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Variation in sexual communication and its role in divergence of two host strains of the noctuid moth *Spodoptera frugiperda*

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Citation for published version (APA):

Unbehend, M. (2013). *Variation in sexual communication and its role in divergence of two host strains of the noctuid moth *Spodoptera frugiperda**.

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Chapter 1

General Introduction

1. Sexual communication in moths

1.1. *The role of sex pheromones as premating signals*

Many Lepidoptera species use sex pheromones to attract a conspecific mate (Tamaki, 1985; Cardé and Minks, 1997; Cardé and Haynes, 2004). In moths, females usually attract males over long distances via a species-specific sex pheromone (Tamaki, 1985; Löfstedt and Kozlov, 1997) that is produced in a pheromone gland located terminal at the abdomen of a female (Percy-Cunningham and MacDonald, 1987). During courtship, females extrude their pheromone gland and expose the gland surface to the wind, which distributes the female pheromone in the environment (Tamaki, 1985; Percy-Cunningham and MacDonald, 1987). Males have sensitive antennae that can detect the female pheromone signal and respond to it by starting flight and following the pheromone plume (Baker et al., 1985; Mafraneto and Cardé, 1994). When the male finds the source of the pheromone signal, i.e. the female, he starts a typical calling behavior by performing wing-fluttering and releasing a male-specific pheromone through its scent brushes or hairpencils (Tamaki, 1985; Birch et al., 1990; Lassance and Löfstedt, 2009). When both mates are attracted to each other at close range, mating will occur.

Females produce a species-specific sex pheromone that is only attractive for conspecific males (Tamaki, 1985; Löfstedt and Kozlov, 1997). On the one hand, species specificity of a sex pheromone is achieved by the use of a specific combination of pheromone components. Some species, like *Cameraria ohridella*, use only one pheromone component to attract males (Svatos et al., 1999), whereas other species, like *Heliothis virescens* or *Spodoptera frugiperda*, use multiple pheromone component blends as sex pheromone (Klun et al., 1980; Tumlinson et al., 1986). Some pheromone components of a complex female blend can also repel males of closely related species to avoid hybridization (Vickers and Baker, 1997;

Groot et al., 2006; Eizaguirre et al., 2007). On the other hand, the relative amount of each pheromone component within a complex female blend contributes to the specificity of sex pheromones (Tamaki, 1985; Jurenka, 2004). The most abundant component in a female blend of one species, e.g. (Z)-9-tetradecenyl acetate in *Spodoptera frugiperda* (Tumlinson et al., 1986), can for example be used in lower relative concentrations by another species, like *Spodoptera litura* (Sun et al., 2002), to avoid cross-attraction. The specificity and diversity of sex pheromones are remarkable and to date more than 1500 different sex pheromone compounds of a large variety of species have been identified (El-Sayed, 2012).

1.2. Biosynthesis of sex pheromones in females

Moth sex pheromones can be divided in so-called Type I (75%), Type II (15%) and miscellaneous (10%) pheromones, according to their chemical structure and biosynthesis (Ando et al., 2004). While Type I pheromones consist of a long carbon chain (C₁₀-C₁₈) with an oxygen-containing functional group, i.e. an alcohol, aldehyde or acetate ester, Type II pheromones are polyunsaturated hydrocarbons and epoxides with longer carbon chains (C₁₇-C₂₃) and no terminal functional group (Millar, 2000; Jurenka, 2003; Ando et al., 2004). The majority of female moths use sex pheromone compounds belonging to Type I, and pheromone biosynthesis of these compounds is based on the products of the fatty acid synthesis, i.e. palmitic acid (C₁₆) and stearic acid (C₁₈) (Jurenka, 2003, 2004). Modification of the long chain fatty acid precursors is achieved by different enzymes, i.e. (a) desaturases, which introduce double bonds at specific positions, (b) β -oxidation enzymes, which are responsible for chain-shortening by two carbons at a time, (c) reductases, which reduce the fatty acid precursors to produce alcohols and aldehydes, (d) oxidases, which oxidize alcohols to aldehydes, and (e) acetyltransferases, which convert fatty alcohols to acetate esters (Roelofs and Bjostad, 1984; Jurenka, 2003, 2004). Due to the action of all these different

enzymes, a great variety of sex pheromone components can be produced to obtain species-specific sex pheromone blends.

Pheromone biosynthesis in moths is activated by a pheromone biosynthesis activating neuropeptide (PBAN), which is produced in the subesophageal ganglion in the brain and released through the corpora cardiaca into the hemolymph (Raina and Menn, 1987; Raina, 1993; Rafaeli, 2005). PBAN binds to specific PBAN-receptors, present in the membrane of pheromone gland cells, and leads to the activation of second messengers, i.e. calcium influx and/or cAMP production, which induce the pheromone production (Raina, 1997; Roelofs and Jurenka, 1997; Rafaeli and Jurenka, 2003). In many moths, PBAN is produced in a circadian rhythm and released at the beginning of the scotophase (Raina, 1997; Rafaeli and Jurenka, 2003), so that mates are reproductively active at night and inactive during the day. Besides the variation in pheromone production between night and day, the female pheromone can also be influenced by many other factors.

1.3. Variation in sexual communication

Variation in the pheromone signal of a female moth is a common phenomenon and can be caused by differential environmental and endogenous factors (Raina, 1998). Many moth species for example exhibit geographic variation in the female pheromone composition (Hansson et al., 1990; McElfresh and Millar, 1999, 2001; Cardé and Haynes, 2004; Groot et al., 2009; Barrozo et al., 2010a). Furthermore, environmental factors like temperature (Delisle and Royer, 1994; Dong and Du, 2002; Raina, 2003), humidity (Royer and McNeil, 1991, 1993; Raina, 2003), photoperiod (Webster and Yin, 1997; Han et al., 1999; Gemeno and Haynes, 2001), host plant volatiles (McNeil and Delisle, 1989; Landolt and Phillips, 1997; Reddy and Guerrero, 2004), or interspecific olfactory cues (Groot et al., 2010a) can have an effect on the female pheromone. It has also been shown that endogenous

female-specific factors like age or mating status can change the sex pheromone blend of a female (Babilis and Mazomenos, 1992; Tang et al., 1992; del Mazo-Cancino et al., 2004; Lima et al., 2008).

Similar to the variation in the female pheromone signal, males exhibit variation in their response to sex pheromones, depending on endogenous, as well as environmental factors. Among other factors, the response of male moths to sex pheromones can be influenced by geographic variation (Wu et al., 1999; Groot et al., 2007; Zhu et al., 2009), humidity (Royer and McNeil, 1993), temperature (Baker and Cardé, 1979; Linn et al., 1988; Dumont and McNeil, 1992; Delisle, 1995), insecticides (Wei et al., 2004; Xu et al., 2010), predator exposure (Svensson et al., 2004; Anton et al., 2011), mating status (Gadenne et al., 2001; Barrozo et al., 2010a, b; Barrozo et al., 2011), age (Payne et al., 1970; Delisle, 1995; Altafini et al., 2010), plant volatiles (Ochieng et al., 2002; Party et al., 2009; Pregitzer et al., 2012), or pre-exposure to sex pheromone (Bartell and Lawrence, 1973; Anderson et al., 2003; Anderson et al., 2007).

Thus, although moth sex pheromones are unique and species-specific, variability in the sender of the signal, i.e. the female, and the receiver of the signal, i.e. the male, exists. Despite the fact that changes in the pheromone signal and response can reflect fitness and mating status of a partner (Johansson and Jones, 2007; Harari et al., 2011), they can also be the start of reproductive isolation between populations and contribute to the formation of new species (Phelan, 1992, 1997; Löfstedt, 1993; Cardé and Haynes, 2004; Smadja and Butlin, 2009; Wicker-Thomas, 2011). This has for example been shown in the European corn borer, *Ostrinia nubilalis*, which is described in more detail below (part 3.1.).

2. Evolution of pheromone diversity in moths

2.1. Dependence of pheromone sender and receiver

The evolution of pheromone diversity in moths is hard to understand because stabilizing selection seems to act on the sexual communication channel of a species, due to the reciprocal dependence of the sender, i.e. the female, and the receiver, i.e. the male, of a pheromone signal (Cardé and Baker, 1984; Phelan, 1992, 1997; Löfstedt, 1993; Linn and Roelofs, 1995). If only stabilizing selection would act on the sexual communication system of moths, females would emit a sex pheromone most attractive for the majority of males, and the male response would be centered according to the most common female blend within a population (Cardé and Baker, 1984; Cardé and Haynes, 2004). Such a strong reciprocal stabilizing selection would lead to the coevolution of sender and receiver and cause the reduction of variation in signal and response, which constrains directional selection and the evolution of new signal-response systems (Phelan, 1992).

When the signal of a female and the response of a male are genetically linked, changes in the signal would consequently lead to changes in the response and *vice versa* (Phelan, 1992). Thus, pleiotropy and/or linkage disequilibrium could contribute to the diversification of sexual communication systems. However, in the studies on moths conducted so far, genetic linkage between pheromone biosynthesis of females and pheromone perception of males was not found (Roelofs et al., 1987; Klun and Huettel, 1988; Löfstedt et al., 1989; Dopman et al., 2004). Furthermore, although the species-specific signal is not variable, the female pheromone signal and the male response can vary to some extent, as mentioned above. Therefore, the question arises whether counter-active selection forces exist that may overcome stabilizing selection and contribute to the great diversity of sex

pheromones and the species richness of moths (Shields, 1989; Kristensen et al., 2007; El-Sayed, 2012).

2.2. Asymmetric tracking hypothesis

The asymmetric tracking hypotheses was proposed by Phelan (1992, 1997), who suggested that selection could act asymmetrically on sender and receiver and that evolution of pheromone diversity in moths is driven by sexual selection via differential parental investments. The main assumption of this hypothesis is the existence of sex-specific parental investment, i.e. females invest more in their offspring and value the quality, not quantity, of males, whereas males invest more in mate finding with regard to the quantity of matings (Phelan, 1992, 1997). Phelan (1992) argued that both sexes differ in their reproductive strategies to maximize their own fitness and therefore, different selection pressures act on sender and receiver. More precisely, the pheromone signal is under weak selection and influenced by “stochastic factors and by avoidance of mating mistakes”, while the male response is under strong selection and determined by the female (he “tracks” the female), as well as intraspecific competition (Phelan, 1992, 1997). The overall conclusion of Phelan’s hypothesis is that the female pheromone signal may change relatively simply due to nonadaptive forces like genetic drift, founder effects or pleiotropy, while the male will track the most common female blend due to a wide response window.

Based on the asymmetric tracking hypothesis, the following evolutionary scenario (step 1 - 4) could explain how a mutation in the female sex pheromone could lead to reproductive isolation within a population and cause the formation of new species (Phelan, 1992, 1997; Löfstedt, 1993; Roelofs et al., 2002; Roelofs and Rooney, 2003; Baker, 2008; Smadja and Butlin, 2009).

First, the female pheromone signal changes (step 1). This could be caused by adaptation to the environment via selection on new mutations or on pre-existing standing genetic variation (Barrett and Schluter, 2008). It has been shown that the female pheromone signal can change, for example, under laboratory conditions, in the noctuid moth *Trichoplusia ni* (Haynes and Hunt, 1990a, b). The mutant *T. ni* females produced a sex pheromone that was significantly different from normal females of field populations and was not attractive for normal males (Haynes and Hunt, 1990a, b).

However, some rare males exist that exhibit a broad response window and are attracted to the new pheromone signal, while they can also respond to the most common pheromone blend of normal females (step 2). Some experiments showed that moth populations can contain rare males, exhibiting a broader pheromone response spectrum than normal males (Liu and Haynes, 1994; Roelofs et al., 2002; Linn et al., 2003; Linn et al., 2007; Hemmann et al., 2008). Thus, it is possible that a mutant female finds a mating partner, i.e. a rare male, and inherits the new pheromone signal to her female offspring, while the male offspring will respond to the new signal.

As a next step, to fix the new pheromone signal in the population, hybrids between mutant females and normal males, and/or crosses between normal females and rare males, need to have a lower fitness (step 3). Due to this hybrid fitness disadvantage, assortative mating can occur between mutant females and rare males, leading to the evolution of reproductive isolation barriers between the ancestral and the derived population (step 4). Once fully established, pre- as well as post-zygotic reproductive isolation mechanisms can drive divergence and contribute to the formation of new species (Coyne and Orr, 2004).

However, it remains an open question how fixation of the new pheromone signal is achieved in the derived population and how this causes the divergence of

populations (Smadja and Butlin, 2009). Furthermore, it is unclear what selective advantage rare males have when they are broadly tuned to a female pheromone blend. If males exhibit a very wide response window, they could also be attracted to females of another species, which would be a selective disadvantage for rare males. Thus, the asymmetric tracking hypothesis describes well the evolution of pheromone divergence in Lepidoptera, although it does not explain all aspects, which leaves other selection forces to shape the mate-signaling system in moths.

2.3. Selective forces in the evolution of pheromone diversity

Other selection forces, like sexual selection (Coltman et al., 2002; Wade and Shuster, 2004; Andersson and Simmons, 2006; Irestedt et al., 2009; Sullivan-Beckers and Cocroft, 2010), host plant adaptation (Nosil, 2007; Wiklund and Friberg, 2008; Smadja and Butlin, 2009; Ohshima, 2010), or geographically varying environmental factors (Cardé and Haynes, 2004), might contribute to the diversification of moth pheromones. Furthermore, selection due to specific environmental interaction with predators and parasitoids (Stowe et al., 1987; Zuk and Kolluru, 1998; Cardé and Haynes, 2004; Anton et al., 2011; Laumann et al., 2011), or the evolution of behavioral antagonists (Vickers and Baker, 1997; Cardé and Haynes, 2004; Groot et al., 2006; Baker, 2008), could overrule stabilizing selection. To understand the evolution of sexual communication systems in moths, intra-specific studies, rather than inter-specific ones, might facilitate the identification of factors causing the divergence of pheromone signals. More precisely, the study of pheromonal strains within a species could help to understand how differentiation in sexual communication systems can arise and lead to reproductive isolation within a population.

3. Pheromone divergence within species: The first step to speciation?

3.1. *The European corn borer Ostrinia nubilalis*

The most prominent example of pheromone divergence within a lepidopteran species is *Ostrinia nubilalis*, which consists of two pheromonal strains, the so-called E-strain and the Z-strain (Roelofs et al., 1985; Lassance, 2010). The female sex pheromone of both strains consists of the two components (Z)-11-tetradecenyl acetate (Z11-14:OAc) and (E)-11-tetradecenyl acetate (E11-14:OAc), which are produced in a 97:3 Z/E ratio in Z-strain females and in a 1:99 Z/E ratio in E-strain females (Kochansky et al., 1975). Due to the strain-specific pheromone, both strains mate assortatively in the field and hybridization between strains is rare (Roelofs et al., 1972; Glover et al., 1987; Linn et al., 1997).

Genetic analyses revealed that different genomic regions are involved in the variation in the female pheromone and the male response (Roelofs et al., 1987; Klun and Huettel, 1988; Löfstedt et al., 1989; Dopman et al., 2004; Olsson et al., 2010). Lassance et al. (2010) showed that the fatty acyl reductase *pgFAR* is responsible for the opposite pheromone ratio found in E- and Z-strain females. The *pgFAR* gene has two strain-specific alleles that have different substrate specificities to the *cis* and *trans* isomer of the pheromone precursors (Z)- and (E)-11-tetradecenoyl and subsequently cause strain-specific pheromone blends (Lassance et al., 2010). Genes responsible for the strain-specific male response have not been identified so far. However, it was shown that the male response is determined by the *resp* locus, located on the sex chromosome (Roelofs et al., 1987; Dopman et al., 2004), and by loci affecting the antennal response, which are both autosomal and sex-linked (Roelofs et al., 1987; Olsson et al., 2010). Different odorant receptor genes, located on the sex chromosome, could partly cause the strain-specific male attraction (Lassance et al., 2011; Yasukochi et al., 2011).

In conclusion, strain-specific sexual communication is a strong prezygotic mating barrier between the Z- and the E-strain and leads to reproductive isolation. The pheromonal differentiation as well as genetic differences suggest that both strains are in the process of speciation and probably semispecies or sibling species (Cardé et al., 1978; Malausa et al., 2007; Lassance, 2010). As a result, *O. nubilalis* has become a model species to study the evolution of sexual communication (Smadja and Butlin, 2009; Lassance, 2010; Wicker-Thomas, 2011).

3.2. *The fall armyworm Spodoptera frugiperda*

Similar to the two strains in *Ostrinia nubilalis*, the fall armyworm *Spodoptera frugiperda* (J. E. Smith) consist of two strains that differ in their female sex pheromone composition (Groot et al., 2008; Lima and McNeil, 2009), and seem to be undergoing ecological speciation in sympatry (see Chapter 5 and 6). The two strains of *S. frugiperda*, the corn-strain and rice-strain, have first been described as host strains, which prefer either corn as host or smaller grasses like rice and Bermuda grass (Pashley et al., 1985; Pashley, 1986). Besides habitat isolation, both strains exhibit behavioral isolation due to strain-specific timing of mating activity in the night (Pashley et al., 1992; Schöfl et al., 2009). While the corn-strain is the “early” strain, the rice-strain is the “late” strain, calling, copulating and ovipositing approximately three hours later than the corn-strain (Schöfl et al., 2009). Behavioral isolation due to allochronic (temporal) isolation can be a strong prezygotic mating barrier (Coyne and Orr, 2004; Devries et al., 2008), because this may cause both strains to rarely encounter each other. However, the reproductively active times of both strains do overlap to some degree and allochronic isolation seems to be asymmetric and less pronounced than previously thought (Schöfl et al., 2009). To determine the role of sexual communication in the divergence of corn- and rice-strain populations, we started to investigate the strain-specific sexual communication system of both *S. frugiperda* strains.

3.3. Strain-specific pheromone variation in *Spodoptera frugiperda*

The sex pheromone of *S. frugiperda* females has first been investigated by Tumlinson et al. (1986), who showed that females emit a multi-component blend consisting of the major pheromone component (Z)-9-tetradecenyl acetate (Z9-14:OAc), the critical secondary component (Z)-7-dodecenyl acetate (Z7-12:OAc) and several minor compounds like (Z)-11-hexadecenyl acetate (Z11-16:OAc), with unknown behavioral function. Although the sex pheromone composition of *S. frugiperda* females is known since 1986, and both strains have first been described in 1985 (Pashley et al., 1985), it took more than 20 years until the existence of a strain-specific corn- and rice-strain pheromone was first identified (Groot et al., 2008; Lima and McNeil, 2009). Interestingly, both studies found different strain-specific female pheromone compositions. First, I will first describe the variation that we found (Groot et al., 2008; Marr, 2009), and then the variation that Lima and McNeil (2009) found.

We examined the pheromone composition of laboratory populations from Florida and found that corn-strain females produced significantly higher relative amounts of Z11-16:OAc than rice-strain females, while rice-strain females exhibited higher relative amounts of Z7-12:OAc and (Z)-9-dodecenyl acetate (Z9-12:OAc) than corn-strain females (Groot et al., 2008; Marr, 2009). The pheromone analysis of hybrid females revealed that the major pheromone component Z9-14:OAc, as well as Z11-16:OAc, were maternally inherited, whereas Z9-12:OAc showed a corn-strain dominant inheritance (Groot et al., 2008; Marr, 2009). Interestingly, the relative amount of the important secondary pheromone component Z7-12:OAc was significantly lower in hybrid CR (corn♀ x rice♂) and RC (rice♀ x corn♂) females than in pure strain females (Groot et al., 2008; Marr, 2009). Because Z7-12:OAc has been shown to be a critical minor component necessary for the attraction of males in the field (Tumlinson et al., 1986), the suppression of this component in

hybrid females suggests that hybrid females may not be as attractive for males as pure-strain females. Based on phenotypic correlations between all pheromone components of the female blend, we constructed a pheromone biosynthesis pathway of *S. frugiperda* and suggested candidate genes that might be responsible for the strain-specific female pheromone composition (Groot et al., 2008; Marr, 2009). Differences in the expression level or substrate specificity of a $\Delta 11$ -desaturase, a $\Delta 9$ -desaturase or a possible $\Delta 7$ -desaturase might cause the strain-specific differences in the relative amount of Z7-12:OAc, Z9-12:OAc and Z11-16:OAc between corn- and rice-strain females (Groot et al., 2008; Marr, 2009). In conclusion, we found strain-specific pheromone differences between corn- and rice-strain females and differential inheritance of single pheromone components, which suggests the involvement of multiple genomic regions leading to differential pheromone blends (Groot et al., 2008; Marr, 2009).

Lima and McNeil (2009) examined laboratory populations that originated from Louisiana, and also found strain-specific pheromone differences between corn- and rice-strain populations. In contrast to our results (Groot et al., 2008; Marr, 2009), corn-strain females from Louisiana exhibited higher relative amounts of Z9-14:OAc than rice-strain females, whereas rice-strain females produced higher relative amounts of Z11-16:OAc than corn-strain females (Lima and McNeil, 2009). The differences between both studies suggest that geographic variation influences the strain-specific variation in the female pheromone composition of *S. frugiperda*. However, strain-specific differences in the relative amount of Z7-12:OAc were similar between females from Florida and Louisiana, namely that corn-strain females have lower amounts of Z7-12:OAc than rice-strain females (Groot et al., 2008; Lima and McNeil, 2009; Marr, 2009). Thus, although geographic variation might affect the female pheromone, similarities between both studies suggest that stabilizing selection acts on the critical sex pheromone

component Z7-12:OAc. Furthermore, Lima and McNeil (2009) showed that Z9-14:OAc was maternally inherited, which was similar to our results (Groot et al., 2008; Marr, 2009). Based on our results (Groot et al., 2008; Marr, 2009) and the research by Lima and McNeil (2009), the aim of my research was to disentangle strain-specific from geographic variation and to determine the genetic basis of the strain-specific female sex pheromone, all findings of which are described in this thesis.

4. The biology of *Spodoptera frugiperda*

4.1. Life cycle

The fall armyworm *Spodoptera frugiperda* (Lepidoptera: Noctuidae) is a noctuid moth that occurs throughout North- and South-America (Luginbill, 1928; Sparks, 1979). Depending on the climate, *S. frugiperda* can persist the whole year or overwinter as pupae, and one life cycle may take 4 to 13 weeks (Sparks, 1979; Andrews, 1988). During the day, adult moths usually hide within the vegetation (MU, personal observation; Fig. 1A, B). During the scotophase, receptive females sit near the top of a host plant and start calling by extruding their pheromone gland (Sparks, 1979).

One female usually attracts several males which fly towards the pheromone source and try to land near the calling female (Sparks, 1979). After landing, receptive males show a typical male calling behavior in which they extrude their hair pencils, perform wing fanning and bend their abdomen to approach a female (MU, personal observations). Females can reject unsuitable males (Sparks, 1979), which is probably caused by close range pheromonal communication between both sexes (Schöfl et al., 2011).

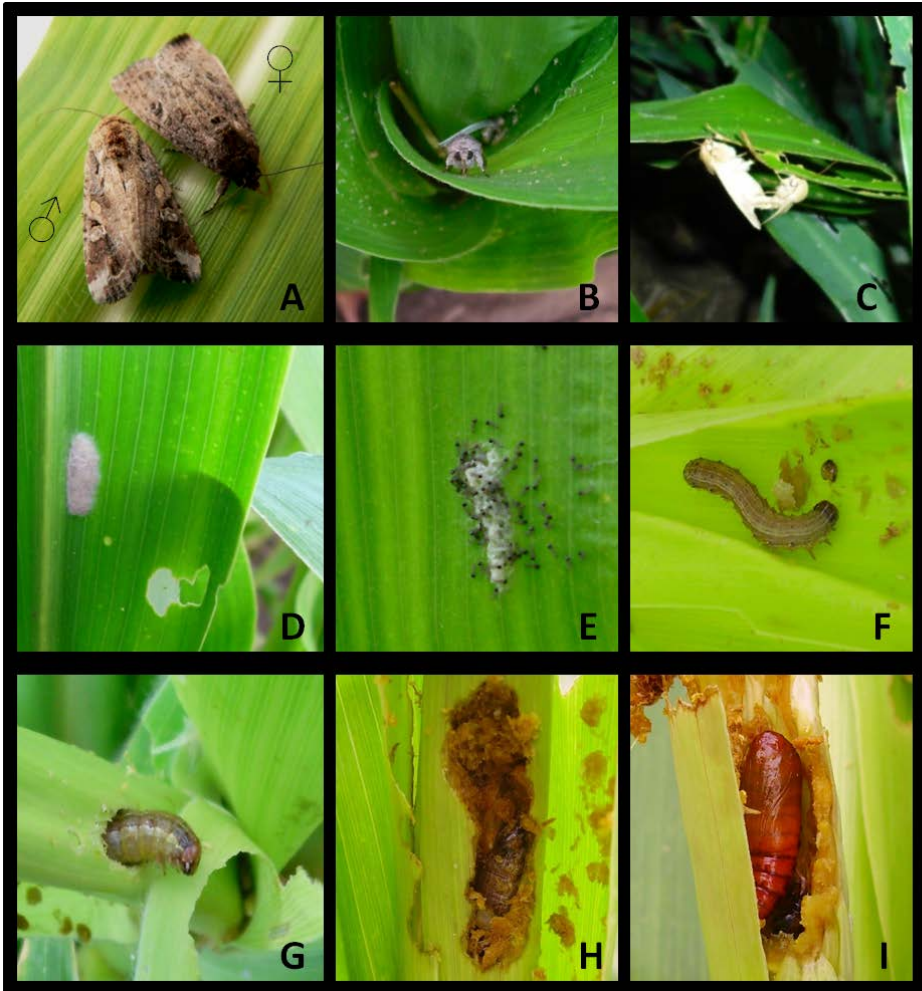


Figure 1. Development of *Spodoptera frugiperda* in the field. (A) Adult moths. (B). Female moth hiding in the whorl of a corn plant during the day. (C) Mating of adult moths in the night. (D) Egg clutch on a corn plant. (E) Hatching larvae. (F) Larva feeding on a corn plant. (G) Last instar larva. (H) Larva goes into pupation stage. (I). Pupae.

When a female accepts a male, both partners will mate with each other (Fig. 1C), and the duration of copulation can take several hours (Schöfl et al., 2009). During copulation, the male transfers a spermatophore, i.e. a capsule containing sperm, into the female (Lamunyon, 2000). Although *S. frugiperda* females mate only once a night (Sparks, 1979), females can mate with multiple partners in different nights and can contain more than one spermatophore (Meagher and Nagoshi, 2010).

After a successful copulation, females search for a suitable oviposition place (Fig. 1D), which includes host plants, non-host foliage as well as artificial substrates like window panes or carts (Sparks, 1979). The use of non-hosts as oviposition site for *S. frugiperda* females may facilitate neonate dispersal or avoidance of predators and parasitoids (Meagher et al., 2011). Females usually lay their eggs in clutches (Fig. 1D), which are covered with scales and contain few up to hundreds of eggs (Sparks, 1979; Meagher et al., 2011). First instars hatch from the egg clutches around two to four days after oviposition (Fig. 1E), and feed on their host plant until the sixth instar (Sparks, 1979; Fig. 1F, G).

Spodoptera frugiperda is known as a generalist species, which can feed on more than 80 plant species from 23 different plant families (Pashley, 1988a). Under experimental conditions, larvae feed for approximately three weeks until they reach their last instar (Fig. 1G, H), and start pupating (Groot et al., 2010b; Nagoshi, 2011). In nature, sixth instars dig themselves into the ground and pupate between one and three meters deep into the soil, where, depending on the temperate, they eclose after one to five weeks (Sparks, 1979). In some cases, larvae pupate within the stem of their host plants (Fig. 1I). After emergence from the pupal case, adults leave the soil and climb onto plants to expand their wings (Sparks, 1979). Newly emerged adults do not mate within their first night (Sparks, 1979), and are usually

reproductively active when they are two to five days old (MU, personal observation).

4.2. *Identification of two host strains*

In 1986, Pashley reported the presence of two strains in *S. frugiperda*, the corn- and the rice-strain, which exhibited genetic differences and a strain-specific host plant choice. Based on the first studies of both strains, Pashley (1986) suggested that both strains may be sibling species, which are reproductively isolated from each other. Since the discovery of both strains, numerous studies investigated the differences between the two morphologically identical strains, regarding genetic differentiation (Pashley, 1989; Lewter et al., 2006; Nagoshi and Meagher, 2008; Nagoshi, 2010), host plant choice (Busato et al., 2004; Nagoshi et al., 2007; Machado et al., 2008; Juárez et al., 2012), development (Pashley, 1988b; Whitford et al., 1988; Meagher et al., 2004; Groot et al., 2010b), reproduction (Pashley et al., 1992; Schöfl et al., 2009; Meagher et al., 2011; Schöfl et al., 2011), and sex pheromone differences (Groot et al., 2008; Lima and McNeil, 2009; Marr, 2009). Due to the fact that both strains differ in so many traits and occur in sympatry throughout North- and South America, *S. frugiperda* has become a model species to study the evolution of reproductive isolation between strains of the same species (Pashley, 1988a; Pashley et al., 1992; Prowell et al., 2004; Groot et al., 2008; Machado et al., 2008; Nagoshi and Meagher, 2008; Marr, 2009; Schöfl et al., 2009; Groot et al., 2010b; Schöfl et al., 2011; Juárez et al., 2012).

In addition to different possible prezygotic mating barriers, i.e. strain-specific host plant choice (Pashley, 1986; Nagoshi et al., 2006a; Nagoshi et al., 2007), timing of reproduction (Pashley et al., 1992; Schöfl et al., 2009), and sex pheromone composition (Groot et al., 2008; Lima and McNeil, 2009; Marr, 2009), both strains also exhibit postzygotic isolation (Pashley and Martin, 1987; Whitford et al., 1988;

Groot et al., 2010b). Laboratory backcross matings of *S. frugiperda* populations from Puerto Rico and Louisiana showed that hybrid RC (rice-strain♀ x corn-strain♂) females produced no fertile offspring when crossed to a pure strain corn- or rice-strain male (Pashley and Martin, 1987). Furthermore, a reduced number of fertile offspring was found when RC hybrid females were crossed to RC hybrid males, as well as in crosses between pure strain females and hybrid RC males (Pashley and Martin, 1987). Backcross experiments with laboratory populations from Louisiana (rice-strain) and Mississippi (corn-strain), conducted by Whitford et al. (1988), also showed that matings between hybrid RC (rice-strain♀ x corn-strain♂) females and males were less fertile than pure strain matings or crosses between CR (corn-strain♀ x rice-strain♂) hybrid individuals. Similarly, Groot et al. (2010b) reported a reduced fertility when laboratory RC (rice-strain♀ x corn-strain♂) hybrid females, originated from Florida, were crossed to both parental strains and hybrid males (CR and RC). On the contrary, crosses between CR (corn-strain♀ x rice-strain♂) hybrid females and pure strain (C, R) as well as CR hybrid males produced similar percentages of fertile offspring as pure strain matings (Groot et al., 2010b).

Interestingly, the vast majority of hybrids in the field are RC (rice-strain♀ x corn-strain♂) hybrid individuals (Nagoshi and Meagher, 2003; Prowell et al., 2004; Nagoshi et al., 2006b), which exhibit a reduced fertility when females are crossed to pure strains or other hybrids (Pashley and Martin, 1987; Whitford et al., 1988; Groot et al., 2010b). The mating incompatibilities of RC hybrid females represent a unidirectional postzygotic isolation barrier that contributes, together with the different prezygotic isolation mechanisms, to reproductive isolation between both strains (Groot et al., 2010b). Thus, *S. frugiperda* is an ideal model organism to study the evolution of pre- as well as post-zygotic mating barriers within a species.

4.3. *Spodoptera frugiperda* as agricultural pest species

Besides being an ideal species to study incipient speciation, *S. frugiperda* is a serious agricultural pest species that causes great damage to a large variety of plants due to its generalistic feeding behavior (Pashley, 1988a). Fall armyworm infestations of field crops in the southeastern United States can cause losses of 93 up to 297 million dollars per year which makes *S. frugiperda* one of the most damaging agricultural pests occurring in the United States (Sparks, 1986). The ability of *S. frugiperda* to overwinter in subtropical and tropical areas like Florida or the Caribbean leads to a continuous damage of larvae feeding on crop plants throughout the year (Luginbill, 1928; Sparks, 1986). Furthermore, adults can migrate large distances and annual population movements from overwintering (sub)tropical areas to temperate zones cause a spread of this pest into many regions (Luginbill, 1928; Sparks, 1979; Nagoshi and Meagher, 2008; Nagoshi et al., 2008; Nagoshi et al., 2009).

Different pest management strategies like insecticide applications (Andrews, 1988; Hruska and Gladstone, 1988; Pitre, 1988; Vergara and Pitre, 2001), trapping with sex pheromone (Mitchell et al., 1985; Andrade et al., 2000; Malo et al., 2001), biological control via predators or parasitoids (Molina-Ochoa et al., 2003; Hoballah et al., 2004; Bueno et al., 2008), resistant host plants (Sparks, 1986; Wiseman and Isenhour, 1988a, b), and the use of plant polycultures and intercrops (Andrews, 1988), have been considered to reduce the agricultural losses caused by *S. frugiperda*. Due to the fact that this pest species consists of two behaviorally and genetically different strains (Pashley, 1986), pest management treatments may have different effects on both strains. Differences between corn- and rice-strain individuals therefore also help to improve pest management strategies. The use of strain-specific pheromone lures could for example facilitate the early detection of

corn- or rice-strain adults in crops, which could then be treated with strain-specific insecticides, pathogens or parasitoids.

5. Main questions of this thesis

Similar to the case of *Ostrinia nubilalis* (Lassance, 2010), strain-specific differences in the sexual communication system of *S. frugiperda* could act as prezygotic mating barrier between both strains and cause assortative mating. The presence of strain-specific differences in the female pheromone composition of *S. frugiperda* (Groot et al., 2008; Lima and McNeil, 2009; Marr, 2009) indicates that assortative mating could occur if males of both strains are strain-specifically attracted to females of their own strain. The main aim of this thesis was to evaluate whether strain-specific sexual communication is a prezygotic mating barrier between corn- and rice-strain populations and contributes to reproductive isolation between both strains. Therefore, we investigated the differences in female pheromone composition and tested with different assays if males of both strains are distinctively attracted to strain-specific females. Furthermore, we studied the variability in the male response to pheromones in different geographic regions and examined the genetic basis of strain-specific corn- and rice-strain pheromones to understand the evolution of both *S. frugiperda* strains.

6. Thesis outline

Chapter 2 describes the pheromonal divergence between the two strains of *S. frugiperda* in Florida (Unbehend et al., 2013b). The main aim of this study was to assess whether strain-specific pheromones act as prezygotic mating barrier and cause assortative mating between both *S. frugiperda* strains in Florida. To assess strain-specific female pheromone differences, we performed pheromone gland extractions of corn- and rice-strain females of laboratory and field populations

originated from Florida. The male response of both strains towards strain-specific pheromone blends was tested in wind tunnel assays, using laboratory females, and in male trapping experiments in Florida, using self-made strain-specific synthetic pheromone lures. Dose-response experiments of different pheromone compounds were conducted in the field to evaluate the importance of single compounds for strain-specific male attraction. Furthermore, all trapping experiments were conducted in a corn-strain-specific habitat (corn field) as well as in a rice-strain-specific habitat (grass field), to determine the influence of different environments on the male response.

Similar to the results of our previous study on laboratory populations (Groot et al. 2008; Marr 2009), we found strain-specific sex pheromone differences between corn- and rice-strain females from Florida field populations in this study. The results of wind tunnel assays and field trapping experiments showed that males were not strain-specifically attracted to females of their own strain. This suggests that strain-specific female sex pheromone differences are not strong enough to cause assortative mating in Florida. Nevertheless, we found strain-specific differences in the male attraction to the critical pheromone component Z7-12:OAc, as well as differential male responses to strain-specific sex pheromone blends in different habitats. Furthermore, dose-response experiments suggested that the minor compounds Z11-16:OAc and Z9-12:OAc are not required for male attraction in Florida.

In Chapter 3, we investigated the variation in sexual attraction of *S. frugiperda* males in different geographic regions (Unbehend et al., 2013c), with the aim to disentangle strain-specific variation from geographic variation. Different male trapping experiments with self-made synthetic pheromone lures were carried out in Canada, North Carolina, Florida, Puerto Rico, Peru and Argentina, to evaluate variability in the response of corn- and rice-strain males. Pheromone traps were

baited with two different synthetic 4-component blends as well as with lures containing different amounts of important pheromone components like Z7-12:OAc or E7-12:OAc. The strain-identity of all trapped males was determined via molecular analysis of the cytochrome oxidase I gene, which exhibits strain-specific sequence differences.

We found that corn-strain males exhibited geographic variation in their response to our two synthetic 4-component blends and to different doses of Z7-12:OAc. In contrast, rice-strain males showed almost no geographic variation in response to different sex pheromone blends. These results suggest that corn-strain males are more restricted in their response to sex pheromone than rice-strain males. *Spodoptera frugiperda* males also showed differential responses towards the minor compound E7-12:OAc, which attracted males in North Carolina, but was unattractive for males in Peru. Furthermore, attraction of males to strain-specific pheromone blends varied between habitats within the same region, which suggests an influence of habitat-specific volatiles on the male attraction to sex pheromone blends.

In Chapter 4, we studied the genetic basis of strain-specific female pheromone differences in *S. frugiperda* (Unbehend et al., 2013a). Female-informative backcrosses were generated by hybridizing both strains and backcrossing the generated hybrid females with corn- and rice-strain males. One backcross family was used for an AFLP marker-based quantitative trait locus (QTL) analysis to determine which genomic regions are involved in the strain-specific pheromone production. We generated a genetic map for *S. frugiperda* and mapped different candidate genes that may cause differential pheromone production of both strains. To investigate the inheritance of strain-specific pheromones, pheromone gland extractions of pure strain, hybrid and backcross females were performed.

In this study, we found that multiple genomic regions are involved in the production of strain-specific female sex pheromone blends. We identified 10 QTL on 9 different chromosomes that explain the strain-specific differences in the relative amounts of Z9-14:OAc, Z11-16:OAc, Z7-12:OAc and Z9-12:OAc. A delta-11-desaturase (*SfLPAQ*) mapped to *Sf* chromosome 2, which explained a significant portion of the variance of Z9-14:OAc and Z11-16:OAc and showed the opposite-to-expected phenotypic pattern for both compounds. Furthermore, the circadian clock protein *vrille* (*SfVRI*) mapped to *Sf* chromosome 28, responsible for the critical secondary sex pheromone component Z7-12:OAc. Interestingly, *vrille* also appears to be responsible for the strain-specific differences in timing of reproduction in the scotophase (Hänniger et al., 2013). Thus, one chromosome (*SfC28*) is associated with the strain-specific variation in two prezygotic mating barriers in *S. frugiperda*, i.e. differential timing of reproduction and female sex pheromone composition. Analysis of the inheritance of strain-specific pheromone differences showed that Z9-14:OAc was overexpressed in CR hybrid females (C♀ x R♂) and paternally inherited in RC (R♀ x C♂) hybrid females, while Z11-16:OAc was suppressed and Z9-12:OAc overexpressed in both hybrids. The critical minor component Z7-12:OAc was rice-strain dominant inherited in CR and RC hybrid females.

Chapter 5 shows an overview of the roles and interactions of different reproductive isolation mechanisms in both *S. frugiperda* strains (Groot et al., 2010b). This review examines how habitat isolation and behavioral isolation through sexual communication and differential timing of reproduction affect reproductive isolation between corn- and rice-strain populations. Possible interactions between these prezygotic isolation barriers as well as their genetic bases are discussed. Furthermore, data on postzygotic incompatibilities as well as the permeability of the host strain genomes are analyzed.

Chapter 1

The main conclusion of this review is that the separate pre- and postzygotic mating barriers seem unlikely to cause reproductive isolation between both strains, but in combination they may act additively or synergistically and thus prevent both strains from merging into one population. Furthermore, strain-specific differences in the mitochondrial mtDNA suggest that both strains separated approximately 600 000 years ago.

Chapter 6 deals with the evolution of reproductive isolation of *S. frugiperda* (Groot et al., 2013). This review comprises data on habitat isolation of both strains due to differential host plant choice, as well as behavioral isolation due to strain-specific timing of reproductive activity at night. Furthermore, the level and direction of hybridization between both strains and an evolutionary scenario on possible reproductive isolation in the two strains is discussed. In this chapter, we also summarize recent data on behavioral isolation of both strains due to variation in sexual communication. Besides inter-strain-specific pheromone differences, we found female pheromone variation within strains, which are described in relation to geographic variation in the female pheromone composition. We also present data on variation in the male response to strain-specific female pheromone blends, as well as on the male attraction to different pheromone compounds in the field.

The main conclusion of this review is that both strains are rather “timing strains” than “host strains” or “pheromonal strains”, and sterility of RC hybrid females (rice-strain♀ x corn-strain♂) is a strong postzygotic mating barrier which contributes to the divergence of the two *S. frugiperda* strains. Furthermore, we suggest a possible evolutionary scenario in which the rice-strain is the ancestral strain and the corn-strain the derived one, because the corn-strain is genetically more homogeneous than the rice-strain. This hypothesis correlates with findings that the corn-strain is more restricted in habitat occurrence and in pheromone response than rice-strain individuals.

In Chapter 7, I summarize and discuss all main findings of this thesis. First, the results are discussed with regard to the evolution of both strains and the contribution of sexual communication differences to the divergence of the corn- and the rice-strain. Secondly, the results are discussed in the light of pest management, because *S. frugiperda* is an important agricultural pest species. Based on the results of the male trapping experiments in the field, I recommended a pheromone blend that can be used to monitor both strains independent of geographic and strain-specific variation, and discussed whether it is possible to reduce *S. frugiperda* populations in the field via the use of mating disruption. A summary of the main findings of this thesis can be found on pages 166-167.

7. References

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