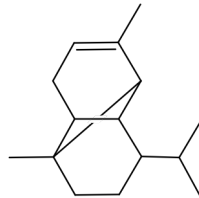


# ODOURS, POTATO AND INSECTS

## HOST FINDING AND REPRODUCTION BEHAVIOR

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## SUMMARY

Plant odours can give important information about plant species. These chemical messengers volatilized from potato plants, mediate host-finding behaviour in insects living on potato. During the development of a potato crop, lasting approximately three months, the pest insects described in this introductory paper have to find the potato plant. When attracted, the insects choose a part of the potato; leaves, tubers, or flowers, where they feed, hide, mate or oviposit. Host plant selection or host preference is not only governed by nutritional quality but also by environmental factors and reproduction success. The synergistic effect of odours from conspecifics and plants can enhance the attractiveness and hence the survival of the species. Pheromone and kairomone response from two Coleopterans, tree Lepidoptera and two Homopteran insects, that are severe pests on potato, are described here as well as their behaviour towards potato crop. Knowledge about insect response to semiochemicals gives indications of how to develop future crop protection management. The enhancement of sex attraction induced by host odours suggests that more effective traps can be devised for the management of insect pests.

This introductory paper is a part of my PhD project “Safe control of Guatemalan potato moth in household storage”. The project is conducted at the Swedish University of Agricultural Sciences, department of Plant Protection Biology, division of Chemical Ecology. Supervisors for my thesis are Göran Birgersson (main), Magali Proffit, Marie Bengtsson, and Ylva Hillbur.

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## 1. Introduction

Potato *Solanum tuberosum* L is grown around the world with an annual production of 300 million tons, which makes it the fourth most important agricultural product (FAO 2005). In five centuries, this diverse and adaptable tuber has spread from its original South America to all elevation zones in temperate regions of all the continents (Kiple 2000). Agricultural activity replaces natural bio diversity into a mono crop system and causes more damage on agro-ecosystems than in natural conditions. Crop losses due to insects have reached 13% worldwide (Pimentel 1997). Losses due to animal pests have increased during the last years for several crops, including potato. In 1965, only 6% of potato production was lost due to animal pests compared to 16% in the years 1991-93 (Oerke and Dehne 1997). Seven potato pest insects are presented herein, as examples of the relation that can be found between potato, insects and odours.

In this introductory paper, volatile compounds or odours, either from the potato or from potato pest insects, are discussed. Some of the compounds act as semiochemicals, transferring information between individuals. The focus is on the compounds that are volatile and perceived by the olfactory system of the insects. The sense of smell, the chemical message from plants and insects, received by the insect's olfactory system, mediates information about the insect's environment. This information can lead to a behaviour response that mostly is determined to improve the current situation. It can provide the insect with information so it can find its host plant or a mating locality. The sexual behaviour of phytophagous insects is often integrated with their host plants. Host plant volatiles may be important cues during reproduction behaviour for the regulation of pheromone production, the insect's physiological development and sexual attractiveness. For many species of insects, it is important that the food site and the oviposition site are coincidental. (Landolt 1989, Landolt et al. 1994, Hartlieb and Rembold 1996, Rojas 1999).

I will in this introductory paper discuss the relation between host-finding and reproductive behaviour and volatile chemical compounds among the selected potato pest insects. I will compile what is documented about volatile compounds from potato, the insect recognition of them, and observe if an integrated insect strategy exists to locate hosts and mates. Do host plants volatily regulate or mediate sexual communication? Do potato odours have an equal importance for these insects that feed and reproduce on potato? Female adult insects search for potatoes, sometimes without feeding on them. Is the reason to oviposit or is it to enhance the probability of mating with a conspecific male? Are insects first attracted to the host plant or their conspecifics?

In the first chapter, volatile compounds from potato are presented. It is followed by a chapter which describes insect olfaction, host-plant orientation and gives a presentation of the most severe potato pest insects. Thereafter some examples are given of what is known about the selected potato pest insects and their odour perception of potato volatiles and of their pheromones. Finally, a brief summary is presented of how insect odour perception is used, and can be used, in pest management.

## 2. Volatile compounds

### 2.1 Volatile plant compound

Plants produce a wide spectrum of compounds and their chemical composition varies between species but also within individual plants of the same species. Plants release substances such as terpenoids, aromatics and fatty acid derivatives (Knudsen et al. 2006, Dudareva et al. 2006). Compounds with a molecular weight less than 200 g/mol can get volatilized under natural conditions from all parts of the plants, including leaves, fruits, flowers and tubers, either through stomata, leaf cuticle or glandular tissues. Several hundred volatile substances can be found in the air around a plant, although only one or a small number of compounds dominate the blend. The major volatiles are aldehydes, esters, or terpenoids (Schoonhoven et al. 2006). The amount of emitted compounds varies from a few pictograms to several micrograms per hour. The largest amounts are released from flowers: from beetle and moth pollinated species (Knudsen et al 2006).

The chemical differences between plants of the same species depends on environmental factors; nutrients in soil, insect attack and light conditions. No two plant individuals have exactly the same profile (Bernays and Chapman 1994, Schoonhoven et al. 2006). The level of compounds also fluctuates with maturity and some plants have a diurnal variation of the compounds (Okolie and Obasi 1993, De Moraes et al. 2001).

### 2.2 Volatile potato compounds

The development of a potato plant can be divided into several different phenological stages; sprout development, vegetative growth, development of tubers, growth of reproduction parts and senescence (Figure 1) (Valbuena 2000, Struik 2007).

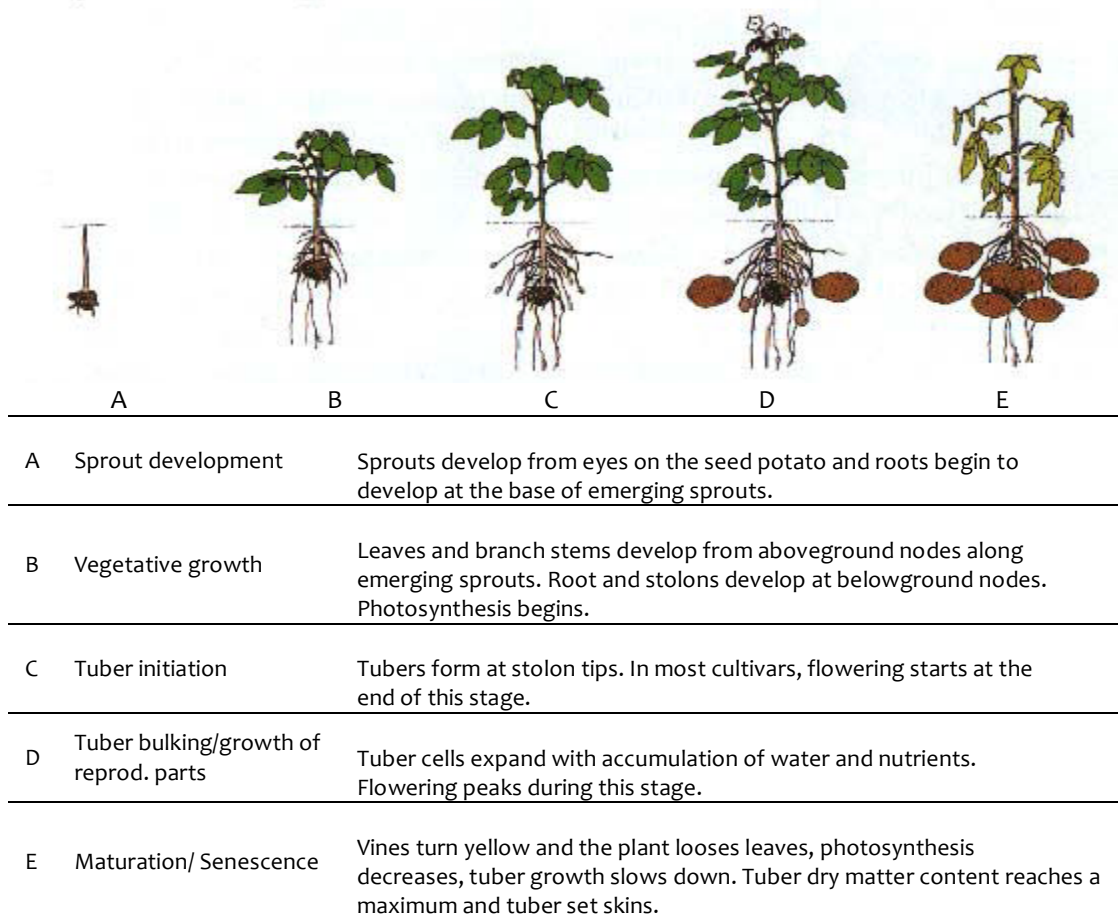


Figure 1: Potato phenological stages

Compounds released from potatoes have been identified in several studies by somewhat different methods. The volatile emission from intact potato foliage is a blend of terpenoids, especially sesquiterpene hydrocarbons and fatty acid derivatives such as aldehydes and alcohols (Avé et al. 1987, Bolter et al. 1997, Agelopoulos et al. 2000). In potato tubers there are no volatile sesquiterpenes found while aldehydes, alcohols and alkanes are the most common compounds (Table 1) (Agelopoulos et al. 2000, Bolter et al. 1997, Fischer and Müller 1991, Szafranek et al. 2005, Visser et al. 1979, Weissbecker et al. 2000,).

Among the sesquiterpene hydrocarbons,  $\beta$ -caryophyllene, (*E*)- $\beta$ -farnesene, (*Z,Z*)- $\alpha$ -farnesene, germacrene D, and  $\beta$ -bisabolene are the major volatile compounds from foliage of undamaged plants. In addition, the monoterpene alcohol linalool, and the fatty acid derivative aldehydes nonanal and decanal are released in high amounts. Ratios between the sesquiterpens are quite stable, with approximately twice as much  $\beta$ -caryophyllene compared to (*E*)- $\beta$ -farnesene, germacrene D, and  $\beta$ -bisabolene, and half as much (*Z,Z*)- $\alpha$ -farnesene compared to these three compounds (Agelopoulos et al. 2000).

In general, there is a major difference in the volatiles released from healthy plants compared to stressed or attacked ones. In addition, plants react in different ways when attacked by insects and fungi. Furthermore, some plants respond differently when damaged by different insect species (Schutz et al. 1999). Chemical analyses based on headspace from infested potato plants indicate that infestation causes the emission of a blend of chemicals that is qualitatively quite similar to that emitted by undamaged plants. The main difference is that the amount released from herbivore infested plants is larger than that from mechanically damaged or undamaged plants.  $\beta$ -caryophyllene and  $\beta$ -selinene were the most abundant compounds after infestation with Colorado potato beetle, *Leptinotarsa decemlineata*, larvae and the amount of chemicals emitted increased 7 to 10-fold. Among the terpenes emitted from infested plants, the two terpenes 4,8-dimethyl-1,3(*E*),7-nonatriene and 4,8,12-trimethyl-1,3(*E*),7(*E*),11-tridecatetraene were most abundant (Bolter et al. 1997). (*Z*)-3-Hexenal, (*E*)-2-hexenal and (*Z*)-3-hexen-1-ol are released in the highest amounts during the first five minutes after damage but after ten minutes these compounds drop to very low levels. This is also the case for many sesquiterpenoids released in high amounts directly after damage (Agelopoulos et al. 1999b). The volatile emission follows a diurnal rhythm and Agelopoulos et al. (2000) found the highest emission of sesquiterpene hydrocarbons from potato foliage during the afternoon.

Table 1: Volatiles identified from potato when foliage is A) intact B) infested by Colorado potato beetle C) mechanically damaged D) from undamaged tubers (•=presence of compound)

Chemicals	A	B	C	D	Chemicals	A	B	C	D
<b>Alipathics</b>					<b>Irregular terpenes</b>				
Acetic acid				•	3-Methylbutanol			•	
2-Methylpropanal				•	Methylcyclohexane				•
Acetone				•	4,8-Dimethyl-1,3,7-nonatriene	•	•		
1-Butanol				•	4,8,12-Trimethyl-1,3(E),7(E),11-tridecatetraene			•	
2-Butenal				•	<b>Monoterpenes</b>				
1-Pentanol				•	Hydrocarbons				
(Z)-2-Penten-1-ol			•		(R)-(+)-Limonene	•	•		
3-Pentanone		•			(S)-(-)-Limonene	•	•		
1-Hexanol				•	Myrcene	•	•		
(E)-2-Hexenal	•	•			Tricylene			•	
(E)-3-Hexen-1-ol			•		Alcohols and aldehydes				
(Z)-3-Hexen-1-ol	•	•			1,8-Cinole			•	
(Z)-3-Hexenol	•	•			(±)-Linalool	•	•		
(Z)-3-Hexenyl acetate		•			α-Pinene	•	•		
2-Ethyl-hexan-1-ol				•	Sabinene			•	
(E)-2-Hexenal			•	•	<b>Sesquiterpenes</b>				
(Z)-3-Hexenal			•		Hydrocarbons				
(Z)-3-Hexenyl butyrate		•			(E)-α-Bergamotene	•	•	•	
Hexanal				•	Bicyclogermacrene	•	•	•	
2-Methylhexane				•	β-Bisabolene	•		•	
Heptanal		•		•	β-Elementene	•			
(E,Z)-2,4-Heptadienal				•	(E)-β-Farnesene	•	•	•	
(E,E)-2,4-Heptadienal				•	(Z)-β-Farnesene	•			
Heptane				•	(Z,Z)-α-Farnesene	•			
1-Octen-3-ol				•	Cadinene	•	•		
Octanal		•		•	β-Caryophyllene	•	•	•	
2-Octenal				•	α-Copaene			•	
Nonanal	•	•			α-Cubebene			•	
(E)-2-Nonenal				•	Curcumene			•	
(E,Z)-2,4-Nonadienal				•	Germacrene-D	•	•	•	
(E,E)-2,4-Nonadienal				•	α-Humulene			•	•
Decanal	•	•		•	(+)-Longifolene			•	
(E,Z)-2,4-Decadienal				•	γ-Muuroloene			•	
(E,E)-2,4-Decadienal				•	α-Selinene	•	•		
Dodecane				•	β-Selinene	•	•		
<b>Benzenoids and Phenyl propanoids</b>					γ-Selinene (tentativ)			•	
Toluene				•	β-Sesquiphellandrene	•	•		
Xylene				•	Sesquisabinene			•	•
2-Phenoxyethanol				•	α-Zingiberene			•	•
Methyl salicylate		•			Alcohols and aldehydes				
<b>Miscellaneous cyclic compounds</b>					Ledol	•	•	•	
Furfural					Germacrene-D-4-ol	•			
2-Furaldehyde					Caryophyllene oxide			•	•
2-Pentylfuran				•					
Cyclohexane									
Indole			•						



## 2.3 Semiochemicals

Chemicals that act as signals by transferring information between individuals are called semiochemicals. Semiochemicals provide signals for recognition and the location of food plants, oviposition sites and mates (Metcalf and Metcalf 1992, Shonhooven et al 2006, Visser 1986). These compounds are nominated according to their communication range (Figure 2). Allelochemicals enable communication between individuals of different species while pheromones are an odour secreted by an individual inducing a certain reaction/behaviour in another individual of the same species (Nordlund and Lewis 1976). Pheromone compounds are often emitted from the insect as blends of 2 to 5 compounds; mainly 5-20 chained carbons coupled with different functional groups such as alcohols, aldehydes and esters.

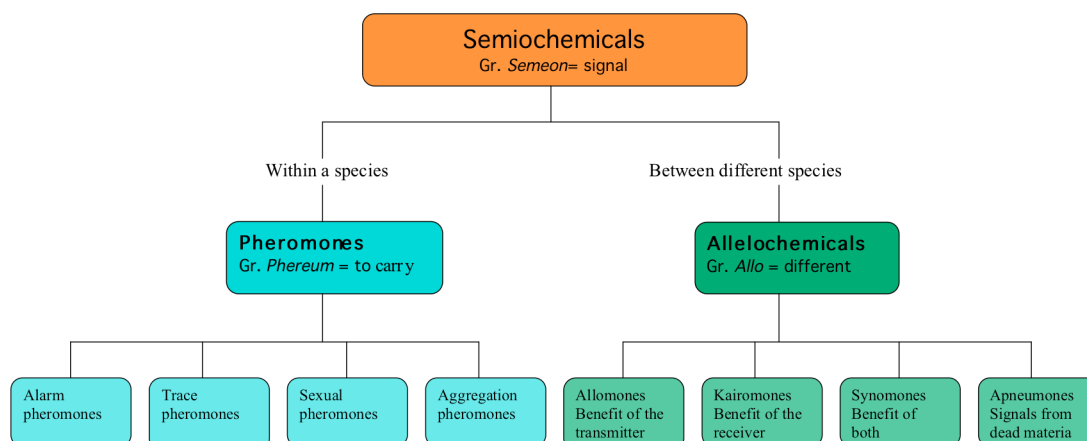


Figure 2: Semiochemical nomenclature

## 3. Insect olfaction

Insects receive numerous sensory inputs including semiochemical cues, such as pheromones and allelochemicals; kairomones, allomonones or synomonones. If the insect perceives the compound through its olfactory system, it can then be processed in the central nervous system. If a correct combination of sensory input is received from a plant, this plant is recognised as a host, and attraction or arrestment occurs (Bruce et al. 2005). Volatiles can provide stimuli that motivate physical response and hence stimulate or deter oviposition and foraging behaviour. Some plant volatile compounds act both as attractants and as repellents in different insects. Volatiles can also act as a defence against herbivores and to attract natural enemies (Bernays and Chapman 1994, Dudareva et al. 2006).

Phytophagous species have evolved olfactory systems with a high sensitivity and selectivity to chemical compounds, produced both by plants and by insects. The olfactory system functions as a filter where olfactory receptor neurons are sensitive to only a limited range of volatile compounds. Most olfactory receptor neurons are found to be tuned to a specific semiochemical (Bruce et al. 2005, Dejong and Visser 1988) and demonstrate a fine-tuning of single neurones to biologically relevant odours, for instance, to host-plant specific volatiles. The fact that olfactory receptor neurons are sensitive to a limited range of relevant volatile chemicals, enable the insects to filter out relevant information about food suitability, presence of predators and sexual status of the opposite sex (Anderson et al. 1995, Bruce et al. 2005, Mustaparta 2002). When odour molecules come in contact with olfactory receptor neurones, an action potential is produced and are then sent to the antennal lobe and thereafter integrated in higher brain centra (Hansson 1999).

In response to host plant cues, insects can release or produce sex pheromones. Some insects, for example bark beetles, use the plant volatiles and convert them into aggregation pheromones (Martin et al 2003). Certain insects sequester or acquire host plant compounds and use them as sex pheromones or sex pheromone precursors. Chemicals from host plants often synergize or enhance insect responses to sex pheromones. Synergistic effects have been found both in antennal response and as a more successful mating rate (Landolt et al. 1994, Reddy and Guerro 2004, Roelofs and Bjorstad 1984).

## 4. Plant as a host

A host plant can provide the insect with food and/or shelter and can also act as an oviposition site for the females. The plant creates a specific microclimate that may provide protection against natural enemies and pathogens. Either the entire plant or only a part of the plant is selected as a host. Host plant selection or host preference is not only governed by nutritional quality but also by environmental factors and reproduction success. Insects respond to very low levels of nutritional and non-nutritional compounds in plants, which influence their acceptance and colonisation of the plant or plant part, and thereby their growth and development. The plant that offers the best overall survival rates can be chosen over a nutritionally optimal plant. (Schoonhoven et al. 2006, Singer et al. 2004). Interestingly, there is no overall correlation between larval survival and female oviposition preference. However, individual female oviposition preference does coincide with larvae growth (Schoonhoven et al. 2006).

The relation between herbivorous insects and plants may lead to a high degree of host-plant specialization. Among Lepidoptera, Hemiptera and Coleoptera, many species are classified as monophagous or oligophagous; only feeding on one or a few closely related plants. It is also argued that host-specialization can be based on plant chemical content. Thus, a herbivore feeding on plants with a specific type of plant chemical may be considered monophagous even though host plants belong to different families (Schoonhoven et al. 2006). The cabbage white butterfly is mostly found in Brassicaceae plants but has also been found on *Tropaelum* and *Reseda*, which belong to other families. However, these plants contain glucosinolates, chemicals that often occur in cruciferous plants (Klausnitzer 1983).

Plants change in their nutritive values during the growing season, which affects the amount and mixture of volatilized plant compounds. This will also affect insects. It is known that insects synchronize their life cycle with their host and it is especially true for food specialists. Synchronization is well achieved when both insect and plant respond to the same environmental changes, such as photoperiod, temperature and humidity. Furthermore, the synchronization can be achieved when insects respond to signals indicating different phenological stages in the host plant. There are many examples of stimuli from plants that affect the development of the insect, such as diapause, morphism, maturation and mating (Schoonhoven et al. 2006).

### 4.1. Host selection

Plants differ in regard to colour, shape, texture and chemical composition. The insect perceives these plant properties via visual, olfactory or gustatory sensory organs (Schoonhoven et al. 2006). Host selection in phytophagous insects consists of a sequence of behavioural responses to an array of stimuli associated with host and non-host plants (Visser 1986). Insect orientation towards a host plant is motivated by optical stimuli, such as light, colour and shape, and/or by chemosensory stimuli created by volatile chemicals. These stimuli mediate behaviour over a long distance, while non-volatile chemicals and tactile stimuli mediate behaviour at a short distance. The dominant theory of insect recognition of host-plant volatiles is that plant discrimination is due to central processing of olfactory signals by the insect, and that it is ratio-specific odour recognition (Bruce et al. 2005).

The olfactory system encodes information from plant odour quality, quantity and spatial distribution. A physiological response in insects' olfaction system provides a chemical message leading to a behaviour response that mostly is determined to improve the current situation (Bernays and Chapman 1994, Schoonhoven et al. 2006). Nevertheless, it is still unknown what message many of the compounds give the insect, regarding the plant as a potential oviposition or feeding host plant (Schoonhoven et al. 2006).

Volatiles released from a plant can exceed hundreds of different substances but the active blends that interact with insects are, with few exceptions, dominated by a small amount of compounds (Bruce et al. 2005, Tasin et al. 2006 Zhang et al. 1999).

## 5. Insect pest on potato

Several insects prefer potato as their host. They might feed from the potato plant, oviposit on the leaves, mate on the plant or in the vicinity of the crop. Insects found on potato constitute a diverse group from many insect orders. Some insects have become serious pests on potato (FAO 2005). Due to insect host specialization, the world's agricultural narrow flora and the fact that insects and plants are introduced into new areas, some insects have become serious pests on potato. Losses due to insect damage are one of the major constraints to potato production nowadays. Infected plant material is often carried forward from one generation to the next; in planting material, in the field, after harvest and in storage, and thereby pest insects are spread among potato producing areas (CIP 1998).

The insects chosen for this introductory paper are among the most severe pest insects in potato production in some regions of the world. Seven insect species from three families; Lepidoptera, Coleopteran and Homoptera were selected (Table 2). The potato tuber moth *Phthorimaea operculella* originated from Southern and Central America and is now widely distributed all over the world, registered in more than 70 countries. It is assumed that the potato tuber moth distribution area is limited naturally to an average annual isotherm of 10°C. The pest distribution area is continuously expanding all over the zones of potato production partly due to climate warming. This is also true for the Colorado potato beetle *Leptinotarsa decemlineata*, which is now a pest in potato in northern America, Europe and south-western Asia. The pest distribution area is continuously expanding, successively spreading all over the zones of potato production due to the wide limits of adaptive variability of this species and due to climate warming (CIP 1998, López-Ávila and Espita 2000, Cevipapa 2004, Larsson 2007 pers. comm.).

The two aphid species, *Aphis frangulae* and *A. nasturtii*, are among the aphids with a worldwide importance in potato production. Damage is caused by piercing/sucking of sap extracts and by transmission of viruses (Radcliffe and Ragsdale 2002, Twengström 2003).

Table 2: Insect pests in potato, described in this introductory paper.

Order	Family	Scientific name	Name
Coleoptera	Chrysomelidae	<i>Leptinotarsa decemlineata</i>	Colorado potato beetle
	Curculionidae	<i>Premnotrypes vorax</i>	Andean potato weevil
Lepidoptera	Gelechiidae	<i>Phthorimaea operculella</i>	Potato tuber moth
		<i>Tecia solanivora</i>	Guatemalan potato moth
	Noctuidae	<i>Agrotis segetum</i>	Turnip moth
Homoptera	Aphididae	<i>Aphis nasturtii</i>	Buckthorn aphid
		<i>Aphis frangulae</i>	-

## 5.1. Colorado potato beetle

*Leptinotarsa decemlineata* Say  
Coleoptera: Chrysomelidae



[http://www.nuzban.scholaris.pl/zwierz/s/stonkzie/stz\\_01](http://www.nuzban.scholaris.pl/zwierz/s/stonkzie/stz_01)

### Host and damage

Host plants of the Colorado potato beetle are exclusively from the Solanaceae family, mainly potato but also eggplant, tomato and wild Solanaceae such as black nightshade, *Solanum nigrum* and woody nightshade, *S. dulcamara*. Adults and larvae feed on the plants and destroy partially or totally the foliage of their host and harvest is greatly reduced when a major invasion occurs (Hare 1990).

### Life cycle

The Colorado potato beetle has one or two generations in Europe and four in the warmest areas of its geographic range (Hare 1990). In the spring, when the ground temperature reaches 14 °C the surviving adults from last year emerges from hibernation in the ground (25-50cm depth) (Hiiesaar et al. 2006). The beetles start to search for a new host; often weeds or early-planted potatoes and they even search down into the soil to attack emerging new plants. First they search for food plants by walking from the field edges. If beetles do not find host plants via walking they will fly some distance in search of food. But during the first days the beetles have to regenerate their flight muscles before they are able to fly. Once host plants are found, the adults begin to feed. Thus, they have to feed before they mate. Some beetles may have mated during the previous fall or late summer but they continue to mate in spring (Boiteau et al. 2003, Ferro et al. 1999, Mhungu and Boiteu 2008)

After mating, the female immediately starts to lay clusters of eggs and one female can lay more than 2000 eggs. Larvae eclose after four to ten days and feed on foliage. They moult three times and complete development in about two weeks. Before pupation, the larva digs itself into the ground (2-20cm) to pupate and after another eight to fifteen days the cycle is completed. In Europe, the total length of the cycle is about five to six weeks but can be less than one month in warmer climates. Some of the newly emerged beetles feed for a few days and then reproduce while others enter the ground to diapause (Hare 1990, Ferro et al. 1999). The summer generation of adult beetles diapauses within the crop or flies to nearby trees or hedgerows before burrowing into the soil. Some adult beetles spend the winter in last year's potato fields, but most move into the woods and bushy borders next to these fields. The main means of natural spread of flying beetle over large areas is by wind-borne migration, particularly of the spring generation. Adults can also be carried over long distances in seawater (Senanayake et al. 2005, Hare 1990).

Both larvae and adults feed on the potato plant. Adults feed both before mating and before hibernating. Therefore, the newly emerged beetles must feed to survive the winter (Hazard 2006). Oviposition continues for several weeks, during which time females may move from older to younger plants feeding voraciously on potato leaves. Larvae feed mostly on the leaves of their host plants. Feeding is almost continuous except when larvae are molting, (Boiteau and Le Blanc 1992).

## 5.2. Andean potato weevil

*Premnotrypes vorax* Hustache  
Coleoptera: Curculionidae



<http://www.redepapa.org/bord>

### Host and damage

The main host plant for the andean potato weevil is the potato *Solanum tuberosum* but the weevil is polyphagous and feeds as well on other Solanaceae (*S. nigrum*, *S. caripense*), Brassicaceae (*Capsella bursa pastoris*, *Brassica campestris*, *Raphanus sativus*) Asteraceae (*Galinsoga parviflora*, *Siegesbeckia cordifolia*) Lamiaceae (*Salvia palefolia*) Fabaceae (*Trifolium repens*) Caryophyllaceae (*Drymaria* sp.) and Polygonaceae (*Rumex acetocella*) (Herrera 2002).

The financial loss is due to larvae excavation and feeding on tubers in fields (Herrera 2002). *Premnotrypes* spp. are among the most serious pest of potatoes at high altitudes in the Andean region (Bolivia, Peru, Ecuador, Colombia, and Venezuela) and *P. vorax* is observed in northern Peru, Ecuador, Colombia and Venezuela, in localizations with altitudes between 2500 and 2800 m.a.s.l. (Alcazar 1997, Heath et al. 2001)

### Life cycle

The Andean potato weevil has a holometabolous development with egg, five larval instars, pupa and adult (Herrera 2002). The total life cycle comprises 85-170 days (Herrera 2002) where the total duration depends on temperature, altitude, humidity in the soil and presence of and type of diet available (López-Ávila and Espita 2000). Eggs are laid on weeds, soil or on potato plants. Eggs are often hidden inside dried straw of Gramineae or residues from last year's crop (Calvache 1987), which can be peas or beans. Eggs can also be placed in the soil, a few centimetres below soil surface (Alcazar 1997, Herrera 2002).

The larvae develop inside tubers, stolons or stems of potato. After the larvae eclose from the eggs, they first move towards the small roots and then to developing tubers. The larvae make tunnels and they may move from one tuber to another. The last larval instars leave the tubers and pupate (Herrera 2002). The weevil pupates in the soil, beneath the tuberization zone (10-15cm deep) (Calvache 1987, Herrera 2002).

Adults develop in soil and when they emerge from the soil they aggregate in groups of about 25 individuals and then walk towards emerged potato plants since they are not able to fly. Directly after emerging from the soil they also mate. After five to ten days the female is ready to lay her eggs, which are laid in clusters with a total of, on average, 250 eggs (Alcazar 1997, Herrera 2002).

During daytime, the weevils are inactive and hide in dark humid places; in residues or in tubers. During the night, activity is enhanced and they climb the shoots of host plants to feed on leaves and stems but they can also feed on tubers (Herrera 2002). The adults live 130 to 365 days (López-Ávila and Espita 2000).

### 5.3. Potato tuber moth

*Phthorimaea operculella* Zeller  
Lepidoptera: Gelechiidae



Photo: Miriam Frida Karlsson

#### Host and damage

Potato tuber moths feed on several Solanaceae plants. The moth is a severe pest on potato and tomato. The moth larvae develop in potato tubers but also occur in the fruit, stem and even in the leaves of potato as well as in tobacco, eggplant and tomato. Larvae of the moth have also been found on weeds and herbs such as thorn-apple leaves *Datura stramonium*, nightshade, *Solanum nigrum* and tamarillo leaves *Cyphomandra betacea*. The potato tuber moth has a worldwide distribution and is one of the most important pests on potato production in the tropics and subtropics (Kroschel and Koch 1994, López-Ávila and Espita 2000).

#### Life cycle

Potato tuber moths have four larval instars and within a year, five or eight generations are developed. Between egg and adult it takes less than 30 days in summer and at least 70 days in winter. In Mediterranean regions hibernation occurs either in the egg, larvae or adult stage. In warmer areas or in places with two potato-growing seasons, the development is not interrupted (Kroschel and Koch 1994). The population is the highest when the average daily temperature is 20-25 °C and the moth survives in temperatures with a daily minimum mean of 5°C (Pratissoli et al. 2003), although the moth can survive short-term temperatures down to -7,5°C if the day-temperature is around 20°C (Kroschel and Koch 1994).

The average fecundity is about 100 to 200 eggs per female and eggs are laid singly or in small clusters. Eggs are usually placed on rough surfaces such as in cracks and indentations of the eyes of potato, in the soil or on hairy undersides of leaves (Fenemore 1988, Kroschel and Koch 1994, Pratissoli et al. 2003).

After 3 to 6 days the eggs hatch and the larvae penetrate the tuber at the level of a crack; it makes a small silken sheath and moults. It then forms a gallery which it coats with silk threads and ejects its frass to the outside. When the eggs are oviposited on the leaves and larva emerges on them, it forms a gallery and then penetrates the petioles, the stems or other leaves. It is the larval stage of the potato tuber moth that causes damage to growing plants by mining leaves in the field and severely infesting potato tubers in field and in storage, which subsequently allows bacterial infection to get a hold (Fenemore 1988). Larvae development is completed 3 days faster on tuber than on potato foliage according to López-Ávila and Espita (2000).

The larvae pupate 15 to 20 days after oviposition and are formed outside the tuber, in the soil, near the base of the host plant, on leaf residues, or in some other suitable sheltered site. Six to 30 days later, depending on climatic conditions, the pupae hatch. Adults are nocturnal and are most active during dusk and dawn initiating their flight 1-2 hours after sunset. The potato tuber moth can fly for more than five hours and in that time move ten kilometres if the wind speed is less than 5-6 m/s (Fenemore 1988). In 25 °C the adults live for one month. They prefer a shadowy and dry site and they feed on nectar and dew (Pratissoli et al. 2003).



Photo: Miriam Frida Karlsson

#### 5.4. Guatemalan potato moth

*Tecia solanivora* Povolny  
Lepidoptera: Gelechiidae

##### Host and damage

The Guatemalan potato moth, *Tecia solanivora*, is a severe pest on potato, *Solanum tuberosum tuberosum*, *S. tuberosum andigenum* and *S. phureja*, in the northern part of South America and throughout Central America. Potato production in the Canary Islands has also been affected. The moth is found at an altitude of 500 to 3500 m.a.s.l. and depending on the temperature, between two and ten generations per year are generated, at 10°C and 25°C respectively. The lowest temperature threshold is related to the survival of the most sensitive stage, prepupa, surviving temperatures above 7°C (Notz 1995). Damage is limited to the tubers and no feeding of foliage has been observed (Torres et al. 1997). The damage is enhanced in times of drought, and the pest is seen in all cultivated varieties of potato (Sánchez et al 2005, Torres 1998).

##### Life cycle

At a temperature of 25°C, the mean duration of the life cycle is approximately 40 days. With even lower temperatures the life cycle mean duration is more than three months (Torres et al. 1997). Adults can fly short distances and are locally spread this way, whereas long dispersal takes place with infested plants or soil (Herrera 1998). Adults have a crepuscular habit and its activity is enhanced during the night as well as in the morning (Torres et al. 1997).

Mating occurs one day after eclosion from the pupa and the sexual activity takes place in the morning. The following night, the first oviposition occurs. Females oviposit during 10-17 days with most eggs laid during the three first days. Each female lays between 200 and 400 eggs (Sotelo 1996) mainly on the soil, on uncovered tubers and on leaves and stems when there are plants in the field. Eggs are also laid in storage directly on the tubers. Around 84% of the oviposition occurs on the soil surface and on the root head of the plant, while only 13% of the eggs are laid on the foliage (López-Ávila and Triana 2004). Contorted surfaces or soil with crevices, such as in the soil close to a stem, are preferred (Torres et al. 1997). This was confirmed by Vargas et al. (2004), who found a preference for oviposition on dirty tubers, under soil adhered to the potato and around the area of the buds.

Eggs hatch in the morning (Torres et al. 1997) and first instar larvae migrate towards potato tubers and penetrate the tuber at the buds. They start feeding initially on the superficial parts, entering thereafter the tuber. Alimentation is highest in the initial part of the fourth instar and reduces totally until the end of the phase (Torres et al. 1997). If the population density is very high, the Guatemalan moth search for other tubers and leave the tuber as fourth instar larvae (Herrera 1998). They pupate in the soil, most of them not deeper than one centimetre. In storage the larvae pupate on the walls, on bags, and occasionally inside the tubers (Herrera 1998, Sotelo 1996, Alvarez, Trillos 1996).

## 5.5. Turnip moth

*Agrotis segetum* Denis and Schiffermüller  
Lepidoptera: Noctuidae



<http://www.biolib.cz/IMG/GAL/BIG/110686>

### Host and damage

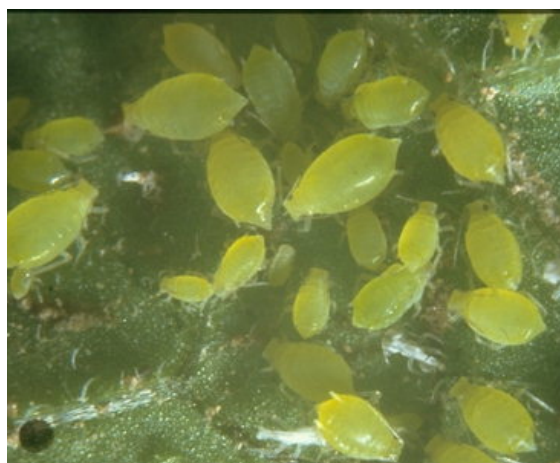
The host plants of *Agrotis segetum* are the weeds *Agropyrum*, bindweed, *Convolvulus*, plantain *Plantago* and the neighbouring vegetables such as beet, potato, cereals, tobacco, wine and many more. The larvae are extremely voracious and the damage is caused predominantly by the biting of the tubers, especially during warm and dry summers (Hedene and Olofsson 1994).

### Life cycle

In Sweden the turnip moth has one generation each year (Hedene and Olofsson 1994) but may have two or three generations in the southern parts of Europe. Females deposit 800 to 1200 eggs and place them singly or in small clusters on plants as well as on bare soil. At 14.5°C the egg hatches after 15 days. During two to three weeks, the larvae stay in the upper surface of the soil (Hedene and Olofsson 1994). The young larvae feed on wild plants and attack afterwards the neighbouring cultivated species. The larvae feed at night, gnawing the foliage and cutting the petioles and stay during the day rolled up under a piece of earth or at a slight depth in the ground. The larvae feed after hatching on plant stems during some weeks. Thereafter the larvae go further down in the soil and feed on tubers and roots. The turnip moth hibernates as larva or as pupate and pupates in the ground (Hedene and Olofsson 1994). Like the Guatemalan potato moth, the turnip moth mates at the beginning of the photophase and oviposits at the end of the photophase and the beginning of the scotophase. Males mate approximately seven times and females only once. The number of matings is positively correlated with longevity in males, but not in females (Svensson et al 1998).

## 5.6. Buckthorn aphid and *Aphis frangulae*

*Aphis nasturtii* Kaltenbach  
*Aphis frangulae* Kaltenbach  
Homoptera: Aphididae



<http://www.inra.fr/hyppz/IMAGES/7010721.jpg>

### Host and damage

*Aphis frangulae* and *Aphis nasturtii*, buckthorn aphid, cause the most severe direct damage on potato among the aphids in Sweden (95-100% of aphid population). *A. frangulae* is among the aphids with a worldwide importance in potato production causing both direct damage and by transmission of virus (Radcliffe and Ragsdale 2002). Other aphids such as *Rhopalosiphum padi* and



*Myzus persicae* are the most severe virus vectors (Sigvald and Lindblad 1999) and the most important virus vectors of potato are aphids (Radcliffe and Ragsdale 2002).

*A. frangulae* is an oligophagous aphid, which is a pest on potato, *Solanum tuberosum*, and has been found on *Solanum nigrum*, *Eupatorium cannabinum* (Asteraceae) (flowers, leaves, shoots), *Capsella bursa-pastoris* (Brassicaceae) (flowers, leaves) (Aksoy et al. 1998).

The buckthorn aphid, *Aphis nasturtii* is a common pest on potato throughout Central Europe. Their direct damage is caused by piercing/sucking of sap extracts from these plants, by inserting its stylet in the phloem hindering plant growth without causing deformation of the leaves. Buckthorn aphid acts as a vector for various viruses and the transmission of virus causes serious indirect damage, in particular, on seed potatoes. Buckthorn aphid acts as a vector for different viruses, such as the potato virus Y (regarded as causing necrosis of the veins of tobacco leaves), A virus (rough mosaic), yellow spot virus, and also M and S viruses (Twengström 2003).

#### **Life cycle of buckthorn aphid**

The buckthorn aphid alters between primary and secondary hosts where the primary host is the common buckthorn, *Rhamnus cathartica* or the alder buckthorn, *Frangula alnus*. Secondary hosts are potato and weeds. Winter-eggs are laid on common buckthorn or on the alder buckthorn and they hatch at the beginning of April. The fundatrix (parthenogenetic viviparous female) emerge in spring from the overwintered eggs and produce, some three weeks later, nymphs, which in turn, produce virginiparous and viviparous females, which mostly are winged. The latter leave the primary host due to abundant population and establish new colonies on various secondary hosts (Hedene and Olofsson 1994).

During the summer, several virginiparous generations follow each other, partly composed of winged individuals and partly of apterous forms. The winged forms attack new summer host plants and can be disseminated over a great distance by the wind, especially warm springs and summers. Once summer development is complete, the aphid in the form of gynoparous females and males return to the primary host, where mating occurs and where the females lay their fertilized eggs at the base of buds and in cracks in the buckthorn bark, where they will spend the winter (Hedene and Olofsson 1994)

## **6. Odours, potato and insects**

The insects described above are all severe pests on potato and in some cases potato is their only or main host. They prefer different part of the potato; some feed, oviposit, and mate on the foliage while others prefer on, or close to, tubers. Their sensory input from the plant, coming from mechanoreceptors and/or chemoreceptors elicit different behaviour in the insects. Even the insect physiology and pheromones production may be influenced.

A summary of volatile compounds described to give a behavioural or electrophysiological response in the insect, is listed in Table 3.

### **6.1 Volatile potato compounds and insect response**

The Colorado potato beetle orientate towards the potato plant to feed, mate and oviposit. This beetle species is one of the most studied insects with respect to plant volatile attraction and it is confirmed that volatile cues from potato attract the beetle. This has been shown both by electrophysiological recordings and behavioural experiments. Specific blends of volatiles emitted by potato have been identified as attractants for Colorado potato beetles and behavioural assays shows that damage and age can influence insect attraction (Visser 1979, 1986, Tibor et al. 1988, Bolter et al. 1997, Dickens 2000b, Dickens et al. 2002). The beetle has a preference for mature plants while small plants become attractive to both male and female beetle only when they are damaged with conspecific or heterospecific herbivores (Bolter et al. 1997, Dickens 2000b).





Synthetic kairomone blends consisting of two or three potato volatiles are as attractive as mechanically damaged potato foliage to both sexes of Colorado potato beetle. A three-component blend consisting of (Z)-3-hexenyl acetate, linalool, and methyl salicylate attracted both larvae and adults of both sexes while single compounds were inactive (Dickens 2000b, Dickens et al. 2002). On the other hand, when tested singly, nonanal (E)-2-hexen-1-ol, (Z)-3-hexen-1-ol, and the sesquiterpene  $\beta$ -caryophyllene were deterrent to the beetle (Dickens 2000b).

Similar to the Colorado potato beetle, the Andean potato weevil search for a potato field as soon as the first potato plants sprout. The activity of the weevil is therefore correlated to the phenological stage of potato, and field captures of Andean potato weevil in *S. phureja* are highest during sprouting and flowering (Galindo and Espanol 2004). While studying adults in the field during an entire year, most adults were captured between preparation of the soil and one week after sprouting (Calvache 1987). Galindo and Espanol (2004) compared the efficiency of two traps; one with potato leave and another with individuals of Andean potato beetles. Traps with potato foliage captured male and female weevils; males mostly during sprouting while traps with conspecific males and females captured most during flowering and had a low capture during sprouting, which may indicate that mating and social behaviours become more important later in season. An alternative hypothesis is that flowering has an effect on the mating. Identification of the plant volatiles that attract the weevils has not been done. Nevertheless, observations of weevil behaviour in relation to potato in field, indicate preferences.

A similar behaviour is observed in the Guatemalan potato moth. The capture of adult male moths is seen to vary during the season and there is a population peak during the first week of the cultivation. Those individuals are moths attracted from fields nearby, from residues or from infested tubers. After the first infestation, the population of flying moths decreases until the initial part of the tuberization stage when the highest population occurs, which coincides with the start of the flowering of the potato (Torres et al. 1997, López-Ávila and Triana 2004, Niño 2004, Rincón et al. 2007). This coincidence of the phenological stage of tuberization stage and flowering, indicates that female moths search oviposition sites when both potato and flowers are found in the field. This might explain the recent findings that females are equally attracted to tubers and flowers. Flowers and tubers attracted together more than 50% of females in a four-armed olfactometer and virgin females were more attracted to potato than mated females (Figure 3) (Rincón et al. 2007).

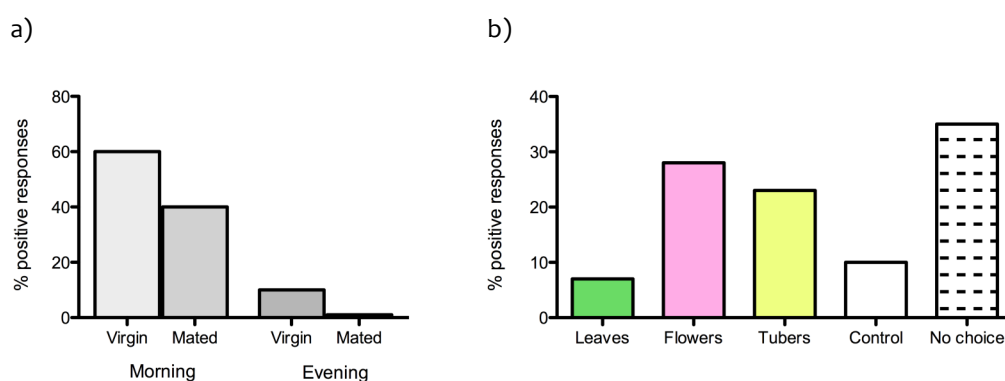


Figure 3: Percentage of positive responses in four-armed olfactometer of females, virgin and mated, Guatemalan potato moth *Tecia solanivora* a) during morning and evening b) to plant parts

Studies on the olfactory receptor neurones in the turnip moth, *Agrotis segetum*, showed a high sensitivity and selectivity to volatile compounds released from potato, such as  $\beta$ -caryophyllene, humulene and to a few alcohols and saturated hydrocarbons (Anderson et al 1996). Also the potato tuber moth has shown to elicit antennal response to volatile compounds from potato, both from leaves and tubers such as hexanal, heptanal, octanal, nonanal, decanal, 2-hexanol, 1-octen-3-

ol and  $\beta$ -farnesene. Predominantly aldehydes and alcohols elicit antennal response in female antenna although very few compounds from other functional classes, such as sesquiterpenes, have been tested (De Cristofaro et al. 2007).

Under field conditions, potato tuber moths oviposit a high portion of their eggs on the soil, or close to host plants, rather than directly on the plant itself, and not around non-host plants (Fenemore 1988). This is confirmed in laboratory studies where females laid their eggs preferable on cages with hidden tubers (De Cristofaro et al. 2007). Potato foliage was shown to stimulate behaviour such as antennal waving, wing fibrillation, running, and non-directional flight (Goldson and Emberson 1977). According to Fenemore (1988) orientation of potato tuber moth adults to plant volatiles seems the most likely mechanism of tuber localization in storages. This concurs with a study by Arab et al. (2007) who observed that mated females had a higher preference for tubers than unmated females. Undamaged tubers were also preferred over damaged ones.

Most potato feeding insects are attracted to their host plant, potato. Interestingly, plant volatiles from the primary host of *Aphis frangulae* did not show any response in an olfactometer study (Lilly and Hardie 1996) although the majority of host-alternating aphid species are highly specialised on both primary and secondary hosts (Narayandas et al. 2006). According to Powell and Hardie (2001) it is more common that aphid species are able to respond to volatile cues released by their primary host plant but there is a difference in individuals from different development stages/phenotypes, and it is found that summer female aphids (virginoparae) do not show selectivity between plants while autumn return migrants (gynoparae and males) show olfactory responses to their primary host plant. Phenotypic differences were also detected by electroantennography between the different female phenotypes, virginoparae and gynoparae and males of *A. fabae* (Powell and Hardie 2001). In accordance with that, the wingless aphid of *Macrosiphum eupliorbiae* is attracted to potato foliage while winged are not. Identification of attractive compounds has not been done but it is shown that the blend of synthetic potato odours, causing aggregation behaviour in both larvae and adults of the Colorado potato beetle, did not attract either winged or wingless aphids of *M. eupliorbiae* (Narayandas et al. 2006).

## 6.2. Pheromone compounds and insect response

Among the insects described in this introductory paper, pheromones have been identified for the Colorado potato beetle and the three moth species described. In all three moth species, sexual pheromones produced by the female are identified. The potato tuber moth females produce a pheromone that is identified as a blend of (E,Z)-4,7-tridecadienyl acetate and (E,Z,Z)-4,7,10-tridecatrienyl acetate (Voerman et al 1977, Mohamed 1980, Kroschel and Koch 1994) in a ratio of 1:1.5 (Raman 1984). Females of the Guatemalan potato moth produce a blend of (E)-3-dodecenyl acetate, the geometric isomer (Z)-3-dodecenyl acetate, and the corresponding saturated dodecyl acetate (Nesbitt et al. 1985, Bosa et al. 2005). Male attraction to the pheromone is optimal with a blend of (E)-3-dodecenyl acetate, (Z)-3-dodecenyl acetate and dodecyl acetate at a ratio of 100:1:20 (Bosa et al. 2005). Another proportion of the three compounds; 2:1:2, a so-called "off-blend" was also tested. In proximity to this blend, male attraction to calling females was suppressed and male response to female pheromone was reduced. This was thus shown to manipulate the sexual communication and mating was disrupted (Bosa et al. 2006). The turnip moth, and its pheromone communication system has been extensively studied both behaviourally and physiologically (Arn et al., 1980; Löfstedt et al., 1982; Hansson et al., 1989; Wu et al., 1995). Almost twenty compounds have been found in the female sex pheromone gland but four of these are enough to elicit optimal attraction of conspecific males, (Z)-5-decenyl acetate, (Z)-7-dodecenyl acetate, (Z)-9-tetradecenyl acetate and (Z)-5-dodecenyl acetate in a ratio of 1:5:2,5:0.1 (Löfstedt et al. 1982, Wu et al. 1995). Svensson et al (2001) showed long-range, pheromone-mediated flight behaviour of individual male moths, demonstrating that male moths have the potential to actively fly over very large distances when searching for mates.

The two most common sex pheromones in Aphidinae are two isomers of nepetalactol. Late-flying gynoparae of *A. nasturtii* and *A. frangulae* additionally utilize the sex pheromone as an aggregation pheromone, enabling them to locate conspecific oviparae on suitable host plants (Pope et al.

2007, Powell and Hardie 2001). Whether nepetalactol also is produced by the aphids *A. nasturtii* and *A. frangulae*, themselves, is not yet known.

Aggregation pheromone is believed to be produced by the Andean potato weevil, as both males and females of the weevil are equally attracted to conspecific individuals of both sexes (Calvache 1987, Galindo and Espanol 2004). This attraction was mainly seen during potato flowering stage and it was supposed to be due to an aggregation pheromone, since weevils have aggregation behaviour during daytime and for mating. The behaviour could also be related to the combined effect between pheromone and potato volatiles (see next chapter).

The existence of a pheromone in the Colorado potato beetle has long been discussed. Recently, a male-produced aggregation pheromone (*S*)-3,7-dimethyl-2-oxo-oct-6-ene-1,3-diol has been identified. (Oliver et al. 2002).

### 6.3. Combination of pheromone and volatile potato compounds and insect response

The interaction of plant semiochemicals and insect pheromones influence the communication between insects. A combination of stimuli from potato plant volatiles and pheromones can increase the response compared to either stimuli alone (Landolt et al 1994, Bartet et al. 1995). Enhanced responsiveness to sex pheromones when combined with host plant volatiles is known to occur in many insect families. Examples from Lepidoptera are the combination of *Spodoptera exigua* pheromone together with the plant volatiles benzaldehyde, phenyl acetaldehyde, (*Z*)-3-hexenyl acetate and linalool, which increases the landing rates of males (Deng 2004). A synergism between pheromone and plant volatiles has also been shown for aphids, Homoptera. Plant odours from the primary host of the black bean aphid *Aphis fabae* enhance the response for the sex pheromone, elicited by mature oviparae aphids, when they return to their host in the autumn (Powell and Hardie 2001). Also gynoparae females and males of the cherry-oat aphid *Rhopalosiphum padi* show an enhanced response to pheromones with host volatiles. *A. fabae*, *R. padi* and *Phorodon humuli* are aphid species for which it has been demonstrated that host plant volatiles increase response to sex pheromones (Powell et al. 2006). In both laboratory bioassays and field experiments with the Colorado potato beetle, a combination of the pheromone plus the three-component plant attractant was preferred over the plant attractant alone (Dickens 2006). Recently it has been found that also the fourth instar larvae show increased positive anemotaxis in response to the combined host plant and pheromone odours (Dickens 2002, Jennifer et al. 2007).

Sexual behaviour of phytophagous insects is often integrated with their host plants. Production or release of sex pheromones can be stimulated as a response to particular host plant cues and some insects are also dependent on host cues to produce pheromones. (Landolt and Phillips 1997). The fecundity of potato tuber moth is enhanced in presence of suitable host-plant material even if the stimuli of a host plant is not required for mating and egg laying to take place (Fenimore 1978). In a closely related Lepidopteran, diamondback moth *Plutella xylostella*, sexual maturation is stimulated with olfaction and gustatory stimuli and it was shown to have a longer pre-reproductive period in absence of its host, cabbage. The specific host-plant volatile of cabbage, allyl isothiocyanate, influenced the ovarian development of the diamondback moth (Schoonhoven et al. 2006). Also for the Colorado potato beetle it has been found that during the first days of adulthood of the beetle, the chemoreceptors mature and both males and females increased their antennal sensitivity from the time of emergence through at least six to eight days. The increased antennal responsiveness to a host plant is correlated with sexual development, which was measured as increased size of testes and ovaries (Dickens 2000a).

Interestingly, volatiles from the host plant can also trigger the production and release of sex pheromones. Females of the corn earworm, *Helicoverpa zea*, can delay their reproductive behaviour, such as secretion of pheromone and oviposition, until they find a suitable host. The

plant hormone ethene induces pheromone production and it is found in ripening fruits, which is a suitable nutrient for the moth larvae (Raina et al 1992).

There are several examples how insects optimize mating and reproduction by using host plant compounds, such as sex pheromone precursors or sequester plant compounds and use them as pheromones (Landolt and Phillips 1997). Volatiles evolved as defence agents in angiosperms and many of these allelomones are related to or are even identical with sex pheromones of insects (Harrewijn et al. 1994). The host plant compounds that attract the Colorado potato beetle are thought to have chemical characteristics close to that of pheromones (Boiteau 1998) (see Table 3). This could concur with the electrophysiological experiments demonstrated by Visser et al. (1979) that the beetle's olfactory receptors are sensitive to a range of similar components, especially hexanols.

The ability to respond to volatile semiochemicals often differs between female and male insects. This despite the fact that male and female antenna of many Lepidopteran species are equally well equipped with receptors eliciting response to volatile plant compounds (Van der Pers 1981). The female of turnip moth is more sensitive to lower concentrations of plant volatiles than males are, but the female is insensitive to pheromone compounds while the male antenna is sensitive both to pheromones and plant volatiles (Hansson et al. 1989). Similarly, electroantennographic studies of the potato tuber moth showed that both sexes responded to volatile compounds from potato but with different response levels. Male antennae are more sensitive to alcohols such as (Z)-2-penten-1-ol, (Z)-3-hexen-1-ol, pentanol and hexanol, than are females while female olfactory sensitivity was high to aldehydes, for example heptanal and octanal. Furthermore, nonanal and heptanal caused an antiovidepment response by the female (De Cristofaro et al. 1999, 2007).

## 7. Pest control

The knowledge about insect response to semiochemicals; allelochemicals and pheromones is not new. Farmers have often used this knowledge to develop agricultural pest management strategies. Control methods such as intercropping, push-pull strategies, trap crops and augmentation of natural enemies are different mechanisms when insect response to semiochemicals plays a role. One of the motives for the agricultural practices intercropping and polyculture, is to confuse the insect or mask the host plant odour with non-host volatiles and thereby disrupt host finding. Aromatic herbs are likewise used to repel insects with their odours (Altieri and Nicholls 2004, Root 1973). Disruption of host-finding behaviour or sexual communication can either involve allelomones or pheromones. Synthetic blends of semiochemicals are now produced that mimic the natural blends and are an increasing part of modern agricultural pest management. Behaviourally active compounds from potato, produced as an attractant synthetic blend of host volatiles might be used in mass-trapping, monitoring or disruption. Compounds that function as a signal for egg-laying females, may be formulated in lures for mass-trapping and might be a method to control females in a population (Oehlschlager et al. 2002, Cork et al. 2003). Potato mimicking blends may also enhance attractiveness to trap crops in order to draw pest insect populations away from cultivated crops to plants with less value or to sacrificial plants.

There are various examples of potential use of semiochemicals in potato production to reduce pest damage (Agelopoulos et al. 1999a, Bosa et al 2006, Kuhar et al 2006, Raman 1988). Monitoring *P. operculella* and *T. solanivora* with pheromones is currently a tool for a more efficient use of chemical insecticides (Mohamed 1980, López-Ávila and Triana 2004). Raman (1988) demonstrated the feasibility of direct control of potato tuber moth both in field and storage with mass trapping. Using the synthetic sex pheromone compounds, (E,Z)-4,7-tridecadienyl acetate and (E,Z,Z)-4,7,10-tridecatrienyl acetate, in a ratio of 1:1.5, tuber damage was reduced by 45% when compared with plots receiving normal insecticidal application with no pheromones. Trap density was one trap per 225 m<sup>2</sup> but with a higher density of traps (one per 110 m<sup>2</sup>), a reduced number of

captures was found, indicating a possible disruption effect (Ortu and Floris 1989). By using pheromones at a high dose or in a different blend than produced by the insect, it is possible to impede insects from finding the opposite sex. Mating disruption of the Guatemalan potato moth has been decent with the pheromone compounds E3-12Ac, Z3-12Ac and 12Ac in a proportion of 2:1:2 instead of 100:1:20, which is produced by the female or with a 1000 fold concentration of 100:1:20 ratio (Bosa et al. 2006). In effective male disruption, male attraction to calling females is suppressed and mating is disrupted (Bosa et al. 2006). By permeating the atmosphere with sex pheromones, disruption of *Agrotis segetum* mating behaviour has been successful and the best effect was achieved by a three-component pheromone blend (Svensson et al. 1995, 2001).

A synthetic blend of potato volatiles has been used in traps for management of the Colorado potato beetle (Martel et al. 2005) and a combination of pheromone and plant volatiles have shown promising results in field tests (Dickens 2006, Kuhar et al. 2006). One other aspect of volatile compounds released from potato is the response that may occur in predators of the Colorado potato beetle when they sense the smell of potato volatiles induced in response to beetle feeding. This can enhance their capability to orientate towards their prey and thus improve the pest control (Dickens 1999).

## 8. Conclusions

Phytophagous insects and plants have co-evolved and it can be assumed that species have been selected for mechanisms that guide them to their host plants. The insects in this introductory paper are all pests on potato. They all orientate towards potato, however during somewhat different phenological stages and/or plant parts. Consequently they are guided by different cues, since the odour profile for different plant parts and stages of the development of the potato, varies. Increased attraction to potato foliage is true for the Colorado potato beetle as the plants mature, while the Andean potato weevil is more attracted to potato in its earlier stages. Nevertheless the Colorado beetle does search for a potato field as soon as the diapause ends. That is when the potato barely is in sprouting stage and before any reproduction takes place since the beetle has to feed before it mates. Higher attraction to mature potato is thus correlated to mating. Attraction to conspecific individuals of the Andean potato weevil is higher to conspecifics at the same time as the potato is mature and flowering. The behaviour of these two Coleopteran species is to some extent similar and it might also be the case for their pheromone production. Although it has not been identified, the Andean potato weevil is supposed to produce aggregation pheromone, just like the Colorado potato beetle. It is known that males of many species of Curculionidae produce pheromones that mediate colonization of susceptible host plants (Bartelt 1999). Combinations of pheromones and host plant volatiles are used to develop methods for mass trapping of many weevil species (Ramirez-Lucas et al. 1996 Piñero et al. 2001, Alpizar et al. 2002).

An enhanced attraction to conspecifics, induced by host odors, is found in two of the potato pest insects portrayed in this introductory paper. The Colorado potato beetle has a higher responsiveness to pheromones in combination with host plant volatiles than to pheromones alone and the potato tuber moth fecundity is enhanced in the presence of suitable host-plant (Fenimore 1978). Sensitivity to pheromone has been shown to be higher in the presence of host plants (Borden et al 2008, Reddy and Guerra 2004, Landolt 1994, 1997), due to synergism of the compounds or the fact that host plant stimulates pheromone release (Raina 1988, Landolt 1994).

The Guatemalan potato moth appears to be highly synchronized with its sole host potato, since the phenological stage tuberization occurs when larval density is increasing in the field. The female seems to be attracted by the flowers in the field just at a suitable time for the larva to develop in the tubers. Population is then increasing during tuber bulking. This is also the time when potato plants do not require much water, which is very destructive for the egg, larvae and pupae located in the soil. Synchronization between potato plant development and population density for the



potato tuber moth resemble that of the Guatemalan potato moth. Synchronization is found (and described) mainly for the monophagous species, the Guatemalan potato moth and the potato tuber moth among insect species dealt with in this introductory paper. The turnip moth, the aphids and the Andean potato weevil are, in contrast, polyphagous. Synchronization between insect life cycle and its host is especially true for food specialists according to Schonhooven (2005).

Response to the entire blend of volatile compounds from potato differs between the insects, with some insects responding to many compounds from the blend and others to only a few. Host plant recognition depends not only on the presence and detection of the individual compounds but more on the ratios of the volatiles. Identification of volatile compounds from potato that elicit an antennal response in electrophysiological recordings has been done for the Coleopteran, Colorado potato beetle, and for the three Lepidopteran species described. Some compounds, like (*E*)- $\beta$ -caryophyllene which is the most abundant volatile compound from potato, elicit responses in the antennae of the Colorado potato beetle, the turnip moth and the Guatemalan potato moth. The Colorado potato beetle is deterred by (*E*)- $\beta$ -caryophyllene while the behavioural response is not known for the moths. Unfortunately there is still not much known for many of the other compounds; whether they are behaviourally active or what kind of behavioural response they generate.

Sesquiterpenes, beside fatty acid derivatives are the most common volatiles components emitted from potato foliage. Some of these compounds, such as (*E*)- $\beta$ -caryophyllene and (*E*)- $\beta$ -farnesene, do give electroantennographic responses in both Coleopterans and Lepidopterans. The ability to detect these compounds might be important to be able to find potato foliage for oviposition and/or for feeding. Most common volatile compounds from tubers are aldehydes and potato tuber moth has shown antennal response to these compounds while the Colorado potato beetle has not. This is in accordance with the feeding behaviour of the two species, hence the Colorado potato beetle does not feed on tubers while the potato tuber moth feed both on tuber and on foliage.

Female adults of these insect species search for potato, sometimes without feeding on them. Virgin females of the Guatemalan potato moth are more attracted to potato plants than mated ones. Is this due to the enhanced probability of encountering a mate or do they feed before they mate? Do they search for a potato to lay their eggs, even before mating? There is not much known about the feeding and oviposition behaviour of the adult moth, but it is assumed that they feed on nectar from potato flowers. Virgin females are, in addition, more attracted to potato in the morning, coinciding with the mating time. This supports the idea of searching to enhance the probability of encountering a male for mating.

Interestingly there are several structural similarities between compounds that attract one species. Some similarity is known within the described potato pest insects, for example in compound preferences of the Colorado potato beetle (Table 3). However, the knowledge about the species described in this introductory paper is unfortunately scarce and more effort has to be given to reveal these types of correlation. Insect orientation and acceptance of oviposition, feeding and mating sites might not be separated, but might be guided by the same type of compounds or compounds with similar chemical structures.

Synergistic effects between semiochemicals emitted by plants and insects, from host and conspecifics, are important for the insect. This is probably one essential issue to consider in the development of new control methods of phytophagous pests. Some compounds that get volatilized from plants act as signals for the insect, and certain compounds elicit attraction behaviour. A trap lure composition based on both kairomones and pheromones, compared to traps based only on pheromone, are likely to be more competitive when placed in the field. More basic studies have to be done on the potato pest insects in order to elucidate which specific compounds are attractive to the different pests. More research is needed to be able to develop pest control methods further, by identifying chemical attractants, pheromones and volatile plant compounds and to characterize the behavioural responses toward the identified compounds. For

this reason it is important to continue to study the relation between mating behaviour and host finding, and the synchronization of hosts' phenological stage and insect behaviour.

## 9. References

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