1983, 1985; Catling and Catling, 1991) if the listed moth-flower interactions did not clearly meet the above criteria. In the special cases of pollinating seed predators, the occurrence of offspring (eggs or caterpillars) was also accepted as an indication of pollination. Occasionally, moth species were named as pollinators based on references to unpublished data. This information has been included in this review but is marked in the Supplemental Data (Appendix II, chapter 10.1).

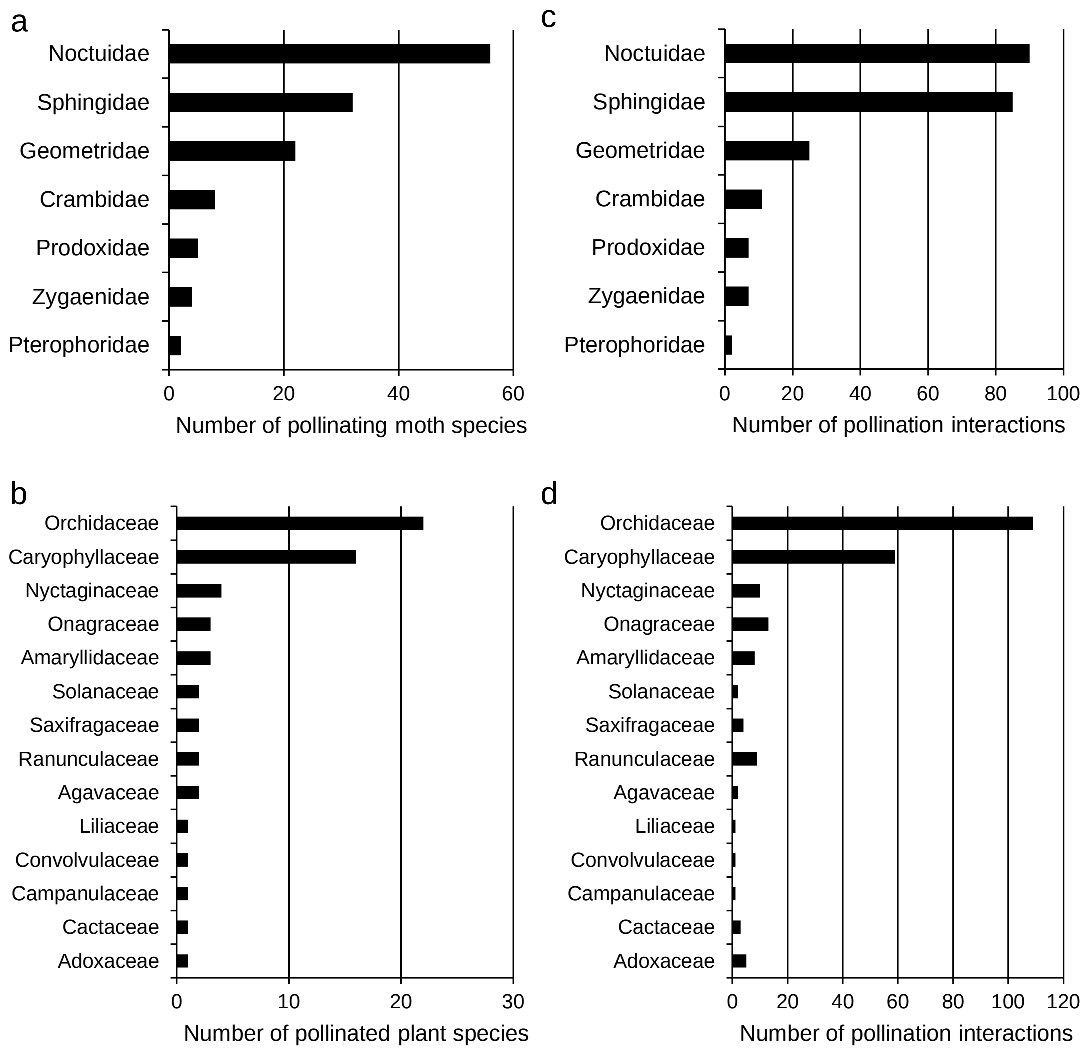


Figure 6-1 Results of the literature search indicating the species number of (a) pollinating moths and (b) pollinated plants per family as well as the number of assessed pollination interactions for (c) moth families and (d) plant families. Details on the pollination interactions and the underlying studies are listed in the Supplemental Data (Appendix II, chapter 10.2).

According to our research, 227 pollination interactions between moth species and plant species have been documented in the literature (Figure 6-1). These interactions include 129 moth species in 7 families (Figure 6-1, Appendix II). Most of the pollination interactions can be attributed to Noctuidae (90 interactions, 56 species) and Sphingidae (85 interactions, 32 species). However, moths of other families, including Microlepidopterans, are responsible for 25% of the interactions. In general, pollination by settling moths has been studied less intensively compared with that of hawkmoths (Sphingidae), although settling moths are considerably more diverse (Atwater, 2013; Okamoto et al. 2008). In tropical ecosystems, numerous tree and other plant species are adapted to hawkmoths as their primary pollinators (e.g., Haber and Frankie 1989), whereas settling moths might be effective pollinators in regions where hawkmoths are less common (Okamoto et al. 2008).

We identified 61 plant species in 14 families for which moths might play a role in pollination (Figure 6-1, Appendix II). Moth pollination was observed in the families Orchidaceae (109 interactions, 22 species) and Caryophyllaceae (59 interactions, 16 species). The breeding system and the pollination of orchids have received attention in research (e.g., Catling and Catling 1991; Argue 2012), and Lepidoptera are known to be the primary pollinators of orchids of the subfamily Orchidoideae (Catling and Catling, 1991). Certain orchids are highly specialized to moths as pollinators, such as the endangered western prairie fringed orchid (*Platanthera praeclara*) for which the only known pollen vectors are certain hawkmoth species (Westwood and Borkowsky, 2004; Borkowsky and Westwood, 2009; Argue, 2012, and references therein). Orchid pollen is often presented in pollinia, which can be attached to specific positions on the body of visiting moths, especially on parts without scales, such as the eyes or the proboscis (e.g., Maad and Nilsson, 2004). Because of these defined pollinia positions, moths can carry the pollen of different orchid species without hybridizing the plants. Furthermore, the pollinia position and form attached to moths can be used to identify visited orchids, even if the visits were not directly observed or moths were trapped using light traps. In this case, it is also possible to obtain information on pollination by examining museum specimens (e.g., Nazarov and Buchsbaum, 2004).

In addition to orchids, approximately 55% of the Caryophyllaceae studied by Kephart *et al*. (2006) were pollinated by Lepidoptera, especially moths. An example of a well-studied plant is white campion (*Silene latifolia*, Caryophyllaceae), a species native to Eurasia that was introduced to North America approximately 200 years ago (Barthelmess *et al*., 2006; Bernasconi *et al*., 2009). The use of this plant by American as well as European pollinators has been studied extensively (Jürgens *et al*., 1996; Young, 2002; Barthelmess *et al*., 2006; Castillo *et al.*, 2014).

The interest of scientists in the pollination of *S. latifolia* (and certain other plant species, see next paragraph) extends to interactions with pollinating seed predators, which are also called nursery pollinators (Kephart *et al*., 2006). The nursery pollinators pollinate flowers; however, females also oviposit in or on flowers, and the hatched caterpillars feed on seeds (Burkhardt *et al*., 2009). Therefore, the interactions between nursery pollinators and their host plants function as model systems for the study of co-evolutionary mutualism (Kephart *et al*., 2006). In general, the relationship between nursery pollinators and plants can range from mutualism to parasitism depending on the amount of seeds consumed by the caterpillars as well as the occurrence and efficiency of co-pollinators.

Research on moth nursery pollinators has focused on five groups (Table 6-1): (1) yucca moths and yucca plants, (2) senita moths and senita cacti, (3) *Epicephala* moths and trees of the family Phyllanthaceae (especially *Glochidion* trees), (4) *Hadena* and *Perizoma* moths and plants of the family Caryophyllaceae (especially *Silene* species), and (5) *Greya* moths and certain plant species of the genus *Lithophragma*. Although *Epicephala* moths and their pollinated Phyllanthaceae plants do not occur in Europe and North America, these interactions are briefly described in Table 6-1.

Table 6-1 Moth nursery pollinators and associated plants.

Interaction between	Moth-plant relationship	Co-pollinators	Information on pollination	References
Yucca plants (*Yucca* and *Hesperoyucca*, Agavaceae) and yucca moths (*Tegeticula* and *Parategeticula*, Prodoxidae)	obligate, mutualistic [1,2]	no [1]	Female yucca moths actively gather pollen and distribute it on the stigma [1,3]. The pollen load of the female *Tegeticula yuccasella* can constitute 10,000 grains and 10% of the female’s body weight [4]. Yucca moths only lay a few eggs per flower and the caterpillars do not consume the complete seeds [1].	[1] Pellmyr, 2003; [2] Pellmyr and Segraves, 2003; [3] Dodd and Linhart, 1994; [4] Pellmyr, 1997
Senita cacti (*Lophocereus schottii*, Cactaceae) and senita moths (*Upiga virescens*, Crambidae)	predominantly obligate, mutualistic [5-7]	yes [6,7]	Senita moths actively pollinate the flowers [5,6]. Under certain circumstances, senita cacti can also be pollinated by bees; however, the pollination efficiency of senita moths is greater compared with other co-pollinators [6,7]. Seed damage by growing caterpillars was observed to be 21% [6].	[5] Fleming and Holland, 1998; [6] Holland and Fleming, 1999; [7] Holland and Fleming, 2002
Phyllanathceae and *Epicephala* moths (Gracillariidae)	obligate, mutualistic [8]	no [12]	According to estimates, more than 500 species of Phyllanathceae are actively pollinated by *Epicephala* moths [9]. The obligate mutualistic relationships demonstrate high degrees of specialization, although not always one-to-one relationships [8,10,11]. Studies of three *Glochidion* tree species revealed that 20-54% of the seeds remain intact after infestations by *Epicephala* moths (and other seed predating, non-pollinating moths) [12].	[8] Kawakita, 2010; [9] Kawakita and Kato, 2009; [10] Kawakita and Kato, 2006; [11] Zhang *et al*., 2012; [12] Kato *et al*., 2003
Silene species and allied Caryophyllaceae (e.g., *Dianthus*) and (1) *Hadena* moths (Noctuidae) or (2) *Perizoma* moths (Geometridae)	facultative, mutualistic to antagonistic [13-19,21]	yes [13-19]	Female *Hadena* and *Perizoma* moths do not actively sample pollen. Male *H. bicruris* moths have also been observed to provide pollination benefits in *S. latifolia* plants [20]. The seed consuming caterpillars can damage 0% to 100% of the seeds per flowers; therefore, the relationship can range from mutualism to parasitism [16,17,21]. In *S. latifolia*, fruit abortion is discussed as a potential control mechanism to reduce seed predators [22].	[13] Pettersson, 1991; [14] Jürgens *et al*., 1996; [15] Westerbergh, 2004; [16] Kephart *et al*., 2006; [17] Gimenez-Benavides *et al*., 2007; [18] Kula *et al*., 2014; [19] Reynolds *et al*., 2012; [20] Labouche and Bernasconi, 2010; [21] Bopp, 2003; [22] Burkhardt *et al*., 2009
Lithophragma plants (Saxifragales) and *Greya* moths (Prodoxidae)	facultative to obligate, mutualistic to antagonistic [23,25]	yes [23]	The interactions between Lithophragma plants and Greya moths are non-obligate; however, the relationships can be strongly mutualistic [23,25]. Caterpillars of *Greya politella* consume approximately 15% to 27% of the seeds of *Lithophragma parviflorum* [24].	[23] Cuautle and Thompson, 2010; [24] Thompson and Pellmyr, 1992; [25] Reynolds *et al*., 2012

6.2.2 Moth pollination in ecosystems

Lepidoptera can be valuable pollinators in ecosystems because butterflies and moths (1) show diurnal, crepuscular, and nocturnal habits, and a number of species visit flowers throughout an entire day; (2) they transport pollen across a range of distances from short to long; and (3) they are a species-rich group of potential pollinators (Travers *et al*., 2012).

However, while several networks of plants and their diurnal pollen vectors have been studied in detail, nocturnal networks have hardly been assessed, although they might represent a significant proportion of plant-visitor interactions (Devoto *et al*., 2011). Moths are likely the most common flower visitors during the night in temperate (and tropical) habitats (Devoto *et al*., 2011). In our literature search, most of the research has focused on individual plant-moth interaction, and only a limited number of studies considered the interactions of several moth species and several plant species in natural communities. These studies were performed in a Scottish boreal pine forest (Devoto *et al*., 2011), the Monahans Sandhills in Texas (Clinebell *et al*., 2004), a sandhill ecosystem in Florida (Atwater, 2013), a semi-arid grassland habitat in Arizona (Alarcon *et al*., 2008), the ketona dolomite glades in Alabama (LeCroy *et al*., 2013) and the grasslands of the Great Plains (Travers *et al*., 2011).

The results of these studies indicate that moth pollination in ecosystems is characterized by high temporal variability. This variability includes species that act as pollen vectors as well as the number of moths carrying pollen in different years (Devoto *et al*., 2011, Alarcon *et al*., 2008). For example, Devoto *et al*. (2011) sampled almost nine-times more moths loaded with pollen in the second year compared with the first year (35 to 304 moths) in their study in a Scottish forest. This difference might have been partly caused by high variances in individual moth species abundances between years. For instance, during a natural outbreak of the hawkmoth *Hyles lineata*, this moth was observed to visit the plant *Nicotiana attenuata* more frequently during an average evening than had been recorded during the previous 16 years of field work (Sime and Baldwin, 2003).

In addition, large differences in the pollen load of moths have been observed, not only between different years (Devoto *et al*., 2011) but also between different moth families and species after foraging on flowers (Atwater, 2013, LeCroy *et al*., 2013). However, most pollen-loaded moths appear to only carry few pollen grains (Atwater, 2013, Devoto *et al*., 2011, Clinebell *et al*., 2004, LeCroy *et al*., 2013). Only approximately 9% of the moths (59 of 622) assessed in the study by Clinebell *et al*. (2004) were loaded with more than 50 pollen grains. However, even with small amounts of pollen grains, moths might be effective pollinators for certain plant species, especially when they are abundant flower visitors (Clinebell *et al*., 2004). Atwater (2013) found that approximately two-thirds of the moths sampled during nectar drinking (64 out of 97) carried pollen, but the pollen presence rates were below 50% for most species when sampled with light traps. However, light trapping might produce biased results when studying moth pollen loads because (1) light attraction differs between moth species (Devoto *et al*.,

2011) and (2) light traps can attract moths before they have visited flowers and contacted pollen grains, which leads to reduced pollen presence rates (Atwater, 2013).

Nevertheless, the results of Clinebell *et al*. (2004) indicate that for three of the assessed plant species (*Gaura villosa*, *G. coccinea*, *Calylophus hartwegii*) moths can be major pollinators because individuals were trapped carrying more than 50 pollen grains. Similarly, Alarcon *et al*. (2008) found large quantities of *Agave palmeri* and *Datura wrightii* pollen on hawkmoth bodies.

The total pollen amount as well as the visited plant species can differ from one year to another (Devoto *et al*., 2011, Alarcon *et al*., 2008). Travers *et al*. (2011) argued that the plant diversity of grassland ecosystems can benefit from diverse pollinators, including moth species. For example, the rare western prairie fringed orchid (*Platanthera praeclara*) depends on hawkmoth pollination and more than 60 grassland plant species were observed to flower coincidentally with *P. praeclara* and were visited by Lepidoptera (Travers *et al.*, 2011).

Overall, limited knowledge is available on the role of moths as pollinators in natural ecosystems. Nonetheless, the results indicate high temporal variation in moth-plant interaction, not only regarding the involved species but also regarding their abundances and pollen loads. In terms of moth pollination in agricultural landscapes, even less information is available, although agriculture represents a major land use both in Europe (approximately 50% of the total EU-27 land area; Stoate *et al*., 2009) as well as in North America (approximately 45% of the total US land area; USDA, 2011).

In agricultural landscapes, studies on pollinators have focused on crop pollination. Although few exceptions occur in which moths might act as co-pollinators (such as blueberry: Cutler *et al*., 2012), crops cultivated in Europe and North America do not appear to rely on moth pollination. However, agro-ecosystems do not exclusively consist of crop plants; there are field margins, hedgerows, meadows, and other semi-natural elements included along with cropped fields, and they are all habitats for numerous non-crop plants. Approximately 40% of the plant species pollinated by moths (see Appendix II, chapter 10.2) can potentially occur in agricultural landscape habitats, such as meadows, pastures, old fields, field margins, and road sides.

Hence, the importance of moths in agricultural landscapes is most likely related to their pollination of non-crop plants, which maintains biodiversity in agro-ecosystems, instead of their pollination of crops, which is commonly valued as an ecosystem service (e.g., Ricketts *et al*., 2008; Power, 2010). This role is of particular importance because a number of organism groups, such as moths (Fox, 2012) and plants (Storkey *et al.*, 2012), are declining in agro-ecosystems and agricultural intensification (e.g., land use changes, input of agrochemicals) has been identified as an important drivers for this reduction.

6.3 Conclusions

Moths are abundant flower visitors and capable of pollinating a range of plant species, of which a number are specialized for moth pollinators (e.g., certain orchids). However, the role of moths as pollinators is most likely underestimated at present because only a limited number of studies on moth pollination are available. Current research at the ecosystem-level and single moth-plant interactional level has showed a high variability in moth populations between years (e.g., Sime and Baldwin, 2003; Alarcon *et al.*, 2008; Devoto *et al.*, 2011). This variability in the abundance of individual species but also in the species composition of moth communities further complicates research on the relevance of moth pollination. In particular, long-term research focusing on ecosystems is necessary to reveal the pollination services of moths according to temporal fluctuations in their abundance.

Moths rely on nectar plants but also on appropriate caterpillar host plants. Hence, preserving and providing habitats rich in plant species might be an effective method of protecting moth-flower interactions. Because Lepidoptera have shown a high sensitivity to various stressors in agro-ecosystems, such as pesticide inputs (Feber *et al.*, 1996; Longley and Sotherton, 1997; Hahn *et al.*, 2015), semi-natural habitats should be protected from such stressors to ensure a diverse Lepidoptera community. Such protection could also benefit further organism groups because Lepidoptera caterpillars and adults are a food source for various bird and bat species (Scoble, 1995; Fox *et al.*, 2006).

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6.4 References

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6.5 Supplemental Data

The Supplemental Data to this manuscript are rather extensive. Therefore, they are presented in Appendix II (chapter 10.2).

7 Summary and general discussion

7.1 The role of narrow field margins for biodiversity

Field margins are common habitat elements in agri-ecosystems; however, agricultural intensification has reduced or eliminated a number of these margins to increase field sizes (Marshall and Moonen, 2002; Robinson and Sutherland, 2002). In recent decades, some attempts have been undertaken to quantify the amount of the remaining field margin habitats in agricultural landscapes (e.g., Kühne *et al.*, 2000; van der Zanden *et al.*, 2013). With the use of Geographic Information Systems (GIS), for example, Kühne *et al.* (2000) estimated the total length of field margins in Germany at approximately 1.3 million kilometers in Germany. However, the length as well as the width are crucial information when working with field margins because the field margin width affects both the (1) habitat quantity and (2) habitat quality for plant and animal species:

(1) Wider field margins provide a greater habitat area and can support a larger number of species and higher abundances of individual species. Consistent with the 'species-area relationship' (Arrhenius, 1921; Würtz and Annila, 2008), plant species richness appears to increase with field margin width (Link and Harrach, 1998; Ma *et al.*, 2002). Furthermore, wider field margins seem to support a greater density of various arthropods, such as grasshoppers (Bundschuh *et al.*, 2012) and hoverflies (Molthan, 1990).

(2) Inputs of agrochemicals decrease with increasing field margin width (Figure 1-4, Table 3-1). The negative effects of agrochemicals in field margins have been demonstrated for various organisms, such as plants (Gove *et al.*, 2007, Kleijn and Snoeijing, 1997) and arthropods (Davis *et al.*, 1991; Langhof *et al.*, 2005). Wider field margins can provide areas with lower pesticide inputs – and thus, higher habitat quality – compared with narrow field margins.

In addition to these ecological aspects of habitat quantity and quality, the width of field margins is also of interest for the risk mitigation measures (RMMs) related to pesticides in Germany (Bundesamt für Verbraucherschutz und Lebensmittelsicherheit, 2015). Although field margins lie outside of fields and can be described as non-target areas for agrochemical applications, narrow margins of less than 3 m width are not included in the RMMs of Germany. Therefore, farmers do not have to maintain distance during pesticide application and can partly overspray them (see chapter 1.2.2), which may result in high pesticide inputs in narrow field margins (Figure 1-4) (Schmitz *et al.*, 2013).

In Paper 1, digital orthophotos were used to assess the amount, width, and vegetation characteristics of field margins in two intensively managed agricultural regions of Germany (RLP: Rhineland-Palatinate; BB: Brandenburg). In both regions, narrow margins with less than 3 m width represented typical landscape elements. In the study region in RLP, approximately 85% of the field margin length belonged to field margins less than 3 m wide, and only a limited number of field margins could be classified as wider than 3 m. Although wider field margins are assumed to offer suitable habitat conditions for a greater number of species, they are likely of minor importance for the biodiversity in the RLP region because of their rarity. In the study region in BB, approximately half of the field margins could be classified as wider than 3 m; however, the overall amount of field margins was strongly reduced compared with that of RLP (RLP: length 119 m/ha, area: 226 m²/ha, BB: length 67 m/ha, area: 84 m²/ha). Hedgerows occurred almost exclusively in field margins wider than 3 m. They are considered valuable elements for biodiversity in agricultural landscapes, because the shrubs, trees, herbaceous plants, and grasses can provide habitat for numerous invertebrate and vertebrate species (e.g., Burel, 1996; Dover and Sparks, 2000; Pollard and Holland, 2006; Stachow, 1988; Tischler, 1948; Zwölfer *et al.*, 1984). Hedgerows provide shelter, foraging habitats for herbivores, pollinators and predators, and roost and nesting sites (Dover and Sparks, 2000; Hinsley and Bellamy, 2000; Pollard *et al.*, 1974). In addition, hedgerows may provide sheltered commuting routes for bats (Boughey *et al.*, 2011). Because of the dominance of narrow field margins, these elements were rather scarce in RLP, with a length of 2 m/ha.

Figure 7-1 Examples of insects observed in narrow vineyard margins in Rhineland-Palatinate.

Nonetheless, even narrow grassy margins provide habitats for various species (Figure 7-1), including plants (Link and Harrach, 1998), spiders and ground beetles (Welling *et al.*, 1994), wasps (Holzschuh *et al.*, 2009), hoverflies (Molthan, 1990), grasshoppers (Bundschuh *et al.*, 2012), butterflies (Feber *et al.*, 1996; Field *et al.*, 2007) and caterpillars (Paper 3). Hence, narrow field margins can positively affect the biodiversity of agro-ecosystems, although these narrow elements might be used predominantly by habitat generalists (e.g., hoverflies; Molthan, 1990). However, habitat with such a linear form may result in a reduced number of individuals (Ewers and Didham, 2007) because of the higher ratio of edge to interior; therefore, species will be exposed to higher pressures from edge-related stressors (e.g., predation, Paton, 1994) relative to non-linear habitats. This might be especially true in the case of narrow field margins because they receive stressors from the field side (agrochemicals) as well as from the road/track side (traffic). As narrow field margins can represent a major component of semi-natural habitats in intensively managed agricultural landscapes (e.g., RLP: 85% (= 102 m/ha) of the field margin length, 65% (= 145 m^2/ha) of the field margin area, Paper 1), their habitat function might still be valuable for biodiversity.

In addition, narrow field margins might serve as corridors between non-linear semi-natural elements and facilitate the movement of species in agro-ecosystems. The abundance and species richness of several wasp species increased in grassy field margins connected with forest edges compared with wasps in highly isolated field margins (Holzschuh *et al.*, 2009). In addition, butterflies prefer to fly along field edges compared with field centers (Dover and Settele, 2009; Fry and Main, 1993), which may be a result of the better availability of resources, such as nectar and host plants. Similar observations have been made for other organisms, like beetles and spiders, whose abundances were also higher close to the field edges and in the field margins than within fields (Welling *et al.*, 1994).

Despite the ecological function of field margins, narrow elements (field margins with widths less than 3 m) are not protected from agrochemical inputs via RMMs in Germany. Thus, the first meter next to the field can receive high application rates (more than 30%, see Figure 1-4 and Schmitz *et al.*, 2013). These inputs can influence plants (Paper 3: Supplemental Data; Schmitz *et al.*, 2014a; Schmitz *et al.*, 2013) and arthropods (Paper 2; Schmitz, 2014) in narrow field margins and might affect food resources for other organisms, such as birds or bats, especially in regions where these elements represent a majority of the available semi-natural habitats.

Therefore, narrow field margins should also be considered in the risk management of pesticides because they are common habitat elements in regions under intensive agricultural use and can fulfill habitat and corridor functions for several species. Reduced inputs of agrochemicals can benefit certain arthropods, such as moths (see chapter 7.2). Furthermore, the habitat quality and resources provided by field margins could be improved by adequate field margin management (e.g., using agri-environmental schemes, see chapter 7.4). For example, the promotion of higher plant diversity, such as through an adapted mowing regime that ensures adequate flowering and seed production of plants or the sowing of diverse seed mixtures in species-poor locations (Carreck and Williams, 2002), could increase the diversity and abundance of herbivores and pollinators (e.g., butterflies, Pywell *et al.*, 2004).

The data presented on field margin widths were recorded in Germany (Paper 1); however, similar assessments of field margin characteristics could also be of interest for other countries in the EU, especially in high-intensity agricultural landscapes because it appears likely that narrow field margins represent common elements in such intensively managed agro-ecosystems. Moreover, country-specific

RMMs and their exceptions (such as the 3 m-width exception in Germany) should be considered when evaluating the semi-natural habitats next to fields and estimating the potential pesticide inputs in these non-target areas.

7.2 Lepidoptera and agrochemicals

7.2.1 Lepidoptera in field margins

Lepidoptera, particularly butterflies, are among the best-studied insect groups (New, 1997, 2004), and a number of species are of conservation interest (e.g., BfN, 1998). Butterflies are regularly monitored in large-scale surveys in various countries (e.g., Van Swaay, 1990; van Swaay *et al.*, 2013; Warren *et al.*, 2001) because they are sensitive to changes in habitat quality. These surveys indicate that strong population declines have occurred in numerous Lepidoptera species in recent decades. The European Grassland Butterfly Indicator (van Swaay *et al.*, 2013) indicated that from 1990 to 2011, the butterfly populations of 17 indicator species have declined by approximately 50% on average compared with the populations in 1990. In Britain, approximately three-quarters of the butterflies analyzed by Warren *et al.* (2001) and approximately two-thirds of the macro-moths studied for the Rothamsted Research project (Conrad *et al.*, 2006) exhibited a declining trend. Agricultural intensification is discussed as one of the main causes of these population declines (Fox, 2012; Fox *et al.*, 2014; Warren *et al.*, 2001), especially habitat loss due to intensified use or abandonment of high-quality habitats (van Swaay *et al.*, 2013), and the use of agrochemicals (Fox *et al.*, 2014).

Semi-natural grasslands, such as extensively managed, flower-rich meadows, represent the main habitat of a number of Lepidoptera species (e.g., for 57% (= 280 species) of the European butterfly species for which information on habitat type is available, van Swaay *et al.*, 2013); however, field margins might serve as surrogates in intensively used agricultural landscapes. Because these margins are vegetated with various grasses, herbs, shrubs, and/or trees, they can provide host and nectar plants for moths and butterflies. Numerous studies have assessed adult Lepidoptera in field margins (e.g., Dover and Sparks, 2000; Feber *et al.*, 1996; Field *et al.*, 2007; Merckx *et al.*, 2009a; Merckx *et al.*, 2012). Adult Lepidoptera were observed to use field margins as foraging habitat; furthermore, their abundance was associated with the availability of floral resources (Feber *et al.*, 1996; Kuussaari *et al.*, 2007; Pywell *et al.*, 2004) and the use of seed mixes that included flowering plant species was found to increase their abundance (Carreck and Williams, 2002; Meek *et al.*, 2002; see also chapter 7.4).

However, only a limited number of studies have assessed the occurrence of caterpillars in field margins, although this developmental stage is likely more sensitive to stressors because caterpillars are often immobile compared with adults and dependent on the availability of suitable host plants. In a survey of narrow cereal field margins in Rhineland-Palatinate, caterpillars belonging to nine families were found (Paper 2). These results indicate that field margins can represent a suitable habitat for the development of Lepidoptera. Nonetheless, the caterpillar abundance in field margins was lower than in meadows (field margin: 4.9 ± 0.9 (May) and 11.7 ± 2.7 (June); meadow: 11.6 ± 2.6 (May) and 18.1 ± 3.6 (June); mean ± SE), which was significant in the sampling phase in May (PerAnova; p = 0.018) but not in June (PerAnova; p = 0.141). This difference might have been caused by differences in habitat area and habitat form (see chapter 4.4) but also by agrochemical inputs. For example, higher abundances of adult Lepidoptera have been observed in unsprayed field edges compared with sprayed field edges (de Snoo *et al.*, 1998; Dover *et al.*, 1990; Dover, 1997; Rands and Sotherton, 1986). Furthermore, studies focusing on the effects of insecticide spray drift on caterpillars found that this life stage can be sensitive to pesticides (e.g., experiments measuring the mortality of *Pieris brassicae* caterpillars after real spray drift events at different wind speeds and in various distances to the field; Davis *et al.*, 1991).

7.2.2 Effects of agrochemicals

Agrochemicals might affect Lepidoptera species in various ways. Thus, direct effects on Lepidoptera and their different development stages are possible (lethal effects of insecticides) as well as indirect effects on the availability or quality of host and nectar plant species (effects of herbicides and fertilizers) can occur (Figure 7-2). In the following sections, an overview of the possible effects of agrochemicals on Lepidoptera is presented.

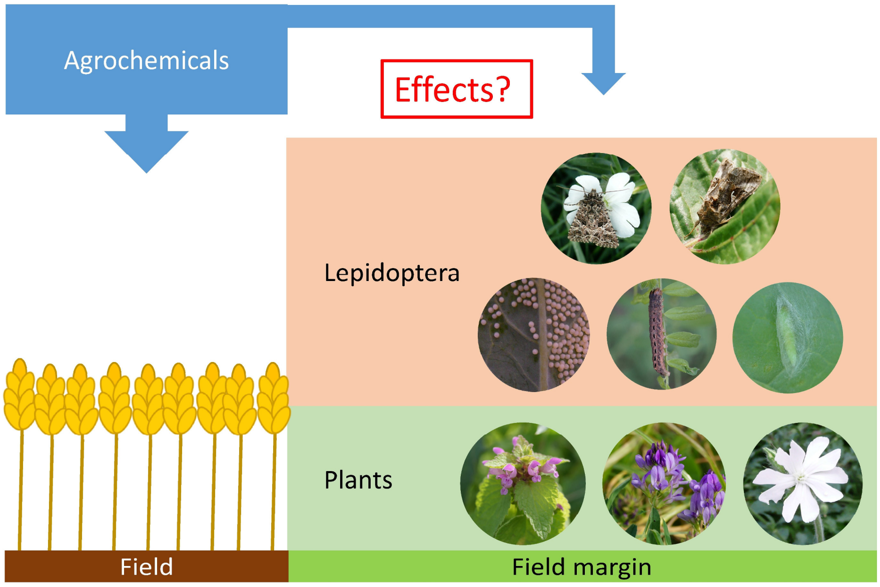

Figure 7-2 Agrochemicals may affect Lepidoptera directly or indirectly because of effects on the host and nectar plants.

7.2.2.1 Insecticides

Insecticides are designed to kill the targeted pest organism(s) in the treated in-field areas. Because certain Lepidoptera can represent major pests (e.g., codling moths *Cydia pomonella* (Tortricidae) for apple, vine moths *Eupoecilia ambiguella* (Tortricidae) for grapes, European corn borer *Ostrinia nubilalis* (Crambidae) for maize), the insecticides used might affect other non-target moth and butterfly species within fields and field margins as well. The insecticides particularly target the caterpillar stage because it is the feeding stage of Lepidoptera and represents the greatest damage to crop plants.

On the one hand, insecticides can cause **lethal effects**. In a field experiment assessing the effects of agrochemicals in narrow field margins using a randomized block design (Schmitz *et al.*, 2013, Paper 2), spraying with the insecticide Karate Zeon (lambda-cyhalothrin, pyrethroid) led to significantly reduced caterpillar numbers in the test plots. Karate Zeon is a non-systemic insecticide against chewing and sucking insects and it rapidly penetrates the insect cuticle and disrupts nerve conduction within minutes, which leads to feeding cessation, reduced muscular control, paralysis, and death (Syngenta, 2015). Laboratory tests with *Mamestra brassicae* caterpillars feeding on leaves treated with various rates of Karate Zeon showed that the LR50 (= lethal rate 50: rate that kills 50% of the test organisms) value was approximately 0.78% (= 0.059 g ha^{-1} active ingredient) of the field rate (Paper 2). This high sensitivity is consistent with the results of other studies; Cilgi and Jepson (1995) tested the toxicity of deltamethrin deposits on cabbage leaves for caterpillars of the butterfly *Pieris brassicae* and found effects at rates of 0.19% of the field application rate (= 0.012 g a.i. ha^{-1}). In addition, field assessments in which young *P. brassicae* caterpillars were placed in field margins showed that real spray drift deposits of insecticide can cause high mortalities in *P. brassicae* caterpillars, but this effect is also influenced by the type of insecticide and the application conditions, especially wind speed (Davis *et al.*, 1991; Sinha *et al.*, 1990). Caterpillars are prey for a number of other species, and they often remain hidden in the vegetation (Scoble, 1995) or the soil (e.g., ‘cutworms’, such as *Agrotis segetum* (Noctuidae); Esbjerg, 1988). Hence, this stage might not come into direct contact with the insecticide spray drift or the overspray. However, even contact with spray deposits on the plants or feeding on sprayed plant material can have lethal effects (Paper 2, Cilgi and Jepson, 1995). In addition to caterpillars, Lepidoptera eggs might also be lethally affected by insecticides; for example, lambda-cyhalothrin is known to have ovicidal properties against eggs of the moth *Spodoptera frugiperda* (Gist and Pless, 1985).

On the other hand, insecticides can also cause **sublethal effects**. Sublethal reactions include weight loss in caterpillars (Abro *et al.*, 1993), reduced pupation times (Kumar and Chapman, 1984), changes in chemical communication and mating behavior of adult moths (Clark and Haynes, 1992; Knight and Flexner, 2007), and reduced reproduction of adult moths (Abro *et al.*, 1993; Han *et al.*, 2012; Knight and Flexner, 2007; Kumar and Chapman, 1984). Thus, unsuitable conditions during caterpillar development might also affect adult moths because there is a positive correlation between pupal weight and adult fecundity (e.g., Calvo and Molina, 2005), with lighter pupae developing into smaller adults, which can result in a reduced egg load in females. Therefore, even if an insecticide does not kill a caterpillar, it might be detrimental to its further development and reproduction.

Moreover, insecticides can act as **repellents**. If a moth species is able to detect an insecticide, it can try to avoid it; caterpillars have been observed to prefer untreated food over insecticide-treated food (Abro *et al.*, 1993; Kumar and Chapman, 1984), and adult females can avoid oviposition on insecticide-treated surfaces (Kumar and Chapman, 1984; Seljasen and Meadow, 2006). Although sublethal effects often reduce the performance of the species, repellence might be beneficial to moths if they are able to switch to uncontaminated oviposition or feeding sites. For example, in a choice experiment, young *M. brassicae* caterpillars did not completely avoid feeding on insecticide treated leaves, but did appear to prefer unsprayed leaves, which indicates minor repellent effects (Paper 2). Their survival increased from 25% to 75% when they could choose between treated and untreated leaves compared with the experiment in which they could only feed on insecticide-treated leaves (treatment: Karate Zeon, 1% of the field rate; Paper 2). Furthermore, in a semi-field study assessing the oviposition behavior of *Hadena bicruris* moths, the females laid 40% fewer eggs on *Silene latifolia* plants sprayed with an insecticide (treatment: Karate Zeon, 30% of the field rate; Paper 2) than on untreated control plants. Considering the high toxicity of this insecticide against *M. brassicae* caterpillars, this avoidance behavior of female *H. bicruris* moths likely reduces the risk of mortality to their offspring.

7.2.2.2 Herbicides

In agricultural landscapes, herbicides and fertilization (see next section) are among the main causes for the observed decline in wild plant species (Andreasen *et al.*, 1996; Carey *et al.*, 2008; Storkey *et al.*, 2012; Wilson *et al.*, 1999). The plant communities in field margins can be strongly affected by inputs of herbicides (Kleijn and Snoeijing, 1997; Schmitz *et al.*, 2014a), and even low rates of herbicides can have detrimental effects on plants (Supplemental Data Paper 3).

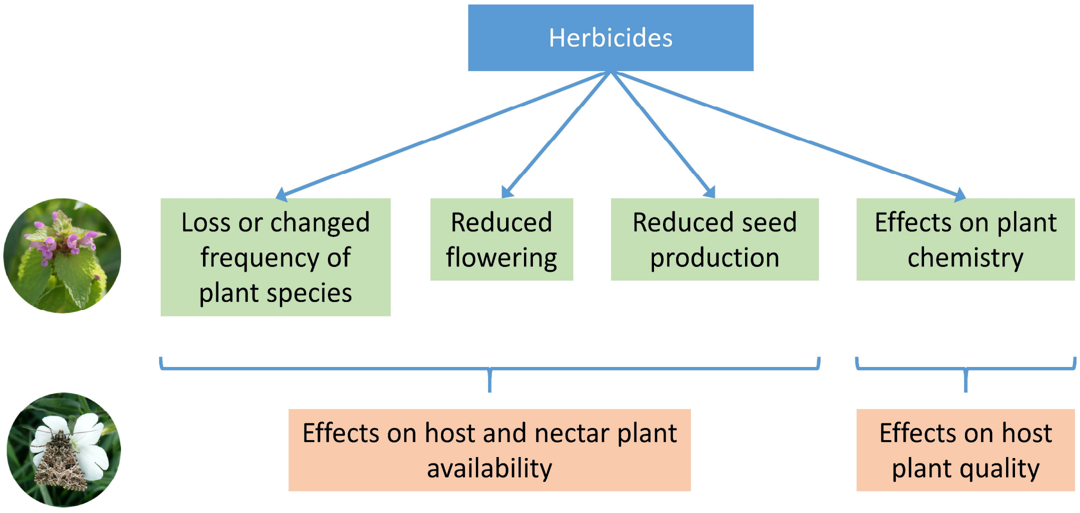

Figure 7-3 Potential effects of herbicides on plants and subsequent effects on Lepidoptera.

Herbicides can affect caterpillars through the **loss or reduced availability of host plants** (Figure 7-3). Thus, mono- and oligophagous Lepidoptera species likely have an increased susceptibility to changes in their host plants relative to polyphagous species, which can switch to another plant species. However, even polyphagous Lepidoptera prefer specific host plants, and less suitable host plant species can influence the caterpillar's performance, including the development rate, body mass, mortality and pupal diapause intensity (Metspalu *et al.*, 2013). Nonetheless, specialized Lepidoptera species have been shown to display stronger population declines compared with generalists (Kotiaho *et al.*, 2005; Kuussaari *et al.*, 2007).

In addition to caterpillar host plants, nectar resources for adult moths can also be affected. A sublethal effect of certain herbicides is a **reduced flowering of plants** (Schmitz *et al.*, 2013, 2014b). Although certain moths do not need to feed on nectar, the longevity and reproductive success of several species is increased by the intake of nectar (Mevi-Schütz and Erhardt, 2005; von Arx *et al.*, 2013), which also enhances their energetic state (Winkler *et al.*, 2009). This effect occurs for females as well as male moths (Cahenzli and Erhardt, 2012). Because the availability of floral resources is among the factors that influence the abundance of Lepidoptera (Meek *et al.*, 2002; Pywell *et al.*, 2004), reduced flowering is presumably detrimental to various Lepidoptera species, particularly in intensively used agricultural landscapes that provide only a limited number of flower-rich semi-natural elements, such as extensively managed meadows. However, certain flowering plants might be more important as nectar sources than others; for example, butterflies appear to prefer legumes (Pywell *et al.*, 2004). Schmitz *et al*. (2014b) studied the effects of a sublethal herbicide rate on the flowering and reproduction of several plant species, including two species of legumes (*Lathyrus pratensis*, *Vicia sepium*); the herbicide treatment surpressed the formation of flowers, and thus, the seed production of both legume species (and a further plant species: *Ranunculus acris*) was significantly reduced. **Reduced seed production** (Schmitz *et al*. 2014b) can not only be detrimental for seed-eating caterpillars (e.g., *H. bicruris*), but it can also reduce the abundance of the plant species, therby reducing the availability of host and nectar plants.

In the field experiment (Paper 2), significant effects of the herbicide applications on caterpillar abundance were not detected. However, the effects of agrochemicals on plants were found to intensify over time. Although individual plant species displayed herbicide effects even during the first year of the field experiment (Schmitz *et al.*, 2013), changes in the plant community were first apparent in the third year (Schmitz *et al.*, 2014a). Hence, the effects on caterpillars might also have been detectable after this time.

In addition to the effects on host and nectar plant availability, herbicides can also **influence host plant quality**. Similar to all other animals, Lepidoptera depend on the appropriate intake of nutrients like carbohydrates, fats, proteins, minerals, and vitamins. In general, juvenile development stages are especially vulnerable to (1) deficiencies in nutrient uptake and (2) the consumption of detrimental substances. Herbicides can affect the quality of host plants for caterpillars in two ways.

First, herbicides alter plant chemistry and can affect the nutritional value of treated host plants. For instance, the effect of glyphosate herbicides is based on the inhibition of an enzyme in the shikimate pathway (Duke and Powles, 2008), and sulfonylurea herbicides inhibit the enzyme acetolactate synthase (Drobny *et al.*, 2012). These enzymes are involved in the synthesis of amino acids in plants. The consumption of amino acids is essential in the development of herbivores (and other organisms); thus, herbicide-treated plants may not meet the nutritional requirements of caterpillars.

Second, herbicides act as stressors for plants and can affect their phytochemistry through the production of secondary metabolites (Kjær *et al.*, 2001). Several secondary metabolites have toxic or deterrent effects on herbivores (e.g., Barbehenn and Constabel, 2011; Bennett and Wallsgrove, 1994; Bosch *et al.*, 2014a) and represent plant defense mechanisms against herbivores. After insect damage or mechanical wounding, several plant species have been observed to increase their concentrations of specific metabolites like tannins (Barbehenn and Constabel, 2011) or jasmonates (Bosch *et al.*, 2014a). Tannins are common secondary metabolites in woody and herbaceous plants, and they are assumed to have deterrent and toxic effects on non-adapted insect herbivores because of the production of high levels of reactive oxygen species after their ingestion (Barbehenn and Constabel, 2011). Tannins supplied in an artificial diet were found to suppress the growth and reduce the survival of caterpillars of *Spodoptera eridania* (Manuwoto and Scriber, 1986) and *Malacosoma disstria* (Karowe, 1989). In the species *Spodoptera exigua* and *Manduca sexta*, jasmonate acid affects oviposition behavior as adults and feeding behavior as caterpillars on tomato plants (Bosch *et al.*, 2014a; Bosch *et al.*, 2014b). However, the reactions of caterpillars to secondary metabolites are species specific; thus, generalist feeders might be deterred by the occurrence of secondary metabolites, whereas specialist feeders may have evolved mechanisms to manage specific secondary metabolites in their diet (e.g., caterpillars of the tobacco hornworm *Manduca sexta*, Glendinning, 2002).

In Paper 3, *Mamestra brassicae* caterpillars feeding on herbicide-treated *Ranunculus acris* plants showed reduced survival and performance (Figure 5-2, Table 5-1). On the one hand, this effect could have been caused by the inhibition of the enzyme acetolactate synthase, which blocks the synthesis of certain amino acids and, thus, affects protein synthesis (Drobny *et al.*, 2012). However, these amino acids (leucine, valine, and isoleucine) are essential for animals, including insects (O'Brien *et al.*, 2005). On the other hand, the plant tissues of *R. acris* are known to contain ranunculin, a substance that can be transformed into the toxin protoanemonin and can be toxic to livestock as well as several insect species (see Sedivy *et al.*, 2012, and references therein). Both of these mechanisms could have negatively affected the survival and development of *M. brassicae* caterpillars. Such detrimental effects of sublethal herbicide rates on host plant quality have been recognized in other studies as well: Kjær and Elmegaard (1996) observed increased mortality of the leaf-eating beetle *Gastrophysa polygoni* (Coleoptera) feeding on *Polygonum convolvulus* plants sprayed with chlorsulfuron; Agnello *et al.* (1986) found reduced longevity of caterpillars of the soybean looper (*Pseudoplusia includes*) on soybean plants sprayed with the growth regulator herbicides fluazifop-butyl; and Speight and Whittaker (1987) noticed extended development times and reduced female egg numbers of the green dock beetle (*Gastrophysa viridula*) on broad-leaved dock (*Rumex obtusifolius*) treated with a systemic herbicide (methyl(4-aminobenzene sulfonyl)carbamate).

Although these herbicide effects on the survival, development, and performance of Lepidoptera and other herbivores were observed, significant effects of the herbicide applications on caterpillar abundance were not detected in the plots of the field experiment (Paper 2). An explanation for this lack of effect might be that herbicide effects on host plant quality and plant resources appear to be species-specific. To identify such effects in the field, a more specific survey method (compared with sweep nets) could be useful, including observations and assessments of caterpillars on their particular host plant.

7.2.2.3 Fertilizer

Similar to herbicides, fertilizers might **affect the availability of host plants and nectar plants** (Figure 7-4) because they can alter the community composition of plants (Kleijn and Verbeek, 2000; Schmitz *et al.*, 2014a). Fertilizers promote the occurrence of (tall) nitrogen-tolerant plants (such as certain grasses; Boatman, 1994; Schmitz *et al.*, 2014a), whereas smaller plant species are more shaded and can suffer from a lack of light (Hautier *et al.*, 2009), which can further reduce the occurrence of smaller species. Hence, in the long run, fertilizers can reduce plant species richness (Kleijn and Verbeek, 2000; Schmitz *et al.*, 2014a).

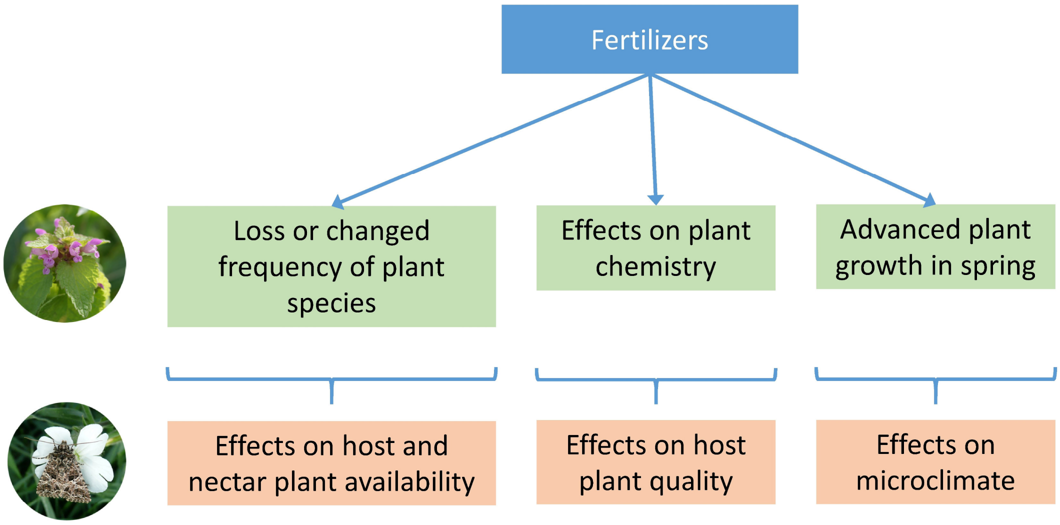

Figure 7-4 Potential effects of fertilizers on plants and subsequent effects on Lepidoptera.

Because caterpillars (and other herbivores) are are dependent on their host plants, fertilizers may also decrease the abundance and diversity of caterpillars and other herbivores. Moth species whose larval host plants are associated with low nitrogen and open environments showed the strongest declines in Britain in recent decades (Fox *et al.*, 2014). However, specific Lepidoptera might also benefit from plant species-poor habitats if the remaining plant community consists of suitable host plants. For example, sown grass strips consisting of two to four grass species have been found to increase the abundance of butterfly species that feed on grasses during their caterpillar stage, such as *Maniola jurtina*, *Thymelicus sylvestris* and *Thymelicus lineola* (Field *et al.*, 2007). Furthermore, the abundance of *Urtica dioica*, a plant species adapted to nitrogen-rich habitats, has strongly increased in the last years in Britain (Carey *et al.*, 2008), which is associated with increasing population trends in several butterflies that use *U. dioica* as a caterpillar host (Smart *et al.*, 2000).

In the field experiment (Paper 2), the fertilized plots were characterized by a significantly increased number of caterpillars during the second sampling period in June. This difference could possibly be attributed to a higher availability of certain host plant species. For example, the frequency of the grass *Dactylis glomerata* significantly increased by approximately 12% in the fertilized plots compared with the control plots (Schmitz *et al.*, 2014a). The internet database 'HOSTS – a database of the World's Lepidopteran hostplants' (Robinson *et al.*, 2010) lists more than 30 Lepidoptera species that feed on this grass in Europe. Hence, caterpillars of these species might have benefited from fertilizer applications. Furthermore, the results of the caterpillar sampling in the field experiment suggested that fertilizer applications affected the composition of the caterpillar community during the sampling in May (Paper 2). Nevertheless, changes in the plant community were initially observed during the third year of the experiment (Schmitz *et al.*, 2014a); therefore, effects on the abundance and community composition of caterpillars might also intensify after a longer time period.

Fertilizers can alter the availability of host and nectar plants and increase the availability of nutrients in the soil, which might **affect the quality of host plants,** especially their nutritional value. Nitrogen is an essential element in the diet of animals, including Lepidoptera, because it is necessary for the building of proteins, and herbivores in particular face the dilemma of gaining enough nitrogen out of their rather nitrogen-poor plant food (Pierce and Berry, 2011). Fertilization increases the nitrogen content in plants (Baylis and Pierce, 1991; Chen *et al.*, 2004), which can be beneficial for herbivores. Several studies have shown positive effects of fertilization on the abundance (Haddad *et al.*, 2000) and populations (Butler *et al.*, 2012) of herbivores as well as the development and performance of caterpillars (Arshad *et al.*, 2013; Baylis and Pierce, 1991; Giertych *et al.*, 2005; Hwang *et al.*, 2008; Kula *et al.*, 2013; Wheeler and Halpern, 1999). In choice experiments, caterpillars of *Spodoptera exigua* fed preferentially on host plants with higher nitrogen content (Chen *et al.*, 2008). In addition, female Lepidoptera have been observed to prefer fertilized host plants as oviposition sites compared with unfertilized host plants (Baylis and Pierce, 1991; Chen *et al.*, 2008; Chen *et al.*, 2004; Prudic *et al.*, 2005). Hence, the increased caterpillar abundance in the fertilized plots in the field experiment (Paper 2) could also have resulted from increased oviposition and improved caterpillar performance.

However, the effects of fertilizers on herbivores are not solely positive (Butler *et al.*, 2012). Fox *et al.* (2014) indicated that moth species whose host plants are adapted to nutrient-poor environments exhibited the strongest population declines. Similarly, Kuussaari *et al.* (2007) found that the host plants of decreasing butterfly species grow in less eutrophic habitats compared with increasing butterfly species. On the one hand, this result may be explained by the negative effects of fertilizers on the availability of host plants; e.g., Schmitz *et al.* (2014a) observed that the number as well as the frequency of several plant species decreased in plots receiving fertilizer treatments. On the other hand, certain caterpillar species are negatively affected by increasing nitrogen concentrations in their host plants, such as the caterpillars of *Cabera pusaria* (Geometridae) (Kula *et al.*, 2014). High nitrogen contents may be detrimental to Lepidoptera species adapted to nutrient poor conditions, including caterpillars that feed on leaves with seasonally decreasing nitrogen content (Kula *et al.*, 2014). Thus, fertilizer inputs may cause a reduced availability of host plants and result in higher nitrogen concentrations in plant tissues, which are unsuitable for certain caterpillars. Moreover, next to effects on the performance and development of individual herbivore species, fertilization may influence processes that affect species at the population level as well, such as parasitism, predation, and competition (see Kytö *et al.*, 1996, for examples on individual and population responses for insects in trees). For instance, fertilizer-induced increases in the biomass of plants may enhance the overall abundance of herbivores but, as a consequence, also the density of general predators; this increased predation might override the positive fertilizer effects for herbivores (Kytö *et al.*, 1996).

Moreover, fertilizers can **affect the microclimate** of habitats. In combination with climate change, fertilizers can advance plant growth in spring, which might increase shading in vegetated habitats and thereby contribute to microclimatic cooling (WallisDeVries and Van Swaay, 2006). Such cooling might be detrimental to thermophilous Lepidoptera species, especially to species hibernating as eggs or caterpillars (WallisDeVries and Van Swaay, 2006).

7.3 Moths as pollinators and effects of agrochemicals on the pollination service

Pollination is a crucial ecosystem service in natural and agricultural terrestrial ecosystems (Klein *et al.*, 2007; Ollerton *et al.*, 2014). In agricultural landscapes, studies have focused on crop pollination and the main crop pollinator, the honey bee. However, other species are also valuable pollinators for crops and wild plants, and declines in honey bee populations have increased the awareness of the role of these species as pollinators, which has remained relatively unknown and unappreciated until recently (Allen-Wardell *et al.*, 1998).

Lepidoptera are among the most common flower visitors (Knuth (1898) in Willmer, 2011) and can be valuable pollinators in ecosystems for three reasons (Travers *et al.*, 2011): First, their diurnal, crepuscular, and nocturnal habits indicate that a number of Lepidoptera species are visiting flowers throughout the entire day. Second, different Lepidoptera species can transport pollen from short to long distances. Third, Lepidoptera are a species-rich group of potential pollinators. However, only a small number of studies have assessed lepidopteran pollination services, and there is even less information available for moths than for butterflies. Nonetheless, in a literature search of the available studies on moth pollination in Europe and North America (Paper 4), approximately 230 pollination interactions between individual moth and plant species were identified. Especially in the plant families Orchidaceae and Caryophyllaceae, a number of examples of moth pollination were observed. However, only six studies considered moth pollination on an ecosystem level (Alarcon *et al.*, 2008; Atwater, 2013; Clinebell *et al.*, 2004; Devoto *et al.*, 2011; LeCroy *et al.*, 2013; Travers *et al.*, 2011). Moths can be among the most common flower visitors in certain ecosystems (Clinebell *et al.*, 2004) and may carry the pollen of various plant species (see Supplemental Data of Paper 4, Appendix II). However, the observed moth-flower interactions often showed a high temporal variability regarding the involved moth and plant species but also in the number of pollen-loaded moths and their particular pollen loads (Alarcon *et al.*, 2008; Devoto *et al.*, 2011). Furthermore, differences were observed in the pollen load and the pollination services of different moth families and species (Atwater, 2013; Devoto *et al.*, 2011).

Although pollination is a valued ecosystem service in agro-ecosystems (Power, 2010), to my knowledge, information is not available on the pollination service provided by moths. Nonetheless, approximately 40% of the plant species analyzed for individual moth-flower interactions (Paper 4) can potentially occur in semi-natural habitats, such as pastures and field margins, in agricultural landscapes (e.g., the moth pollinated *Silene latifolia*, Jürgens *et al.*, 1996 and personal observations). Hence, although moths are most likely of low importance with regards to the pollination of crops in temperate regions, their pollination service might benefit the overall biodiversity of agricultural ecosystems.

However, agrochemicals can negatively affect the pollination service of moths. On the one hand, insecticides can affect moth pollinators. In a semi-field experiment, the number of pollinated *S. latifolia* flowers was significantly reduced on plants treated with 30 % of the field rate of an insecticide (Paper 2). This reduction was most likely caused by repellent effects of the insecticide (lambda-cyhalothrin) against *Hadena bicruris* moths, the main-pollinator of *S. latifolia* (Kephart *et al.*, 2006). This hypothesis is consistent with the observation that insecticide-treated plants carried 40% less moth eggs (Paper 2), as *H. bicruris* moths are pollinating seed predators, with adult females pollinating flowers during oviposition and caterpillars feeding on the seeds (Figure 1-7). Although the overall seed production was similar between treated and control plants in the case of *S. latifolia* (insecticide treatment: 194 ± 28 seeds per flower, control: 206 ± 25 seeds per flower, Paper 2) and negative effects on the population of *S. latifolia* were not expected, the results might be different for other plant species, such as plant species that produce fewer seeds per plant. Furthermore, because of the high temporal variability of moth pollination, long-term studies are necessary to reveal the pollination interactions of moths and the effects of agrochemicals.

On the other hand, agrochemicals can affect plants and might thereby alter pollination interactions. For example, the inputs of sulfonyl-urea herbicides can reduce the flower formation of various plant species (Schmitz *et al.*, 2014b). Settlings moths may seek nectar from clusters of flowers (inflorescences) (Atwater, 2013; Oliveira *et al.*, 2004). Herbicide inputs typical for narrow field margins (30% of the in-field rate) reduced the flowering intensity of *Ranunculus acris* plants by 85% (Schmitz *et al.*, 2013). Such scattered flowers might attract fewer settling moths and reduce the pollination success and seed production. However, addition research is needed to assess the potential effects of herbicide-caused flower suppression on the foraging and pollination behavior of (settling) moths.

7.4 Protection of Lepidoptera in agricultural landscapes

Many species of Lepidoptera occur as caterpillars (Paper 3, Facey *et al.*, 2014) and adults (e.g., Feber *et al.*, 1996; Fuentes-Montemayor *et al.*, 2011; Merckx *et al.*, 2012) in agricultural landscapes. Thus, Lepidoptera play an integral role in these landscapes: First, because of their species richness, Lepidoptera contributes to the diversity of agro-ecosystems. Second, they provide services such as pollination and breaking down live plant tissue (Scoble, 1995). Third, they constitute a major food resource for species of higher trophic levels, like birds and bats (Scoble, 1995; Vaughan, 1997; Wilson *et al.*, 1999). Hence, the protection of moths and butterflies is of interest for the protection of biodiversity in agricultural areas.

An option for improving the protection of moths in agricultural landscapes could be to adapt the risk assessment procedure for pesticides. As mentioned in the introduction, the current arthropod test species are predominantly predators, and herbivores are not included. Lepidoptera have shown sensitivity to (low rates of) pesticides. Furthermore, the current test species do not represent the typical species occurring in field margins. Therefore, it has been recommended in the ESCORT 2 workshop to improve the available information on the pesticide effects on NTAs (Candolfi *et al.*, 2000), such as Lepidoptera. In addition, indirect effects, such as a lack of food sources or changes in food quality caused by herbicides (as described in Paper 2), are not included in the risk assessment for NTAs.

Currently, the guidance document on terrestrial risk assessments is revised, and the protection of biodiversity is considered as a general protection goal (EFSA, 2015). A new risk assessment scheme for NTAs is proposed in a scientific opinion of the EFSA (EFSA, 2015). The scheme recommends to test at least four arthropod species of different taxonomic groups and lifestyles for the tier 1 level of the risk assessment, and the selected test species should include lepidopteran caterpillars to represent herbivorous NTAs (oral toxicity study). Furthermore, it is suggested to assess the reproductive effects of pesticides beginning at tier 1 (EFSA, 2015).

Although this recommended scheme is most likely more suitable for identifying the direct effects of insecticides (especially lethal and possibly also certain sublethal effects) on Lepidoptera, indirect effects, such as herbicide-induced changes in host plant quality, are not addressed. Such indirect effects are difficult to assess experimentally because they most likely depend on the herbicide as well as the herbivore and plant species. Thus, testing all of these combinations would be unrealistic. A more appropriate option for the protection of moths and butterflies in agricultural landscapes would include a focus on RMMs to ensure that the amount of pesticide inputs is further reduced in non-target habitats next to agricultural sites (e.g., via the use of buffer strips; EFSA, 2015).

On the other hand, Lepidoptera could benefit from agri-environmental schemes (AESs). In Europe, AESs are implemented to encourage farmers to protect and enhance the environment on their farmland by providing payments in return to such services (European Commission, 2005). In general, AESs aim to decrease management intensity regarding (parts of) agriculturally used fields (e.g., application of agrochemicals) and/or the management of semi-natural habitats according to certain prescriptions (Ekroos *et al.*, 2014). Although there is a debate on the effectiveness of AESs regarding the protection of farmland biodiversity (Berendse *et al.*, 2004; Ekroos *et al.*, 2014; Kleijn and Sutherland, 2003; Primdahl *et al.*, 2003), there is evidence that at least certain organism groups can benefit from the implementation of several AESs (Boatman *et al.*, 2008; Haaland *et al.*, 2011; Kleijn *et al.*, 2006; Marshall *et al.*, 2006; Taylor and Morecroft, 2009), including Lepidoptera species (Facey *et al.*, 2014; Fox, 2012; Fuentes-Montemayor *et al.*, 2011; Merckx *et al.*, 2010a; Merckx *et al.*, 2009b).

First, Lepidoptera can benefit from schemes implemented at agricultural sites. For example, measures to increase the diversity of crops as well as non-crop plants in fields benefit arthropod predator populations and reduce the negative impacts of pest organisms, which leads to reduced pesticide inputs to the fields (Letourneau *et al.*, 2011) and field margin habitats. This reduced pesticide inputs would most likely favor Lepidoptera in these habitats. In addition, weedy patches in fields, such as herbicide-free crop edges with flowering non-crop plants, provide nectar resources for adult Lepidoptera (Pywell *et al.*, 2004) and other flower visiting insects. The cultivation of flower strips within the fields or at the crop edges can greatly enhance the availability of nectar and pollen, which can increase the abundance and diversity of adult Lepidoptera (Haaland and Bersier, 2011; Haaland and Gyllin, 2010; Korpela *et al.*, 2013). Although individual caterpillars have been observed in flower strips, the suitability of this habitat element for juvenile Lepidoptera can be increased by the inclusion of appropriate host plant species in the seed mix and a multi-year time span between sowing and ploughing (Haaland and Bersier, 2011) as well as an adapted management of the strips (e.g., mowing can cause high caterpillar mortality; Humbert *et al.*, 2010). ‘Grass only’ strips, which are a common AES implemented in Great Britain, are less suitable habitats for Lepidoptera. Although such grass strips can promote the abundance of individual species, such as *Maniola jurtina*, the lack of nectar and host plants limits their benefit for Lepidoptera species (Field *et al.*, 2005, 2007). Nonetheless, unsprayed crop edges and in-field flower or grass strips can act as a buffer for inputs of agrochemicals in adjoining field margins.

Second, moths and butterflies can benefit from AESs that target field margin habitats. For instance, AESs that enlarge field margin widths can increase the abundance and species richness of moth species (Merckx *et al.*, 2009a; Merckx *et al.*, 2012). This effect might be attributed to the greater availability of habitat for adult and juvenile Lepidoptera as well as improved habitat quality in relation to pesticide inputs because spray drift decreases with increasing distance to the field. Furthermore, plant species richness increases with margin width (e.g., Link and Harrach, 1998), which most likely also increases the availability of host and nectar plants. However, appropriate management of field margins is also important because mowing causes high caterpillar mortalities (Humbert *et al.*, 2010). Furthermore, mowing time and frequency can influence the availability of floral resources (Noordijk *et al.*, 2009; Smith *et al.*, 1994). In the short term, mowing also affects the plant species richness of field margins, whereas in the long term, it predominantly influences the composition of the plant community (Smith *et al.*, 2010). Hedgerows and hedgerow trees can also positively affect the abundance, species richness and diversity of moths (Merckx *et al.*, 2009a; Merckx *et al.*, 2012). These elements provide additional host plants for species feeding on trees and bushes (such as several mining species), as well as lichens. In addition to these direct effects on host plant availability, hedgerow trees can provide shelter and a warmer microclimate, which is most likely another reason for the increased abundance and species richness of moths next to hedgerow trees (Merckx *et al.*, 2012). Furthermore, hedgerows and trees might act as stepping stone habitats and hence can reduce the fragmentation of agricultural landscapes (Slade *et al.*, 2013). Thus, the management of hedgerows (e.g., cutting frequency and time) can affect the abundance of certain feeding guilds as well as the parasitism rates of caterpillars (Facey *et al.*, 2014).

Although schemes are implemented at a local level (i.e., individual farmers, individual fields), the benefits of these AESs for Lepidoptera may be optimized at the landscape level because the mobility can differ considerably between Lepidoptera species (Merckx *et al.*, 2009a; Merckx *et al.*, 2009b). Furthermore, the efficiency of AESs may vary among different landscapes (Ekroos *et al.*, 2014). The beneficial effects of wider margins and hedgerow trees were shown to increase in landscapes with a higher occurrence of AESs (Merckx *et al.*, 2009b). In addition, the abundance of micro-moths was positively related to the percentage of semi-natural habitat in a distance of 250 m (Fuentes-Montemayor *et al.*, 2011), whereas macro-moths appeared to be affected by their surroundings in a radius of 800 m and might benefit from the implementation of AESs at this scale (Merckx *et al.*, 2012; but also see the results of Fuentes-Montemayor *et al.*, 2011).

However, most AES may primarily favor mobile habitat generalists, whereas habitat specialists and poor dispersers likely need AESs that are tailored to their habitat requirements (Ekroos *et al.*, 2010), but adequate information on the specific needs of numerous species is often lacking (Merckx *et al.*, 2010a). Nonetheless, rare or declining species can also benefit from more generalized AESs (Merckx *et al.*, 2010a; Merckx *et al.*, 2012), especially when implemented at relatively small spatial scales (Merckx *et al.*, 2012).

8 Conclusions and outlook

Agriculture is a dominant land use in Europe (Stoate *et al.*, 2009) and worldwide (Foley *et al.*, 2005). Because of human population growth, increasing demands for agricultural products, such as food and fuel, will most likely further increase the area of cultivated land as well as the cultivation intensity.

In general, wildlife species provide crucial ecosystem services in agricultural landscapes and enhance agricultural production (Power, 2010). While traditional land use systems create and preserve diverse habitats and enable numerous wildlife species to survive in these landscapes, agricultural intensification poses a major threat to biodiversity (e.g., Krebs *et al.*, 1999; Stoate *et al.*, 2009). For example, a myriad of moths and butterflies act as herbivores, pollinators and prey organisms in ecosystems. In agricultural landscapes under intensified use, Lepidoptera are not only influenced by the loss of suitable habitats, but also by inputs of agrochemicals in the remaining non-crop elements, such as field margins. Agrochemicals can affect Lepidoptera directly (e.g., lethal effects of insecticides) and indirectly through changes in the quantity and quality of host and nectar plants (herbicides and fertilizers) and repellent effects.

Further research on the ecological services provided by Lepidoptera and the effects of agricultural management, especially the impacts of agrochemicals, on this (and other) organism group(s) is necessary to better understand the risks and threats of intensified agro-ecosystems to biodiversity and design appropriate measurements (such as AESs) to mitigate negative effects. For example, on the basis of the results of the present thesis as well as other research, the improved protection of field margin habitats from agrochemicals is recommended because of its potential benefits to Lepidoptera (and other organisms, such as plants).

Furthermore, not only should the agricultural management be improved, but also agricultural products should be used more efficient. One third of food production is lost or wasted globally (Gustavsson *et al.*, 2011), and another third is used inefficiently as livestock feed (Tscharntke *et al.*, 2012). In addition, agricultural sites are used for the growth of biofuel feedstocks and approximately 12% of coarse corn, 14% of vegetable oil, and 30% of sugarcane production globally will likely be used for biofuel until 2023 (OECD-FAO, 2014). Thus, a more efficient use of agricultural products would reduce the pressure on agro-ecosystems and might even allow the extensification of existing agricultural systems or, at least, prevent further agricultural intensification.

9 References

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10 Appendices

10.1 Appendix I: Details Table 1-2

10.1.1 Details on the literature search

In Table 10-1 the results of a literature search are presented. Table 10-1 is based on the results of Hahn *et al.* (2013) but has been modified and extended. In the following, details on the approach for this literature research are provided.

Overall, 45 studies were analyzed by extracting the potential factors affecting the presence and/or abundance of (macro-) Lepidoptera (with a focus on European species). Subsequently, these relationships were evaluated as positive, neutral, or negative:

Positive:	higher plant species richness leads to higher species diversity
Neutral:	the percentage of semi-natural habitat does not influence abundance
Negative:	species richness was reduced in plots with higher pesticide usage

In certain cases, a distinct relationship may not have been described in the analyzed study, although a factor influencing the Lepidoptera was mentioned in the presented data (for example, mowing influences the community composition and vegetation height influences abundance). These results were listed separately.

A study could contain information for several factors (e.g., plant species richness, mowing, pesticides) but was counted only once per relationship (positive, neutral, negative), even if this relationship comprises several parameters (e.g., abundance, diversity, mortality).

For example: Ekroos *et al.* (2008) mentioned the *"positive effects of nectar flower abundance on lepidopterans […] abundance"* while *"organic farming did not show any significant effects on lepidopteran diversity"*. Therefore, this study was classified as showing (1) a positive relationship of the factor flower abundance on the parameter Lepidoptera abundance and (2) a neutral relationship of the factor organic agriculture on the parameter Lepidoptera diversity.

An overview of the evaluated literature and detailed information on the relationships and parameters is provided below in Table 10-1.

Table 10-1 Evaluated literature and results for Lepidoptera. Green (+): positive relationship, yellow (o): neutral relationship, red (-): negative relationship, blue (wr): influencing factor without clear relationship. The listed indices refer to Table 1-2.

Indices	Reference	Parameters
Plant species richness/flower abundance		
a: (+)	Ekroos *et al.*, 2008	Lepidoptera abundance (butterflies and diurnal moths), butterfly abundance, butterfly species richness
	Kuussaari *et al.*, 2007	species richness (butterflies and diurnal moths)
	Munguira and Thomas, 1992	species number and diversity of butterflies and burnets
	Ockinger and Smith, 2007	species number, density
	Saarinen, 2002	abundance (4 butterfly species)
	Sparks and Parish, 1995	species richness and abundance (butterflies)
	Winkler *et al.*, 2009	sugar content of *Plutella xylostella* in fields next to flowering vs. grass margins
	Brittain *et al.*, 2010	butterfly species richness (at field scale)
	Franzen and Nilsson, 2008	species number of burnets
	Rundlöf *et al.*, 2008	butterfly species richness and abundance
	Kirkham *et al.*, 1999	number and species diversity of butterflies
b: (o)	Munguira and Thomas, 1992	number of individuals
	Franzen and Nilsson, 2008	species richness of butterflies, number of red-listed burnets
c: (wr)	Haaland and Bersier, 2011	butterfly abundance, butterfly species richness
Vegetation structure/ height		
d: (+)	Kuussaari *et al.*, 2007	butterfly species richness
	Ockinger and Smith, 2007	species richness (day active moths)
	Franzen and Nilsson, 2008	species number of burnets
e: (o)	Sjodin *et al.*, 2008	species richness and abundance of butterflies
f: (-)	Marini *et al.*, 2009	species richness of butterflies (field scale)
g: (wr)	Sjodin *et al.*, 2008	species composition (butterflies)
	Sparks and Parish, 1995	butterfly populations
Presence/ proportion of forests or woody habitats		
h: (+)	Haaland and Bersier, 2011	butterfly species richness
Percentage of semi-natural habitat in agricultural landscapes		
i: (+)	Franzen and Nilsson, 2008	species number of burnets
j: (o)	Franzen and Nilsson, 2008	species richness of butterflies, number of red-listed burnets
k: (wr)	Fuentes-Montemayor *et al.*, 2011	macromoth abundance, macromoth species richness
Field margins/ hedges		
l: (+)	Ekroos *et al.*, 2008	Lepidopteran diversity, abundance of Lepidoptera, butterflies and meadow-preferring butterflies, butterfly species richness
	Feber *et al.*, 1997	abundance of non-pest butterflies
	Field *et al.*, 2005	abundance of butterflies, abundance of *Maniola jurtina*
	Field *et al.*, 2007	abundance of *Maniola jurtina*, *Thymelicus sylvestris* and *Thymelicus lineola*, butterfly abundance
	Hodgson *et al.*, 2010	butterfly density, butterfly species
	Meek *et al.*, 2002	abundance of butterflies
	Merckx *et al.*, 2009	abundance of moths
	Feber *et al.*, 2007	abundance of butterflies
m: (o)	Field *et al.*, 2005	butterfly species richness, abundance of *Pyronia tithonus*, *Thymelicus* spp., and *Ochlodes venata*
"Ackerschonstreifen"/ headlands		
n: (+)	de Snoo, 1999	butterfly abundance and species number
	Dover, 1997	foraging activity (butterflies)

	Dover *et al.*, 1990	abundance of butterflies
	Dover, 1991	number of butterfly species, abundance of butterflies
	Rands and Sotherton, 1986	butterfly abundance
"Blühstreifen"/ beetle banks/ grass strips		
o: (+)	Haaland and Bersier, 2011	butterfly abundance
	Haaland and Gyllin, 2010	butterfly abundance, butterfly species number (sown wildflower strips vs. greenways)
	Meek *et al.*, 2002	abundance of butterflies (especially Meadow Brown and *Aphantopus hyperantus*)
p: (o)	Haaland and Bersier, 2011	species richness
Agricultural intensification		
q: (+)	Saarinen, 2002	abundance of *Aglais urticae* (1 out of 39 butterfly species)
r: (o)	Saarinen, 2002	species richness (butterflies), abundance (38 out of 39 butterfly species)
	Sjodin *et al.*, 2008	species richness and abundance (butterflies)
s: (-)	Marini *et al.*, 2009	diversity of butterflies (field scale)
	Saarinen, 2002	diversity (butterflies)
	Brittain *et al.*, 2010	species richness of butterflies (regional scale)
	Ekroos *et al.*, 2010	α- and β-Diversity of butterflies and geometrid moths
Isolation/ fragmentation		
t: (-)	Ockinger and Smith, 2007	species richness, density
Organic agriculture		
u: (+)	Feber *et al.*, 1997	abundance of non-pest butterflies
	Hodgson *et al.*, 2010	butterfly density
	Jonason *et al.*, 2011	butterfly species richness, butterfly abundance
	Rundlöf *et al.*, 2008	butterfly species richness, butterfly abundance, α-, γ-diversity (butterflies)
	Rundlöf and Smith, 2006	butterfly species richness and abundance
	Wickramasinghe *et al.*, 2004	abundance of different moth families
	Feber *et al.*, 2007	abundance and species richness of butterflies
v: (o)	Ekroos *et al.*, 2010	Lepidopteran diversity
	Hodgson *et al.*, 2010	butterfly species richness
	Weibull *et al.*, 2000	butterfly diversity and number of species, number of observations (butterflies)
Pesticides		
w: (o)	Brittain *et al.*, 2010	species richness of butterflies (landscape scale)
	Frampton and Dorne, 2007	Lepidoptera larvae abundance (meta-analysis)
x: (-)	Longley *et al.*, 1997	mortality of *Pieris brassicae* larvae
	Longley and Sotherton, 1997	mortality of *Spodoptera littoralis* larvae
	Russell and Schultz, 2010	survival, wing size and pupal weight of *Pieris rapae* (study from USA)
	Sparks and Parish, 1995	butterfly abundance
	Cilgi and Jepson, 1995	mortality of *Pieris rapae* larvae and *P. brassicae* larvae, weight of *P. brassicae* larvae, size of adults (*P. rapae*, *P. brassicae*)
	Feber *et al.*, 1996	butterfly abundance
	Frampton and Dorne, 2007	adult Lepidoptera abundance, species richness and total Lepidoptera catches
	Sinha *et al.*, 1990	mortality of *Pieris brassicae* (ranking of 8 insecticides)
	Tan, 1981	maximum larval and pupal weights of *Pieris brassicae*, duration of larval period (*P. brassicae*), consumed leaf area (*P. brassicae*)

Fertilizer		
y: (+)	Arshad *et al.*, 2013	body weight of *Chilo partellus* caterpillars
	Giertych *et al.*, 2005	performance of *Lymantria dispar* caterpillars (especially in the ammonium treatment)
	Kula *et al.*, 2013	higher survival, higher caterpillar weight, shorter development time, and higher female pupae weight of *Lymantria dispar* feeding on leaves with higher nitrogen content
z: (-)	Kula *et al.*, 2014	lower survival, longer development time, decreased caterpillar and pupae weights of *Cabera pusaria* feeding on birch leaves with a higher nitrogen content; anomalies at pupation.

10.1.2 References

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10.2 Appendix II: Supplemental Data Paper 4

10.2.1 Supplemental Data of Paper 4

Table 10-2 Pollination interactions between moths and plants extracted from literature. To avoid confusion about taxonomic synonyms, next to the species names mentioned in literature the currently valid species names (as far as we know) are also listed.

Interactions: fv: observed flower visit, p: pollination, p1: pollen/pollinia attached to moths, p2: pollen deposition, p3: seed development, p4: eggs/caterpillars of nursery pollinators, ( ) interactions observed in laboratory experiments, L: interaction described in the publication is based upon further (e.g., unpublished) references which has been not checked separately.

moth family	**moth species (valid name)**	**moth species (name in paper)**	**plant family**	**plant species (valid name)**	**plant species (name in paper)**	**interaction**	**country**	**references**
Crambidae	*Anageshna primordialis* (Dyar, 1907)	*Anageshna primordialis* (Dyar)	Orchidaceae	*Platanthera obtusata* (Banks ex Pursh) Lindley	*Habenaria obtusata* (Pursh) Richardson	fv, p1	USA, Michigan	Voss and Riefner, 1983
Crambidae	*Anageshna primordialis* (Dyar, 1907)	*Anageshna primordialis*	Orchidaceae	*Platanthera flava* (L.) Lindley	*Platanthera flava* (L.) Lindley	p1	no information	Light, 1998
Crambidae	*Catoptria speculalis* Hübner 1825	*Catoptria speculalis* (Hbn.)	Orchidaceae	*Gymnadenia odoratissima* (L.) Rich.	*Gymnadenia odoratissima* (L.) Rich.	p1	Switzerland	Huber *et al*., 2005
Crambidae	*Crambus ericella* (Hübner 1813)	*Crambus ericella*	Orchidaceae	*Pseudorchis albida* (L.) A. & D. Löve	*Pseudorchis albida* (L.) A. & D. Löve	fv, p1	Czech Republic	Jersáková *et al*., 2011
Crambidae	*Crambus lathoniellus* (Zincken 1817)	*Crambus lathoniellus*	Orchidaceae	*Pseudorchis albida* (L.) A. & D. Löve	*Pseudorchis albida* (L.) A. & D. Löve	fv, p1	Czech Republic	Jersáková *et al*., 2011
Crambidae	*Eudonia lugubralis* (Walker, 1866)	*Eudonia lugubralis* (Walker)	Orchidaceae	*Platanthera obtusata* (Banks ex Pursh) Lindley	*Platanthera obtusata* (Banks ex Pursh) Lindley	p1	USA, Alaska	Gorham, 1976
Crambidae	*Pyrausta perrubralis* (Packard, 1873)	*Pyrausta perrubralis* (Packard)	Orchidaceae	*Piperia yadonii* Morgan and Ackerman	*Piperia yadonii* Morgan and Ackerman	L: p	USA, California	Doak and Graff, 2001, in Argue, 2012

moth family	**moth species (valid name)**	**moth species (name in paper)**	**plant family**	**plant species (valid name)**	**plant species (name in paper)**	**interaction**	**country**	**references**
Crambidae	*Udea profundalis* (Packard, 1873)	*Udea profundalis* (Packard)	Orchidaceae	*Piperia yadonii* Morgan and Ackerman	*Piperia yadonii* Morgan and Ackerman	L: p	USA, California	Doak and Graff, 2001, in Argue, 2012
Crambidae	*Upiga virescens* (Hulst, 1900)	*Upiga virescens*	Cactaceae	*Pachycereus schottii* (Engelm.) D. R. Hunt	*Lophocereus schottii*	p4	USA, Arizona	Holland *et al.*, 2004
Crambidae	*Upiga virescens* (Hulst, 1900)	*Upiga virescens*	Cactaceae	*Pachycereus schottii* (Engelm.) D. R. Hunt	*Pachycereus schottii*	p	USA, Arizona	Holland and Chamberlain, 2007
Crambidae	*Upiga virescens* (Hulst, 1900)	*Upiga virescens* (Hulst)	Cactaceae	*Pachycereus schottii* (Engelm.) D. R. Hunt	*Pachycereus schottii* (Englem.)	fv, p4, p3	Mexico	Holland and Fleming, 1999
Geometridae	*Anagoga occiduaria* (Walker)	*Anagoga occiduaria* (Walker)	Orchidaceae	*Platanthera stricta* Lindley	*Platanthera stricta* Lindley	fv, p1	USA, Washington	Patt *et al.*, 1989
Geometridae	*Aplocera plagiata* (Linnaeus, 1758)	*Aplocera plagiata* (L.)	Orchidaceae	*Platanthera chlorantha* (Custer) Reichb.	*Platanthera chlorantha* (Cust.) Rchb.	fv, p1	Sweden	Nilsson, 1978
Geometridae	*Drepanulatrix baueraria* Sperry, 1948	*Drepanulatrix baueraria* Sperry	Orchidaceae	*Piperia yadonii* Morgan and Ackerman	*Piperia yadonii* Morgan and Ackerman	L: p	USA, California	Doak and Graff, 2001, in Argue, 2012
Geometridae	Elophos dilucidaria (Denis & Schiffermüller, 1775)	*Elophos dilucidaria* (Den. & Sch.)	Orchidaceae	*Gymnadenia odoratissima* (L.) Rich.	*Gymnadenia odoratissima* (L.) Rich.	p1	Switzerland	Huber *et al*., 2005
Geometridae	*Entephria caesiata* (Denis & Schiffermüller, 1775)	*Entephria caesiata* (Den. & Sch.)	Orchidaceae	*Gymnadenia odoratissima* (L.) Rich.	*Gymnadenia odoratissima* (L.) Rich.	p1	Switzerland	Huber *et al*., 2005

moth family	moth species (valid name)	moth species (name in paper)	plant family	plant species (valid name)	plant species (name in paper)	interaction	country	references
Geometridae	*Entephria caesiata* (Denis and Schiffermüller, 1775)	*Entephria caesiata*	Orchidaceae	*Platanthera bifolia* (L.) Rich.	*Platanthera bifolia*	p, p1	Sweden	Boberg *et al*., 2014
Geometridae	*Eupithecia* Curtis 1825	*Eupithecia* Curtis sp.	Orchidaceae	*Piperia unalascensis* (Sprengle) Rydberg	*Piperia unalascensis* (Sprengle) Rydberg	p	USA, Michigan	Ackerman, 1977
Geometridae	*Eupithecia* Curtis 1825	*Eupithecia sp.*	Orchidaceae	*Platanthera stricta* Lindley	*Platanthera stricta* Lindley	fv, p1	USA, Washington	Patt *et al*., 1989
Geometridae	*Eupithecia venosata* (Fabricius 1787)	*Eupithecia venosata* (F.)	Caryophyllaceae	*Silene uniflora* Roth	*Silene uniflora* Roth	p4?	Sweden	Pettersson, 1997
Geometridae	*Eustroma fasciata* Barnes and McDunnough, 1918	*Eustroma fasciata* (B. & McD.)	Orchidaceae	*Platanthera stricta* Lindley	*Platanthera stricta* Lindley	fv, p1	USA, Washington	Patt *et al*., 1989
Geometridae	*Glacies alpinata* (Scopoli 1763)	*Glacies alpinata* (Sc.)	Orchidaceae	*Gymnadenia odoratissima* (L.) Rich.	*Gymnadenia odoratissima* (L.) Rich.	p1	Switzerland	Huber *et al*., 2005
Geometridae	*Gnophos obfuscata* (Denis & Schiffermüller 1775)	*Gnophos obfuscatus* (Den. & Sch.)	Orchidaceae	*Gymnadenia odoratissima* (L.) Rich.	*Gymnadenia odoratissima* (L.) Rich.	p1	Switzerland	Huber *et al*., 2005
Geometridae	*Hydriomena renunciata* (Walker, 1862)	*Hydriomena renunciata*	Orchidaceae	*Platanthera obtusata* (Banks ex Pursh) Lindley	*Habenaria obtusata*	p1	USA, Wisconsin	Thien and Utech, 1970
Geometridae	*Mesoleuca ruficillata* (Guenée, [1858])	*Mesoleuca ruficillata* (Guenee)	Orchidaceae	*Platanthera obtusata* (Banks ex Pursh) Lindley	*Habenaria obtusata*	p1	USA, Wisconsin	Thien and Utech, 1970

moth family	**moth species (valid name)**	**moth species (name in paper)**	**plant family**	**plant species (valid name)**	**plant species (name in paper)**	**interaction**	**country**	**references**
Geometridae	*Mesotype verberata* (Scopoli 1763)	*Perizoma verberata* (Sc.)	Orchidaceae	*Gymnadenia odoratissima* (L.) Rich.	*Gymnadenia odoratissima* (L.) Rich.	p1	Switzerland	Huber *et al*., 2005
Geometridae	*Ourapteryx sambucaria* (Linnaeus 1758)	*Ourapteryx sambucaria* (L.)	Orchidaceae	*Platanthera chlorantha* (Custer) Reichb.	*Platanthera chlorantha* (Cust.) Rchb.	fv, p1	Sweden	Nilsson, 1978
Geometridae	*Perizoma affinitata* (Stephens 1831)	*Perizoma affinitatum*	Caryophyllaceae	*Silene dioica* (L.) Clairville	*Silene dioica*	fv, p1, p4, p2	Finnland	Westerbergh, 2004
Geometridae	*Semiothisa* Hübner 1818	*Semiothisa* Hubner sp.	Orchidaceae	*Piperia yadonii* Morgan and Ackerman	*Piperia yadonii* Morgan and Ackerman	L: p	USA, California	Doak and Graff, 2001, in Argue, 2012
Geometridae	*Speranza marcescaria* (Guenée, [1858])	*Elpiste marcescaria* (Guenee)	Orchidaceae	*Piperia yadonii* Morgan and Ackerman	*Piperia yadonii* Morgan and Ackerman	L: p	USA, California	Doak and Graff, 2001, in Argue, 2012
Geometridae	*Thallophaga taylorata* (Hulst, 1896)	*Thallophaga taylorata* (Hulst)	Orchidaceae	*Piperia transversa* Suksdorf	*Piperia transversa* Suksd.	p	USA, California	Ackerman, 1977
Geometridae	*Xanthorhoe abrasaria* (Herrich-Schäffer, [1855])	*Xanthorhoe abrasaria*	Orchidaceae	*Platanthera obtusata* (Banks ex Pursh) Lindley	*Habenaria obtusata*	p1	USA, Wisconsin	Thien and Utech, 1970
Geometridae	*Xanthorhoe decoloraria* (Esper 1806)	*Xanthorhoe munitata*	Orchidaceae	*Platanthera obtusata* (Banks ex Pursh) Lindley	*Habenaria obtusata*	fv, p1	USA, Michigan	Stoutamire, 1971
Geometridae	*Xanthorhoe decoloraria* (Esper, 1806)	*Xanthorhoe munitata*	Orchidaceae	*Platanthera obtusata* (Banks ex Pursh) Lindley	*Platanthera obtusata* (Banks ex Pursh) Lindley	p1	USA, Michigan	Gorham, 1976
Geometridae	*Xanthorhoe lacustrata* (Guenée, [1858])	*Xanthorhoe lacustrata*	Orchidaceae	*Platanthera obtusata* (Banks ex Pursh) Lindley	*Habenaria obtusata*	p1	USA, Wisconsin	Thien and Utech, 1970

moth family	**moth species (valid name)**	**moth species (name in paper)**	**plant family**	**plant species (valid name)**	**plant species (name in paper)**	**interaction**	**country**	**references**
Geometridae	*Xanthorhoe lagganata* (Swett & Cassino)	*Xanthorhoe lagganata* (Swett & Cassino)	Orchidaceae	*Platanthera stricta* Lindley	*Platanthera stricta* Lindley	fv, p1	USA, Washington	Patt *et al*., 1989
Noctuidae	*Abrostola triplasia* (Linnaeus 1758)	*Abrostola triplasia* (L.)	Caryophyllaceae	*Silene vulgaris* (Moench) Garcke	*Silene vulgaris* (Moench) Garcke	fv, p1, p2	Sweden	Pettersson, 1991
Noctuidae	*Abrostola triplasia* (Linnaeus 1758)	*Abrostola triplasia* (L.)	Orchidaceae	*Platanthera chlorantha* (Custer) Reichb.	*Platanthera chlorantha* (Cust.) Rchb.	fv, p1	Sweden	Nilsson, 1978
Noctuidae	*Agrotis ipsilon* (Hufnagel, 1766)	*Agrotis ipsilon* (Hufnagel)	Orchidaceae	*Piperia yadonii* Morgan and Ackerman	*Piperia yadonii* Morgan and Ackerman	L: p	USA, California	Doak and Graff, 2001, in Argue, 2012
Noctuidae	*Agrotis* Ochsenheimer 1816	*Agrotis sp.*	Orchidaceae	*Platanthera blephariglottis* (Willdenow) Lindley	*Platanthera blephariglottis* (Willdenow) Lindley	fv, p1	USA, Michigan	Smith and Snow, 1976
Noctuidae	*Anagrapha falcifera* (Kirby, 1837)	*Anagrapha falcifera* Kirby	Orchidaceae	*Platanthera lacera* (Michaux) G. Don	*Platanthera lacera* (Michaux) G. Don	fv, p1	USA, Illinois	Little *et al*., 2005
Noctuidae	*Anarta oregonica* (Grote, 1881)	*Discestra oregonica* (Grote)	Orchidaceae	*Platanthera dilatata* (Pursh) Lindl. ex Beck	*Platanthera dilatata* (Pursh) Lindley ex Beck var. *dilatata*	fv, p1	USA, Oregon	Larson, 1992
Noctuidae	*Anorthoa munda* (Denis & Schiffermüller 1775)	*Orthosia munda* Denis & Schiffmüller	Adoxaceae	*Adoxa moschatellina* L.	*Adoxa moschatellina* L.	p1	UK	Holmes, 2005
Noctuidae	*Apamea anceps* (Denis & Schiffermüller 1775)	*Apamea anceps* (Den. & Schiff.)	Orchidaceae	*Platanthera chlorantha* (Custer) Reichb.	*Platanthera chlorantha* (Cust.) Rchb.	fv, p1	Sweden	Nilsson, 1978

moth family	**moth species (valid name)**	**moth species (name in paper)**	**plant family**	**plant species (valid name)**	**plant species (name in paper)**	**interaction**	**country**	**references**
Noctuidae	*Apamea furva* (Denis & Schiffermüller 1775)	*Apamea furva* (D. & S.)	Caryophyllaceae	*Silene vulgaris* (Moench) Garcke	*Silene vulgaris* (Moench) Garcke	fv, p1, p2	Sweden	Pettersson, 1991
Noctuidae	*Apamea furva* (Denis & Schiffermüller 1775)	*Apamea furva* (Den. & Schiff.)	Orchidaceae	*Platanthera chlorantha* (Custer) Reichb.	*Platanthera chlorantha* (Cust.) Rchb.	fv, p1	Sweden	Nilsson, 1978
Noctuidae	*Apamea lateritia* (Hufnagel 1766)	*Apamea lateritia* (Hufn.)	Caryophyllaceae	*Silene vulgaris* (Moench) Garcke	*Silene vulgaris* (Moench) Garcke	fv, p1, p2	Sweden	Pettersson, 1991
Noctuidae	*Apamea lateritia* (Hufnagel 1766)	*Apamea lateritia* (Hufn.)	Orchidaceae	*Platanthera chlorantha* (Custer) Reichb.	*Platanthera chlorantha* (Cust.) Rchb.	fv, p1	Sweden	Nilsson, 1978
Noctuidae	*Apamea monoglypha* (Hufnagel 1766)	*Apamea monoglypha* (Hufn.)	Caryophyllaceae	*Silene vulgaris* (Moench) Garcke	*Silene vulgaris* (Moench) Garcke	fv, p1, p2	Sweden	Pettersson, 1991
Noctuidae	*Apamea monoglypha* (Hufnagel 1766)	*Apamea monoglypha* (Hufn.)	Orchidaceae	*Platanthera chlorantha* (Custer) Reichb.	*Platanthera chlorantha* (Cust.) Rchb.	fv, p1	Sweden	Nilsson, 1978
Noctuidae	*Apamea* Ochsenheimer 1816	*Apamea ssp.*	Orchidaceae	*Platanthera bifolia* (L.) Rich.	*Platanthera bifolia* (L.) L. C. Rich.	p	Sweden	Maad and Nilsson, 2004
Noctuidae	*Apamea* Ochsenheimer 1816	*Apamea ssp.*	Orchidaceae	*Platanthera chlorantha* (Custer) Reichb.	*Platanthera chlorantha* (Custer) Reichb.	p	Sweden	Maad and Nilsson, 2004
Noctuidae	*Apamea sublustris* (Esper 1788)	*Apamea sublustris* (Esp.)	Caryophyllaceae	*Silene vulgaris* (Moench) Garcke	*Silene vulgaris* (Moench) Garcke	fv, p1, p2	Sweden	Pettersson, 1991
Noctuidae	*Apamea sublustris* (Esper 1788)	*Apamea sublustris* (Esp.)	Orchidaceae	*Platanthera chlorantha* (Custer) Reichb.	*Platanthera chlorantha* (Cust.) Rchb.	fv, p1	Sweden	Nilsson, 1978

moth family	**moth species (valid name)**	**moth species (name in paper)**	**plant family**	**plant species (valid name)**	**plant species (name in paper)**	**interaction**	**country**	**references**
Noctuidae	*Autographa bractea* (Denis & Schiffermüller 1775)	*Autographa bractea* Schiff.	Caryophyllaceae	*Dianthus superbus* L.	*Dianthus superbus* L.	fv, p1	Switzerland	Erhardt, 1991
Noctuidae	*Autographa bractea* (Denis & Schiffermüller 1775)	*Autographa bractea* (D. & S.)	Caryophyllaceae	*Silene vulgaris* (Moench) Garcke	*Silene vulgaris* (Moench) Garcke	fv, p1	Sweden	Pettersson, 1991
Noctuidae	*Autographa bractea* (Denis & Schiffermüller 1775)	*Autographa bractea* (Den. & Sch.)	Orchidaceae	*Gymnadenia conopsea* (L.) R. Br.	*Gymnadenia conopsea* (L.) R.Br. s.l.	p1	Switzerland	Huber *et al*., 2005
Noctuidae	*Autographa bractea* (Denis & Schiffermüller 1775)	*Autographa bractea* (Den. & Schiff.)	Orchidaceae	*Platanthera chlorantha* (Custer) Reichb.	*Platanthera chlorantha* (Cust.) Rchb.	fv, p1	Sweden	Nilsson, 1978
Noctuidae	*Autographa californica* (Speyer, 1875)	*Autographa californica* (Speyer)	Orchidaceae	*Platanthera dilatata* (Pursh) Lindl. ex Beck	*Platanthera dilatata* var. *leucostachys* (Lindley) Luer	L: fv, p1	USA, California	Kipping, 1971, in Argue, 2012
Noctuidae	*Autographa gamma* (Linnaeus, 1758)	Autographa gamma L.	Caryophyllaceae	*Dianthus gratianopolitanus* Vill.	*Dianthus gratianopolitanus* Vill.	fv, p1	Switzerland	Erhardt, 1990
Noctuidae	*Autographa gamma* (Linnaeus, 1758)	*Autographa gamma* (L.)	Caryophyllaceae	*Saponaria officinalis* L.	*Saponaria officinalis* (L.)	fv, p2	Germany	Wolff *et al*., 2006
Noctuidae	*Autographa gamma* (Linnaeus, 1758)	*Autographa gamma* (L.)	Caryophyllaceae	*Silene vulgaris* (Moench) Garcke	*Silene vulgaris* (Moench) Garcke	fv, p1, p2	Sweden	Pettersson, 1991
Noctuidae	*Autographa gamma* (Linnaeus, 1758)	*Autographa gamma* (L.)	Orchidaceae	*Platanthera chlorantha* (Custer) Reichb.	*Platanthera chlorantha* (Cust.) Rchb.	fv, p1	Sweden	Nilsson, 1978
Noctuidae	*Autographa* Hübner 1821	*Autographa* (Hubner) sp.	Orchidaceae	*Piperia elegans* (Lindl.) Rydberg	*Piperia elegans* (Lindl.) Rydberg	p	USA, California	Ackerman, 1977

moth family	**moth species (valid name)**	**moth species (name in paper)**	**plant family**	**plant species (valid name)**	**plant species (name in paper)**	**interaction**	**country**	**references**
Noctuidae	*Autographa jota* (Linnaeus 1758)	*Autographa jota* (L.)	Caryophyllaceae	*Silene vulgaris* (Moench) Garcke	*Silene vulgaris* (Moench) Garcke	fv, p1, p2	Sweden	Pettersson, 1991
Noctuidae	*Autographa jota* (Linnaeus 1758)	*Autographa jota* (L.)	Orchidaceae	*Platanthera chlorantha* (Custer) Reichb.	*Platanthera chlorantha* (Cust.) Rchb.	fv, p1	Sweden	Nilsson, 1978
Noctuidae	*Autographa precationis* (Guenée 1852)	*Autographa precationis*	Caryophyllaceae	*Silene stellata* (L.) W.T. Aiton	*Silene stellata*	fv, p2	USA, Virginia	Kula *et al.*, 2014
Noctuidae	*Autographa pseudogamma* (Grote, 1875)	*Autographa pseudogamma* Grote	Nyctaginaceae	*Abronia ammophila* Greene	*Abronia ammophila* Greene	fv, p1	USA, Wyoming	Saunders and Sipes, 2006
Noctuidae	*Autographa pulchrina* (Haworth 1809)	*Autographa pulchrina* (Haw.)	Caryophyllaceae	*Silene vulgaris* (Moench) Garcke	*Silene vulgaris* (Moench) Garcke	fv, p1, p2	Sweden	Pettersson, 1991
Noctuidae	*Autographa pulchrina* (Haworth 1809)	*Autographa pulchrina* (Hw.)	Orchidaceae	*Platanthera chlorantha* (Custer) Reichb.	*Platanthera chlorantha* (Cust.) Rchb.	fv, p1	Sweden	Nilsson, 1978
Noctuidae	*Copablepharon viridisparsa* Dod, 1916	*Copablepharon viridisparsa* Dod	Nyctaginaceae	*Abronia ammophila* Greene	*Abronia ammophila* Greene	fv, p1	USA, Wyoming	Saunders and Sipes, 2006
Noctuidae	*Cucullia absinthii* (Linnaeus 1761)	*Cucullia absynthii* (L.)	Caryophyllaceae	*Silene vulgaris* (Moench) Garcke	*Silene vulgaris* (Moench) Garcke	fv, p1, p2	Sweden	Pettersson, 1991
Noctuidae	*Cucullia intermedia* Speyer, 1870	*Cucullia intermedia* (Speyer)	Orchidaceae	*Platanthera huronensis* (Nuttall) Lindley	*Platanthera huronensis* (Nutt.) Lindley	p1	USA, Colorado	Catling and Catling, 1989
Noctuidae	*Cucullia luna* Morrison, 1875	*Nycterophaeta luna* (Morr.)	Nyctaginaceae	*Abronia fragrans* Nutt. ex Hook.	*Abronia fragrans* Nutt.	fv, p1	USA, Nebraska	Keeler and Fredricks, 1979
Noctuidae	*Cucullia lychnitis* Rambur 1833	*Cucullia lychnitidis* Ramb.	Caryophyllaceae	*Silene vulgaris* (Moench) Garcke	*Silene vulgaris* (Moench) Garcke	fv, p1, p2	Sweden	Pettersson, 1991
Noctuidae	*Cucullia umbratica* (Linnaeus 1758)	*Cucullia* c.f. *umbratica* L.	Caryophyllaceae	*Dianthus superbus* L.	*Dianthus superbus* L.	fv, p1	Switzerland	Erhardt, 1991

moth family	**moth species (valid name)**	**moth species (name in paper)**	**plant family**	**plant species (valid name)**	**plant species (name in paper)**	**interaction**	**country**	**references**
Noctuidae	*Cucullia umbratica* (Linnaeus 1758)	*Cucullia umbratica* (L.)	Caryophyllaceae	*Silene vulgaris* (Moench) Garcke	*Silene vulgaris* (Moench) Garcke	fv, p1, p2	Sweden	Pettersson, 1991
Noctuidae	*Cucullia umbratica* (Linnaeus 1758)	*Cucullia umbratica* (L.)	Orchidaceae	*Platanthera chlorantha* (Custer) Reichb.	*Platanthera chlorantha* (Cust.) Rchb.	fv, p1	Sweden	Nilsson, 1978
Noctuidae	*Diachrysia chrysitis* (Linnaeus 1758)	*Diachrysia chrysitis* (L.)	Caryophyllaceae	*Silene vulgaris* (Moench) Garcke	*Silene vulgaris* (Moench) Garcke	fv, p1, p2	Sweden	Pettersson, 1991
Noctuidae	*Diachrysia chrysitis* (Linnaeus 1758)	*Diachrysia chrysitis* (L.)	Orchidaceae	*Platanthera chlorantha* (Custer) Reichb.	*Platanthera chlorantha* (Cust.) Rchb.	fv, p1	Sweden	Nilsson, 1978
Noctuidae	*Diarsia mendica* (Fabricius 1775)	*Diarsia mendica* (F.)	Orchidaceae	*Platanthera chlorantha* (Custer) Reichb.	*Platanthera chlorantha* (Cust.) Rchb.	fv, p1	Sweden	Nilsson, 1978
Noctuidae	*Euchalcia variabilis* (Piller 1783)	*Euchalcia variabilis* Pill.	Caryophyllaceae	*Dianthus gratianopolitanus* Vill.	*Dianthus gratianopolitanus* Vill.	fv, p1	Switzerland	Erhardt, 1990
Noctuidae	*Hada plebeja* (Linnaeus 1761)	*Hada nana* (Hufn.)	Caryophyllaceae	*Silene vulgaris* (Moench) Garcke	*Silene vulgaris* (Moench) Garcke	fv, p1, p2	Sweden	Pettersson, 1991
Noctuidae	*Hada sutrina* (Grote, 1881)	*Hada sutrina* Grote	Nyctaginaceae	*Abronia ammophila* Greene	*Abronia ammophila* Greene	fv, p1	USA, Wyoming	Saunders and Sipes, 2006
Noctuidae	*Hadena albimacula* (Borkhausen 1792)	*Hadena albimacula* (Bkh.)	Orchidaceae	*Platanthera chlorantha* (Custer) Reichb.	*Platanthera chlorantha* (Cust.) Rchb.	fv, p1	Sweden	Nilsson, 1978
Noctuidae	*Hadena bicruris* (Hufnagel 1766)	*Hadena bicruris* Hufn.	Caryophyllaceae	*Silene dioica* (L.) Clairville	*Silene dioica* (L.) Clairville	p4	Germany	Bopp 2003; Bopp and Gottsberger 2004
Noctuidae	*Hadena bicruris* (Hufnagel 1766)	*Hadena bicruris*	Caryophyllaceae	*Silene latifolia* Poiret	*Silene latifolia*	p4	Central/ northern Europe	Magalhaes *et al*., 2011

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Noctuidae	*Hadena bicruris* (Hufnagel 1766)	*Hadena bicruris*	Caryophyllaceae	*Silene latifolia* Poiret	*Silene latifolia* Poiret	fv, p1	The Netherlands	van Putten *et al*., 2007
Noctuidae	*Hadena bicruris* (Hufnagel 1766)	*Hadena bicruris* Hufn. (female)	Caryophyllaceae	*Silene latifolia* Poiret	*Silene latifolia* Poiret	(fv, p4, p3)	France	Labouche and Bernasconi, 2010
Noctuidae	*Hadena bicruris* (Hufnagel 1766)	*Hadena bicruris* Hufn. (male)	Caryophyllaceae	*Silene latifolia* Poiret	*Silene latifolia* Poiret	(fv, p3)	France	Labouche and Bernasconi, 2010
Noctuidae	*Hadena bicruris* (Hufnagel 1766)	*Hadena bicruris* Hufn.	Caryophyllaceae	*Silene latifolia* Poiret	*Silene latifolia* Poiret ssp. *alba* (Miller) Greuter & Burdet	p4	Germany	Bopp 2003; Bopp and Gottsberger 2004
Noctuidae	*Hadena bicruris* (Hufnagel 1766)	*Hadena bicruris* (Hufn.)	Caryophyllaceae	*Silene vulgaris* (Moench) Garcke	*Silene vulgaris* (Moench) Garcke	fv, p1, p2	Sweden	Pettersson, 1991
Noctuidae	*Hadena caesia* (Denis & Schiffermüller 1775)	*Hadena caesia* Schiff.	Caryophyllaceae	*Dianthus gratianopolitanus* Vill.	*Dianthus gratianopolitanus* Vill.	fv, p1	Switzerland	Erhardt, 1990
Noctuidae	*Hadena compta* (Denis & Schiffermüller 1775)	*Hadena compta* Schiff.	Caryophyllaceae	*Dianthus sylvestris* Wulfen	*Dianthus sylvestris* Wulf.	p	no information	Collin *et al*., 2002
Noctuidae	*Hadena compta* (Denis & Schiffermüller 1775)	*Hadena compta* Schiff.	Caryophyllaceae	*Dianthus sylvestris* Wulfen	*Dianthus sylvestris* Wulf.	p1	Switzerland, Swiss Alps	Erhardt, 1988
Noctuidae	*Hadena compta* (Denis & Schiffermüller 1775)	*Hadena compta* (Den. & Schiff.)	Orchidaceae	*Platanthera chlorantha* (Custer) Reichb.	*Platanthera chlorantha* (Cust.) Rchb.	fv, p1	Sweden	Nilsson, 1978
Noctuidae	*Hadena confusa* (Hufnagel 1766)	*Hadena confusa* (Hufn.)	Caryophyllaceae	*Silene uniflora* Roth	*Silene uniflora* Roth	p4	Sweden	Pettersson, 1997
Noctuidae	*Hadena confusa* (Hufnagel 1766)	*Hadena confusa* (Hufn.)	Caryophyllaceae	*Silene vulgaris* (Moench) Garcke	*Silene vulgaris* (Moench) Garcke	fv, p1, p2	Sweden	Pettersson, 1991

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Noctuidae	*Hadena consparcatoides* (Schawerda 1928)	*Hadena consparcatoides*	Caryophyllaceae	*Silene ciliata* Pourr.	*Silene ciliata*	fv, p4	Spain	Gimenez-Benavides *et al*., 2007
Noctuidae	*Hadena ectypa* (Morrison, 1875)	*Hadena ectypa*	Caryophyllaceae	*Silene stellata* (L.) W.T. Aiton	*Silene stellata*	p	no information	Reynolds *et al*., (unpublished) in Kephart *et al*., 2006
Noctuidae	*Hadena ectypa* (Morrison, 1875)	*Hadena ectypa*	Caryophyllaceae	*Silene stellata* (L.) W.T. Aiton	*Silene stellata*	fv, p4, p2	USA, Virginia	Reynolds *et al*., 2012
Noctuidae	*Hadena ectypa* (Morrison, 1875)	*Hadena ectypa* Morrison	Caryophyllaceae	*Silene stellata* (L.) W.T. Aiton	*Silene stellata* (L.) W.T. Aiton	fv, p4, p2	USA, Virginia	Castillo *et al*., 2013
Noctuidae	*Hadena ectypa* (Morrison, 1875)	*Hadena ectypa*	Caryophyllaceae	*Silene stellata* (L.) W.T. Aiton	*Silene stellata*	fv, p2	USA, Virginia	Kula *et al*., 2014
Noctuidae	*Hadena perplexa* (Denis & Schiffermüller 1775)	*Hadena perplexa* (D. & S.)	Caryophyllaceae	*Silene vulgaris* (Moench) Garcke	*Silene vulgaris* (Moench) Garcke	fv, p1, p2	Sweden	Pettersson, 1991
Noctuidae	*Hadena perplexa* (Denis & Schiffermüller 1775)	*Hadena perplexa* (Den. & Schiff.)	Orchidaceae	*Platanthera chlorantha* (Custer) Reichb.	*Platanthera chlorantha* (Cust.) Rchb.	fv, p1	Sweden	Nilsson, 1978
Noctuidae	*Hadena* Schrank 1802	*Hadena*	Caryophyllaceae	*Dianthus sylvestris* Wulfen	*Dianthus sylvestris* Wulf.	p4	Italy	Collin *et al*., 2002
Noctuidae	*Hadena variolata* (Smith 1888)	*Hadena variolata*	Caryophyllaceae	*Silene douglasii* Hook	*Silene douglasii*	p	no information	Kephart *et al*., 2006
Noctuidae	*Lithophane socia* (Hufnagel 1766)	*Lithophane hepatica* Clerck.	Adoxaceae	*Adoxa moschatellina* L.	*Adoxa moschatellina* L.	p1	UK	Holmes, 2005
Noctuidae	*Mniotype adusta* (Esper 1790)	*Mniotype adusta* (Esp.)	Caryophyllaceae	*Silene vulgaris* (Moench) Garcke	*Silene vulgaris* (Moench) Garcke	fv, p1, p2	Sweden	Pettersson, 1991
Noctuidae	*Mythimna oxygala* (Grote, 1881)	*Aletia oxygala* (Grote)	Orchidaceae	*Platanthera huronensis* (Nuttall) Lindley	*Platanthera huronensis* (Nutt.) Lindley	p1	USA, Colorado	Catling and Catling, 1989

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Noctuidae	*Orthosia cerasi* (Fabricius 1775)	*Orthosia cerasi* Fabricius	Adoxaceae	*Adoxa moschatellina* L.	*Adoxa moschatellina* L.	p1	UK	Holmes, 2005
Noctuidae	*Orthosia gothica* (Linnaeus 1758)	*Orthosia gothica* L.	Adoxaceae	*Adoxa moschatellina* L.	*Adoxa moschatellina* L.	p1	UK	Holmes, 2005
Noctuidae	*Orthosia incerta* (Hufnagel 1766)	*Orthosia incerta* Hufnagel	Adoxaceae	*Adoxa moschatellina* L.	*Adoxa moschatellina* L.	p1	UK	Holmes, 2005
Noctuidae	*Papestra quadrata* (Smith, 1891)	*Papestra quadrata* Smith	Nyctaginaceae	*Abronia ammophila* Greene	*Abronia ammophila* Greene	fv, p1	USA, Wyoming	Saunders and Sipes, 2006
Noctuidae	*Plusia festucae* (Linnaeus 1758)	*Autographa festucae* (L.)	Caryophyllaceae	*Silene vulgaris* (Moench) Garcke	*Silene vulgaris* (Moench) Garcke	fv, p1, p2	Sweden	Pettersson, 1991
Noctuidae	*Plusia festucae* (Linnaeus 1758)	*Plusia festucae* (L.)	Orchidaceae	*Platanthera chlorantha* (Custer) Reichb.	*Platanthera chlorantha* (Cust.) Rchb.	fv, p1	Sweden	Nilsson, 1978
Noctuidae	*Plusia putnami* (Grote 1873)	*Plusia putnami* (Grote)	Orchidaceae	*Platanthera chlorantha* (Custer) Reichb.	*Platanthera chlorantha* (Cust.) Rchb.	fv, p1	Sweden	Nilsson, 1978
Noctuidae	*Polia bombycina* (Hufnagel 1766)	*Polia bombycina* (Hufn.)	Caryophyllaceae	*Silene vulgaris* (Moench) Garcke	*Silene vulgaris* (Moench) Garcke	fv, p1, p2	Sweden	Pettersson, 1991
Noctuidae	*Polia bombycina* (Hufnagel 1766)	*Polia bombycina* (Hufn.)	Orchidaceae	*Platanthera chlorantha* (Custer) Reichb.	*Platanthera chlorantha* (Cust.) Rchb.	fv, p1	Sweden	Nilsson, 1978
Noctuidae	*Polia hepatica* (Clerck 1759)	*Polia hepatica* (Cl.)	Orchidaceae	*Platanthera chlorantha* (Custer) Reichb.	*Platanthera chlorantha* (Cust.) Rchb.	fv, p1	Sweden	Nilsson, 1978
Noctuidae	*Polia nebulosa* (Hufnagel 1766)	*Polia nebulosa* (Hufn.)	Orchidaceae	*Platanthera chlorantha* (Custer) Reichb.	*Platanthera chlorantha* (Cust.) Rchb.	fv, p1	Sweden	Nilsson, 1978
Noctuidae	*Sideridis reticulata* (Goeze 1781)	*Heliophobus reticulata* (Goeze)	Orchidaceae	*Platanthera chlorantha* (Custer) Reichb.	*Platanthera chlorantha* (Cust.) Rchb.	fv, p1	Sweden	Nilsson, 1978

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Noctuidae	*Sideridis rivularis* (Fabricius 1775)	*Hadena rivularis*	Caryophyllaceae	*Silene dioica* (L.) Clairville	*Silene dioica* (L.) Clairv.	p4	England	Goulson and Jerrim, 1997
Noctuidae	*Sideridis rivularis* (Fabricius 1775)	*Hadena rivularis*	Caryophyllaceae	*Silene latifolia* Poiret	*Silene latifolia* Poiret	p4	England	Goulson and Jerrim, 1997
Noctuidae	*Sideridis rivularis* (Fabricius 1775)	*Hadena rivularis*	Caryophyllaceae		*Silene latifolia* x *Silene dioica* hybrids	p4	England	Goulson and Jerrim, 1997
Noctuidae	*Trichordestra dodii* (Smith, 1904)	*Trichordestra dodii* (Strecker)	Orchidaceae	*Platanthera huronensis* (Nuttall) Lindley	*Platanthera huronensis* (Nutt.) Lindley	p1	USA, Colorado	Catling and Catling, 1989
Prodoxidae		*Greya spec.*	Orchidaceae	*Platanthera stricta* Lindley	*Platanthera stricta* Lindley	fv, p1	USA, Washington	Patt *et al.*, 1989
Prodoxidae	*Greya obscura* Davis and Pellmyr, 1992	*Greya obscura*	Saxifragaceae	*Lithophragma parviflorum* (Hook.) Nutt. ex Torr. & A. Gray	*Lithophragma parviflorum*	fv, p3	USA, California	Cuautle and Thompson, 2010
Prodoxidae	*Greya politella* (Walsingham, 1888)	*Greya politella* (female)	Saxifragaceae	*Lithophragma heterophyllum* (Hook. &. Arn.) Torr. &. A. Gray	*Lithophragma heterophyllum*	fv, p3	USA, California	Cuautle and Thompson, 2010
Prodoxidae	*Greya politella* (Walsingham, 1888)	*Greya politella*	Saxifragaceae	*Lithophragma parviflorum* (Hook.) Nutt. ex Torr. & A. Gray	*Lithophragma parviflorum*	fv, p3	USA, Washington + Idaho	Pellmyr and Thompson, 1996
Prodoxidae	*Greya politella* (Walsingham, 1888)	*Greya politella* (Walsingham)	Saxifragaceae	*Lithophragma parviflorum* (Hook.) Nutt. ex Torr. & A. Gray	*Lithophragma parviflorum* (Hook.) Torr. & Gray	fv, p4, p3	USA, Washington	Thompson and Pellmyr, 1992
Prodoxidae	*Tegeticula antithetica* Pellmyr 2003	*Tegeticula antithetica* Pellmyr	Agavaceae	*Yucca brevifolia* Engelm.	*Yucca brevifolia*	p4	USA, Utah	Pellmyr and Segraves, 2003

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Prodoxidae	*Tegeticula yuccasella* (Riley, 1872)	*Tegeticula yuccasella* (Riley)	Agavaceae	*Yucca glauca* Nutt.	*Yucca glauca*	fv, p2	USA, Colorado	Dodd and Linhart, 1994
Pterophoridae	*Hellinsia didactylites* (Ström 1783)	*Hellinsia didactylites*	Orchidaceae	*Pseudorchis albida* (L.) A. & D. Löve	*Pseudorchis albida* (L.) A. & D. Löve	fv, p1	Czech Republic	Jersáková *et al*., 2011
Pterophoridae	*Hellinsia osteodactylus* (Zeller 1841)	*Hellinsia osteodactylus*	Orchidaceae	*Pseudorchis albida* (L.) A. & D. Löve	*Pseudorchis albida* (L.) A. & D. Löve	fv, p1	Czech Republic	Jersáková *et al*., 2011
Sphingidae	*Agrius convolvuli* (Linnaeus 1758)	*Herse convolvuli* L.	Caryophyllaceae	*Dianthus superbus* L.	*Dianthus superbus* L.	fv, p1	Switzerland	Erhardt, 1991
Sphingidae	*Darapsa versicolor* Harris 1839	*Darapsa versicolor*	Orchidaceae	*Platanthera blephariglottis* (Willdenow) Lindley	*Platanthera blephariglottis* (Willdenow) Lindley	fv, p1	USA, Michigan	Smith and Snow, 1976
Sphingidae	*Deilephila elpenor* (Linnaeus 1758)	*Deilephila elpenor* (L.)	Orchidaceae	*Platanthera chlorantha* (Custer) Reichb.	*Platanthera chlorantha* (Cust.) Rchb.	fv, p1	Sweden	Nilsson, 1978
Sphingidae	*Deilephila porcellus* (Linnaeus 1758)	*Deilephila porcellus*	Caryophyllaceae	*Silene uniflora* Roth	*Silene uniflora*	p	no information	H. Prentice (unpublished) in Kephart *et al*., 2006
Sphingidae	*Deilephila porcellus* (Linnaeus 1758)	*Deilephilia porcellus* (L.)	Caryophyllaceae	*Silene vulgaris* (Moench) Garcke	*Silene vulgaris* (Moench) Garcke	fv, p1, p2	Sweden	Pettersson, 1991
Sphingidae	*Deilephila porcellus* (Linnaeus 1758)	*Deilephila porcellus*	Orchidaceae	*Platanthera bifolia* (L.) Rich.	*Platanthera bifolia* (L.) L. C. Rich.	p, p1	Sweden	Maad and Nilsson, 2004, Boberg *et al*., 2014
Sphingidae	*Deilephila porcellus* (Linnaeus 1758)	*Deilephila porcellus*	Orchidaceae	*Platanthera chlorantha* (Custer) Reichb.	*Platanthera chloranatha* (Custer) Reichb.	p	Sweden	Maad and Nilsson, 2004
Sphingidae	*Deilephila porcellus* (Linnaeus 1758)	*Deilephila porcellus* (L.)	Orchidaceae	*Platanthera chlorantha* (Custer) Reichb.	*Platanthera chlorantha* (Cust.) Rchb.	fv, p1	Sweden	Nilsson, 1978

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Sphingidae	*Dolba hyloeus* (Drury 1773)	*Dolba hyloeus*	Amaryllidaceae	*Hymenocallis coronaria* (Le Conte) Kunth	*Hymenocallis coronaria* (Le Conte) Kunth	p1	USA, Georgia	Graham, 2010
Sphingidae	*Dolba hyloeus* (Drury 1773)	*Dolba hyloeus*	Amaryllidaceae	*Hymenocallis occidentalis* (Le Conte) Kunth	*Hymenocallis occidentalis* (Le Conte) Kunth	p1	USA, Alabama	Graham, 2010
Sphingidae	*Eumorpha achemon* (Drury, 1773)	*Pholus achemon* Drury	Nyctaginaceae	*Mirabilis multiflora* (Torr.) A. Gray	*Mirabilis multiflora* (Torr.) Gray	fv, p1, p2	USA, Utah	Cruden, 1970
Sphingidae	*Eumorpha achemon* (Drury, 1773)	*Philampelus achemon* Dru.	Orchidaceae	*Platanthera leucophaea* (Nuttall) Lindley	*Habenaria leucophaea* Gray.	p1	USA, Illinois	Robertson, 1893
Sphingidae	*Eumorpha achemon* (Drury, 1773)	*Eumorpha achemon*	Orchidaceae	*Platanthera leucophaea* (Nuttall) Lindley	*Platanthera leucophaea* (Nuttall) Lindley	L: p1	USA, Wisconsin	Cuthrell, 1994, in Argue, 2012
Sphingidae	*Eumorpha achemon* (Drury, 1773)	Eumorpha achemon (Drury)	Orchidaceae	*Platanthera praeclara* Sheviak & Bowles	*Platanthera praeclara* Sheviak & Bowles	L: p1	USA, North Dakota	Cuthrell and Rider, 1994, in Jordan *et al*., 2006
Sphingidae	*Eumorpha achemon* (Drury, 1773)	*Eumorpha achemon*	Ranunculaceae	*Aquilegia chrysantha* Gray	*Aquilegia chrysantha* Gray	fv, p1	USA, Arizona	Miller, 1985
Sphingidae	*Eumorpha fasciatus* (Sulzer, 1776)	*Eumorpha fasciatus*	Onagraceae	*Oenothera grandiflora* L'Hér. ex Aiton.	*Oenothera grandiflora* L'Hér.	p1	USA, Alabama, Florida	Graham, 2010
Sphingidae	*Eumorpha pandorus* (Hübner 1821)	*Eumorpha pandorus*	Onagraceae	*Oenothera grandiflora* L'Hér. ex Aiton.	*Oenothera grandiflora* L'Hér.	p1	USA, Alabama, Florida	Graham, 2010
Sphingidae	*Hemaris* Dalman, 1816[1817]	*Hemaris* sp.	Caryophyllaceae	*Silene caroliniana* Walter	*Silene caroliniana*	fv, p2	USA, Maryland	Reynolds and Fenster, 2008

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Sphingidae	*Hemaris* Dalman, 1816[1817]	*Hemaris* sp.	Orchidaceae	*Platanthera blephariglottis* (Willdenow) Lindley	*Platanthera blephariglottis* (Willdenow) Lindley	p1	USA, Maine	Cole and Firmage, 1984
Sphingidae	*Hemaris diffinis* (Boisduval, 1836)	*Hemaris diffinis*	Campanulaceae	*Lobelia spicata* Lam.	*Lobelia spicata* Lam.	fv, p1	USA, Illinois	Griffin and Byers, 2012
Sphingidae	*Hemaris diffinis* (Boisduval, 1836)	*Hemaris diffinis*	Orchidaceae	*Platanthera peramoena* (A. Gray) A. Gray	*Platanthera peramoena* (A. Gray) A. Gray	p1	USA, Pennsylvania	Hapeman, 1997
Sphingidae	*Hemaris diffinis* (Boisduval, 1836)	*Sesia diffinis*	Orchidaceae	*Platanthera psycodes* (L.) Lindley	*Platanthera psycodes*	fv, p1	no information	Guignard, 1885
Sphingidae	*Hemaris thysbe* (Fabricius, 1775)	*Hemaris thysbe*	Amaryllidaceae	*Hymenocallis coronaria* (Le Conte) Kunth	*Hymenocallis coronaria* (Le Conte) Kunth	p1	USA, Georgia	Graham, 2010
Sphingidae	*Hemaris thysbe* (Fabricius, 1775)	*Hemaris thysbe*	Orchidaceae	*Platanthera blephariglottis* (Willdenow) Lindley	*Platanthera blephariglottis* (Willdenow) Lindley	fv, p1	USA, Michigan	Smith and Snow, 1976
Sphingidae	*Hemaris thysbe* (Fabricius, 1775)	*Haemorrhagis thysbe*	Orchidaceae	*Platanthera lacera* (Michaux) G. Don	*Platanthera lacera* (Michx) G. Don	p1	USA, Michigan	Stoutamire, 1974
Sphingidae	*Hemaris thysbe* (Fabricius, 1775)	*Hemaris thysbe*	Orchidaceae	*Platanthera peramoena* (A. Gray) A. Gray	*Platanthera peramoena* (A. Gray) A. Gray	fv, p1	USA, Pennsylvania	Hapeman, 1997
Sphingidae	*Hemaris thysbe* (Fabricius, 1775)	*Haemorrhagis thysbe*	Orchidaceae	*Platanthera psycodes* (L.) Lindley	*Platanthera psycodes* (L.) Lindley	fv, p1	USA, Michigan	Stoutamire, 1974

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Sphingidae	*Hemaris thysbe* (Fabricius, 1775)	*Sesia thysbe*	Orchidaceae	*Platanthera psycodes* (L.) Lindley	*Platanthera psycodes*	fv, p1	no information	Guignard, 1885
Sphingidae	*Hyles euphorbiae* (Linnaeus 1758)	*Celerio euphorbiae* L.	Caryophyllaceae	*Dianthus superbus* L.	*Dianthus superbus* L.	fv, p1	Switzerland	Erhardt, 1991
Sphingidae	*Hyles euphorbiae* (Linnaeus 1758)	*Hyles euphorbiae* (L.)	Orchidaceae	*Platanthera praeclara* Sheviak & Bowles	*Platanthera praeclara* Sheviak & Bowles	p1	USA, North Dakota	Jordan *et al*., 2006, Phillips, 2003
Sphingidae	*Hyles gallii* (Rottemburg, 1775)	*Hyles gallii* (Rott.)	Orchidaceae	*Platanthera chlorantha* (Custer) Reichb.	*Platanthera chlorantha* (Cust.) Rchb.	fv, p1	Sweden	Nilsson, 1978
Sphingidae	*Hyles gallii* (Rottemburg, 1775)	*Hyles gallii* (Rottenburg)	Orchidaceae	*Platanthera praeclara* Sheviak & Bowles	*Platanthera praeclara* (Sheviak & Bowles)	p1	Canada, Manitoba	Westwood and Borkowsky, 2004
Sphingidae	*Hyles* Hübner, 1819	*Hyles*	Ranunculaceae	*Aquilegia caerulea* James	*Aquilegia caerulea* var. *pinetorum* (Tidestrom)	fv, p1	USA, Arizona	Miller, 1981
Sphingidae	*Hyles* Hübner, 1819	*Hyles*	Ranunculaceae	Aquilegia caerulea James	*Aquilegia caerulea* James	fv, p1	USA, Colorado	Miller, 1981
Sphingidae	*Hyles lineata* (Fabricius, 1775)	*Hyles lineata* Fabricius	Nyctaginaceae	*Abronia ammophila* Greene	*Abronia ammophila* Greene	fv, p1	USA, Wyoming	Saunders and Sipes, 2006
Sphingidae	*Hyles lineata* (Fabricius, 1775)	*Hyles lineata*	Nyctaginaceae	*Mirabilis multiflora* (Torr.) A. Gray	*Mirabilis multiflora*	fv, p2	USA, California	Hodges, 1995
Sphingidae	*Hyles lineata* (Fabricius, 1775)	*Hyles lineata*	Onagraceae	*Oenothera caespitosa* Nutt.	*Oenothera cespitosa* Nutt. subsp. *cespitosa* Nutt.	fv, p3	USA, Wyoming	Artz *et al*., 2010

moth family	moth species (valid name)	moth species (name in paper)	plant family	plant species (valid name)	plant species (name in paper)	interaction	country	references
Sphingidae	*Hyles lineata* (Fabricius, 1775)	*Hyles lineata*	Onagraceae	*Oenothera caespitosa* Nutt.	*Oenothera cespitosa* Nutt. subsp. *navajoensis* (W. L. Wagner, Stockhouse and Klein) Cronq.	fv, p3	USA, Utah	Artz *et al.*, 2010
Sphingidae	*Hyles lineata* (Fabricius, 1775)	*Hyles lineata*	Orchidaceae	*Platanthera blephariglottis* (Willdenow) Lindley	*Platanthera blephariglottis* (Willdenow) Lindley	fv, p1	USA, Michigan	Smith and Snow, 1976
Sphingidae	*Hyles lineata* (Fabricius, 1775)	*Hyles lineata* (Fabricius)	Orchidaceae	*Platanthera praeclara* Sheviak and Bowles	*Platanthera praeclara* Sheviak and Bowles	p1	USA, North Dakota	Fox *et al.*, 2013
Sphingidae	*Hyles lineata* (Fabricius, 1775)	*Hyles lineata* (Fabricius)	Ranunculaceae	*Aquilegia caerulea* James	*Aquilegia caerulea* James	fv, p1	USA, Colorado	Miller, 1978
Sphingidae	*Hyles lineata* (Fabricius, 1775)	*Hyles lineata*	Ranunculaceae	*Aquilegia caerulea* James	*Aquilegia caerulea*	fv, p3	USA, Utah	Brunet and Holmquist, 2009
Sphingidae	*Hyles livornica* (Esper 1780)	*Hyles livornica* Esper	Caryophyllaceae	*Dianthus inoxianus* Gallego	*Dianthus inoxianus* Gallego	L: p	Spain, SW Iberian Peninsula	Balao, 2010, in Balao *et al.*, 2011
Sphingidae	*Hyloicus pinastri* Linnaeus 1758	*Hyloicus pinastri*	Orchidaceae	*Platanthera bifolia* (L.) Rich.	*Platanthera bifolia*	p, p1	Sweden	Boberg *et al.*, 2014
Sphingidae	*Lintneria eremitus* (Hübner, 1823)	*Sphinx eremitis* (Hübner)	Orchidaceae	*Platanthera leucophaea* (Nuttall) Lindley	*Platanthera leucophaea* (Nutt.) Lindl.	p1	USA	Bowles, 1983; Sheviak and Bowles, 1986
Sphingidae	*Lintneria eremitus* (Hübner, 1823)	*Sphinx eremitis* (Hübner)	Orchidaceae	*Platanthera praeclara* Sheviak and Bowles	*Platanthera praeclara* Sheviak and Bowles	p1	USA, North Dakota	Fox *et al.*, 2013

moth family	**moth species (valid name)**	**moth species (name in paper)**	**plant family**	**plant species (valid name)**	**plant species (name in paper)**	**interaction**	**country**	**references**
Sphingidae	*Macroglossum stellatarum* (Linnaeus 1758)	*Macroglossum stellatarum* L.	Caryophyllaceae	*Dianthus sylvestris* Wulfen	*Dianthus sylvestris* Wulf	p1	Switzerland, Swiss Alps	Erhardt, 1988
Sphingidae	*Macroglossum stellatarum* (Linnaeus 1758)	*Macroglossum stellatarum*	Amaryllidaceae	*Narcissus papyraceus* Ker Gawl.	*Narcissus papyraceus*	fv, p1	Spain	Perez-Barrales *et al*., 2007
Sphingidae	*Macroglossum stellatarum* (Linnaeus 1758)	*Macroglossum stellatarum* L.	Caryophyllaceae	*Dianthus gratianopolitanus* Vill.	*Dianthus gratianopolitanus* Vill.	fv, p1	Switzerland	Erhardt, 1990
Sphingidae	*Macroglossum stellatarum* (Linnaeus 1758)	*Macroglossum stellatarum* L.	Caryophyllaceae	*Dianthus sylvestris* Wulfen	*Dianthus sylvestris* Wulf.	p	no information	Collin *et al*., 2002
Sphingidae	*Macroglossum stellatarum* (Linnaeus 1758)	*Macroglossum stellatarum* (L.)	Orchidaceae	*Gymnadenia conopsea* (L.) R. Br.	*Gymnadenia conopsea* (L.) R.Br. s.l.	p1	Switzerland	Huber *et al*., 2005
Sphingidae	*Manduca quinquemaculata* (Haworth, 1803)	*Manduca quinquemaculata*	Nyctaginaceae	*Mirabilis longiflora* L.	*Mirabilis longiflora*	fv, p1	USA, Arizona	Grant and Grant, 1983
Sphingidae	*Manduca quinquemaculata* (Haworth, 1803)	*Manduca quinquemaculata*	Orchidaceae	*Platanthera blephariglottis* (Willdenow) Lindley	*Platanthera blephariglottis* (Willdenow) Lindley	fv, p1	USA, Michigan	Smith and Snow, 1976
Sphingidae	*Manduca rustica* (Fabricius, 1775)	*Manduca rustica* Fabricius	Amaryllidaceae	*Hymenocallis coronaria* (Le Conte) Kunth	*Hymenocallis coronaria* (Le Conte) Kunth	p1	USA, Georgia	Graham, 2010
Sphingidae	*Manduca rustica* (Fabricius, 1775)	*Manduca rustica* Fabricius	Amaryllidaceae	*Hymenocallis occidentalis* (Le Conte) Kunth	*Hymenocallis occidentalis* (Le Conte) Kunth	p1	USA, Alabama	Graham, 2010
Sphingidae	*Manduca rustica* (Fabricius, 1775)	*Manduca rustica* Fabricius	Onagraceae	*Oenothera biennis* L.	*Oenothera biennis* L.	p1	USA, Alabama	Graham, 2010
Sphingidae	*Manduca rustica* (Fabricius, 1775)	*Manduca rustica* Fabricius	Onagraceae	*Oenothera grandiflora* L'Hér. ex Aiton.	*Oenothera grandiflora* L'Hér.	p1	USA, Alabama, Florida	Graham, 2010

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Sphingidae	*Manduca sexta* Linnaeus, 1763	*Manduca sexta* L.	Amaryllidaceae	*Hymenocallis coronaria* (Le Conte) Kunth	*Hymenocallis coronaria* (Le Conte) Kunth	p1	USA, Georgia	Graham, 2010
Sphingidae	*Manduca sexta* Linnaeus, 1763	*Phlegethontius sexta* Joh.	Convolvulaceae	*Ipomoea alba* L.	*Calonyction aculeate* House	p1	USA, California	Tillett, 1966
Sphingidae	*Manduca sexta* Linnaeus, 1763	*Manduca sexta* L.	Onagraceae	*Oenothera biennis* L.	*Oenothera biennis* L.	p1	USA, Alabama	Graham, 2010
Sphingidae	*Manduca sexta* Linnaeus, 1763	*Manduca sexta* L.	Onagraceae	*Oenothera grandiflora* L'Hér. ex Aiton.	*Oenothera grandiflora* L'Hér.	p1	USA, Alabama, Florida	Graham, 2010
Sphingidae	*Manduca sexta* Linnaeus, 1763	*Manduca sexta*	Orchidaceae	*Platanthera leucophaea* (Nuttall) Lindley	*Platanthera leucophaea* (Nutt.) Lindl.	(p1)	USA	Sheviak and Bowles, 1986
Sphingidae	*Manduca sexta* Linnaeus, 1763	*Manduca sexta*	Solanaceae	*Datura wrightii* Regel	*Datura wrightii* Regel	p3	USA, Arizona	Bronstein *et al.*, 2009
Sphingidae	*Manduca sexta* Linnaeus, 1763	*Manduca sexta* (L.)	Solanaceae	*Nicotiana attenuata* Torrey ex Watson	*Nicotiana attenuata* Torrey ex Watson	(fv, p3)	USA, Utah	Sime and Baldwin, 2003
Sphingidae	*Paratrea plebeja* (Fabricius, 1777)	*Paratrea plebeja*	Amaryllidaceae	*Hymenocallis coronaria* (Le Conte) Kunth	*Hymenocallis coronaria* (Le Conte) Kunth	p1	USA, Georgia	Graham, 2010
Sphingidae	*Paratrea plebeja* (Fabricius, 1777)	*Paratrea plebeja*	Onagraceae	*Oenothera biennis* L.	*Oenothera biennis* L.	p1	USA, Alabama	Graham, 2010
Sphingidae	*Paratrea plebeja* (Fabricius, 1777)	*Paratrea plebeja*	Onagraceae	*Oenothera grandiflora* L'Hér. ex Aiton.	*Oenothera grandiflora* L'Hér.	p1	USA, Alabama, Florida	Graham, 2010
Sphingidae	*Paratrea plebeja* (Fabricius, 1777)	*Paratraea plebeja*	Orchidaceae	*Platanthera praeclara* Sheviak & Bowles	*Platanthera praeclara* Sheviak and Bowles	p1	USA, Missouri	Phillips, 2003
Sphingidae	*Sphinx asella* (Rothschild and Jordan, 1903)	*Sphinx asella*	Ranunculaceae	*Aquilegia chrysantha* Gray	*Aquilegia chrysantha* Gray	fv, p1	USA, Arizona	Miller, 1985

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Sphingidae	*Sphinx chersis* (Hübner, 1823)	*Sphinx chersis* Huebner	Nyctaginaceae	*Mirabilis multiflora* (Torr.) A. Gray	*Mirabilis multiflora* (Torr.) Gray	fv, p1?, p2?	USA, Utah	Cruden, 1970
Sphingidae	*Sphinx chersis* (Hübner, 1823)	*Sphinx chersis*	Ranunculaceae	*Aquilegia chrysantha* Gray	*Aquilegia chrysantha* Gray	fv, p1	USA, Arizona	Miller, 1985
Sphingidae	*Sphinx dollii* Neumoegen, 1881	*Sphinx dollii coloradus*	Onagraceae	*Oenothera caespitosa* Nutt.	*Oenothera caespitosa*	fv, p1	USA, Utah	Grant, 1983
Sphingidae	*Sphinx drupiferarum* (J. E. Smith, 1797)	*Sphinx drupiferarum* J.E. Smith	Orchidaceae	*Platanthera praeclara* Sheviak & Bowles	*Platanthera praeclara* (Sheviak & Bowles)	p1	Canada, Manitoba	Westwood and Borkowsky, 2004
Sphingidae	*Sphinx drupiferarum* (J. E. Smith, 1797)	*Sphinx drupiferarum* J. E. Smith	Orchidaceae	*Platanthera praeclara* Sheviak & Bowles	*Platanthera praeclara* Sheviak & Bowles	L: p1	USA, North Dakota	Cuthrell and Rider, 1994, in Jordan *et al.*, 2006
Sphingidae	*Sphinx drupiferarum* (J. E. Smith, 1797)	*Sphinx drupiferarum*	Orchidaceae	*Platanthera orbiculata* (Pursh) Lindley	*Habenaria orbiculata*	p1	no information	Guignard, 1885
Sphingidae	*Sphinx ligustri* Linnaeus 1758	*Sphinx ligustri*	Orchidaceae	*Platanthera bifolia* (L.) Rich.	*Platanthera bifolia*	p, p1	Sweden	Boberg *et al.*, 2014
Sphingidae	*Sphinx pinastri* Linnaeus 1758	*Hyloicus pinastri* (L.)	Orchidaceae	*Platanthera bifolia* (L.) Rich.	*Platanthera bifolia* (L.) L. C. Rich.	p	Sweden	Maad, 2000
Sphingidae	*Sphinx pinastri* Linnaeus 1758	*Hyloicus pinastri* (L.)	Orchidaceae	*Platanthera bifolia* (L.) Rich.	*Platanthera bifolia* (L.) L. C. Rich.	p	Sweden	Maad and Nilsson, 2004
Sphingidae	*Sphinx pinastri* Linnaeus 1758	*Hyloicus pinastri*	Orchidaceae	*Platanthera chlorantha* (Custer) Reichb.	*Platanthera chlorantha*	fv, p1	Norway	Steen, 2012
Sphingidae	*Sphinx sequoiae* Boisduval, 1868	*Sphinx sequoiae*	Liliaceae	*Chlorogalum pomeridianum* (DC.) Kunth	*Chloragalum pomeridianum*	fv, p1	USA, California	Grant, 1983

moth family	**moth species (valid name)**	**moth species (name in paper)**	**plant family**	**plant species (valid name)**	**plant species (name in paper)**	**interaction**	**country**	**references**
Sphingidae	*Sphinx vashti* Strecker, 1878	*Sphinx vashti*	Onagraceae	*Oenothera caespitosa* Nutt.	*Oenothera caespitosa*	fv, p1	USA, Utah	Grant, 1983
Sphingidae	*Sphinx vashti* Strecker, 1878	*Sphinx vashti*	Onagraceae	*Oenothera caespitosa* Nutt.	*Oenothera cespitosa* Nutt. subsp. *cespitosa* Nutt.	fv, p3	USA, Wyoming	Artz *et al*., 2010
Sphingidae	*Sphinx vashti* Strecker, 1878	*Sphinx vashti* Strecker	Ranunculaceae	*Aquilegia caerulea* James	*Aquilegia caerulea* var. *pinetorum* (Tidestrom)	fv, p1	USA, Arizona	Miller, 1981
Sphingidae	*Sphinx vashti* Strecker, 1878	*Sphinx vashti*	Ranunculaceae	*Aquilegia caerulea* James	*Aquilegia caerulea*	fv, p3	USA, Utah	Brunet and Holmquist, 2009
Sphingidae	*Xylophanes tersa* (Linnaeus, 1771)	*Chaerocampa tersa* (L.)	Orchidaceae	*Platanthera leucophaea* (Nuttall) Lindley	*Habenaria leucophaea* Gray.	fv, p1	USA, Illinois	Robertson, 1893
Zygaenidae	*Zygaena exulans* (Hohenwarth 1792)	*Zygaena exulans* Hochenw. & Rainer	Caryophyllaceae	*Dianthus glacialis* Haenke	*Dianthus glacialis* Haenke	fv, p1	Switzerland, Swiss Alps	Erhardt and Jäggi, 1995
Zygaenidae	*Zygaena exulans* (Hohenwarth 1792)	*Zygaena exulans* Hochenw. & Rainer	Caryophyllaceae	*Silene acaulis* (L.) Jacq.	*Silene acaulis* (L.) Jacq.	fv, p1	Switzerland, Swiss Alps	Erhardt and Jäggi, 1995
Zygaenidae	*Zygaena exulans* (Hohenwarth 1792)	*Zygaena exulans* (Hochw.)	Orchidaceae	*Gymnadenia odoratissima* (L.) Rich.	*Gymnadenia odoratissima* (L.) Rich.	p1	Switzerland	Huber *et al*., 2005
Zygaenidae	*Zygaena filipendulae* (Linnaeus 1758)	*Zygaena filipendulae* (Linnaeus, 1758)	Orchidaceae	*Anacamptis pyramidalis* (L.) Rich.	*Anacamptis pyramidalis* (L.) Rich	fv, p1	Ireland	Vallius *et al*., 2013
Zygaenidae	*Zygaena lonicerae* (Scheven 1777)	Zygaena lonicerae (Scheven)	Orchidaceae	*Gymnadenia conopsea* (L.) R. Br.	*Gymnadenia conopsea* (L.) R. Br.	p1	Germany	Nazarov and Buchsbaum, 2004

moth family	**moth species (valid name)**	**moth species (name in paper)**	**plant family**	**plant species (valid name)**	**plant species (name in paper)**	**interaction**	**country**	**references**
Zygaenidae	*Zygaena minos* (Denis & Schiffermüller 1775)	*Zygaena minos* (Denis & Schiffermüller)	Orchidaceae	*Anacamptis pyramidalis* (L.) Rich.	*Anacamptis pyramidalis* (L.)	p1	Sweden	Lind, 1994
Zygaenidae	*Zygaena minos* (Denis & Schiffermüller 1775)	*Zygaena minos* (Denis & Schiffermüller)	Orchidaceae	*Gymnadenia odoratissima* (L.) Rich.	*Gymnadenia odoratissima* (L.) Rich.	p1	Germany	Nazarov and Buchsbaum, 2004

10.2.2 References

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10.3 Appendix III: Declaration

I, the undersigned author of this work, declare that this thesis is my own work and has not been submitted in any form for another degree or diploma at any university or other institution of tertiary education.

Information derived from the published or unpublished work of others has been acknowledged in the text and a list of references is given.

………………………………………..	………………………………………………..
date	signature

10.4 Appendix IV: Curriculum Vitae

PERSONAL INFORMATION

Name	Melanie Hahn
Date of birth	01.06.1984 (in Landau)
E-Mail	hahn@uni-landau.de
Nationality	German

EDUCATION AND WORK EXPERIENCE

2010 – 2015	PhD student, Institute for Environmental Sciences, University Koblenz-Landau Working group: Ecotoxicology and Environment Title of the dissertation: Lepidoptera in agricultural landscapes – The role of field margins, the effects of agrochemicals and moth pollination services.
2010 – 2013	Research associate at the Institute for Environmental Sciences, University Koblenz-Landau, for a Research and Development Project (Nr. 3709 65 421) on behalf of the German Federal Environment Agency (Umweltbundesamt) Project: Protection of biodiversity in the risk assessment and risk management of pesticides (plant protection products & biocides) with a focus on arthropods, soil organisms, and amphibians.
2009	Diploma in Environmental Sciences, University Koblenz-Landau, Campus Landau Title of the diploma thesis: Untersuchung zu Diversität und Abundanz nachtaktiver Insekten – mit Schwerpunkt auf Nachtfaltern (Lepidoptera) – auf verschiedenen landwirtschaftlich genutzten Flächen.
2003 – 2009	Studies of Environmental Sciences • Main subjects: Biodiversity & Sustainability, Applied Ecology, Geo-ecology • Minor subjects: Ecotoxicology, Environmental Economics

10.5 Appendix V: Publications and presentations at scientific conferences

PUBLICATIONS (DOCTORAL THESIS)

Hahn, M., Lenhardt, P. & Brühl, C.A. (2014): Characterization of field margins in intensified agro-ecosystems – Why narrow margins should matter in terrestrial pesticide risk assessment and management. Integrated Environmental Assessment and Management, 10(3): 456–462

Hahn, M., Geisthardt, M. & Brühl, C.A. (2014): Effects of herbicide-treated host plants on the development of *Mamestra brassicae* L. caterpillars. Environmental Toxicology and Chemistry, 33(11): 2633–2638

Hahn, M., Schotthöfer, A., Schmitz, J., Franke, L.A. & Brühl, C.A. (2015): The effects of agrochemicals on Lepidoptera, with a focus on moths, and their pollination service in field margin habitats. Agriculture, Ecosystems and Environment, 207: 153–162.

Hahn, M. & Brühl, C.A. (submitted): The secret pollinators – Moth pollination with a focus on Europe and North America. Manuscript.

FURTHER PUBLICATIONS

Schmitz, J., **Hahn, M.**, Brühl, C.A. (2014): Agrochemicals in field margins – An experimental field study to assess the impacts of pesticides and fertilizers on a natural plant community. Agriculture, Ecosystems and Environment 193, 60-69.

Stahlschmidt, P., **Hahn, M.**, Brühl, C.A. (in prep.): Bat activity in the agricultural landscape – the ultrasonic silence? Manuscript.

REPORTS

Brühl, C.A., Alscher A., Berger G., Bethwell C, Graef F., **Hahn M.**, Schmidt T., Weber B. (2013): Protection of biodiversity in the risk assessment and risk management of pesticides with a focus on arthropods, soil organisms, and amphibians. Report of the Research and Development Project Nr 3709 65 421. German Federal Environment Agency (Umweltbundesamt), p. 244.

PRESENTATIONS AT SCIENTIFIC CONFERENCES

Hahn, M. & Brühl, C.A. (2013): Indirect effect of an insecticide on an ecosystem service: pollination by moths. Oral presentation at the SETAC Europe 23rd Annual Meeting 2013, Glasgow, Scotland.

Hahn, M., Schotthöfer, A., Geisthardt, M., Schmitz, J., Lenhardt, P. & Brühl, C.A. (2012): Caterpillars and protection goals: The role of field margins as habitats and the effects of pesticide applications. Poster presentation at the SETAC Europe 22nd Annual Meeting/6th SETAC World Congress 2012, Berlin, Germany.

Geisthardt, M., **Hahn, M.** & Brühl, C.A. (2011): Effekte von Herbiziden auf die Futterpflanzen-Qualität phytophager Insekten. Poster presentation at the SETAC GLB 16th Annual Meeting 2011, Landau, Germany.

Schotthöfer, A., **Hahn, M.** & Brühl, C.A. (2011): Raupendiversität in Feldsäumen verschiedener landwirtschaftlicher Kulturen. Poster presentation at the SETAC GLB 16th Annual Meeting 2011, Landau, Germany.

Hahn, M., Lenhardt, P., Vollmar, T. & Brühl, C.A. (2010): Erfassung der Breiten von Saumstrukturen landwirtschaftlicher Flächen auf digitalen Orthophotos (DOPs). Oral presentation at the 4th joint Annual Meeting of the SETAC GLB and the GDCh (Section Environmental chemistry and Ecotoxicology) 2010, Dessau, Germany.

Hahn, M., Stahlschmidt, P. & Brühl, C.A. (2009): Biomass, abundance and diversity of nocturnal insects – with a focus on moths (Lepidoptera) – in organic and conventionally managed vineyards. Poster Presentation, Young Environmental Scientist Meeting (YES-Meeting), Landau.

10.6 Appendix VI: Teaching involvement

During my PhD study at the University Koblenz-Landau, Campus Landau, I co-supervised several research projects. These research studies are listed below and they were integrated into my PhD project. All of these studies were supervised by Dr. Carsten Brühl.

Co-supervised projects:

Geisthardt, M. (2011): Der Einfluss von Herbiziden auf die Wirtspflanzenqualität phytophager Insekten. Fallstudie. Universität Koblenz-Landau.

Vollmar, T. (2011): Analyse von Saumstrukturen landwirtschaftlicher Flächen in Rheinland-Pfalz und Brandenburg. Bachelorarbeit. Universität Koblenz-Landau.

Schotthöfer, A. (2012): Untersuchung zur Eignung von Feldsäumen verschiedener landwirtschaftlicher Kulturen als Entwicklungshabitat für Schmetterlingsraupen (Lepidoptera) unter Berücksichtigung der Auswirkungen von Agrarchemikalieneinträgen - eine quantitative Analyse. Diplomarbeit. Universität Koblenz-Landau. (note: further co-supervisor: Juliane Schmitz)

Geisthardt, M. (2012): Effekte von Herbiziden auf phytophage Insekten am Beispiel der Kohleule *Mamestra brassicae*. Diplomarbeit. Universität Koblenz-Landau.

Franke, L. A. (2014): Toxic and repellent effects of an insecticide on cabbage moth caterpillars (*Mamestra brassicae* L.). Research Project Report. Universität Koblenz-Landau.

In addition, I was involved in teaching and co-supervising students in the course “Ökotoxikologische Testmethoden II – Assessment and Monitoring of Effects” in the years 2011 and 2012. Furthermore, I was involved in teaching in the course “Landschaftsmaßstab – Integrative Effekte”, which is part of the “Postgradualstudium Ökotoxikologie (GDCh / SETAC GLB)”, in the years 2010, 2011, 2012 and 2014.