THE EFFECTS OF NON-HOST VOLATILES ON HABITAT LOCATION BY PHYTOPHAGOUS INSECTS

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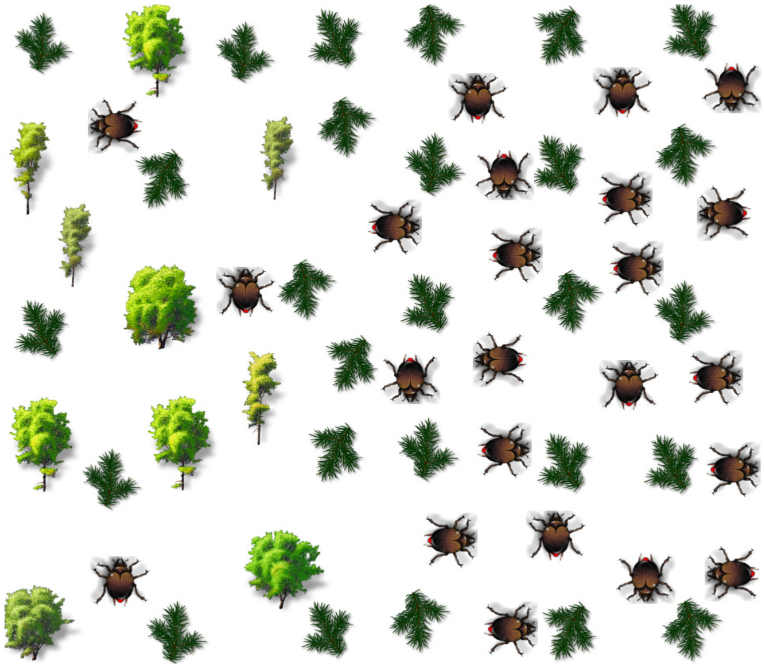
Introductory Paper at the Faculty of Landscape Planning, Horticulture and
Agricultural Science 2007 : 1
Swedish University of Agricultural Sciences
Alnarp, April 2007



ISSN 1654-3580

PREFACE

This paper was written in order to obtain a better understanding of olfactory-guided habitat location mechanisms in phytophagous insects. Focus is on the involvement of volatile chemicals from non-host plants that modulate the insects' response to attractive odours. Most of the relevant literature is covered; a complete review of the several topics discussed would be way beyond the scope of this review. Literature was searched in the BIOSIS database during August 2006, and the paper was written, mainly, during October and November 2006. Cited literature is dated from 1937 to 2007. Apart from my supervisors, Fredrik Schlyter and Mattias Larsson, useful input was provided by Sylvia Anton and Birgitta Rämert. The review is part of my FORMAS funded PhD project: "Semiochemical diversity and insect dynamics" (# 230-2005-1778), and part of the Linnaeus (ICE^3) programme. Personally, writing this paper was very interesting and definitely resulted in in-depth knowledge in several fields of chemical ecology.

The review is divided into three parts, which could be read relatively independent of each other depending on the reader's previous knowledge in the respective fields of research. First, general theories about habitat and host location in phytophagous insects are discussed. In the second part, the 'stability-diversity hypothesis' is presented, and the effects of increased biodiversity on pest populations in agricultural ecosystems is summarized. The third and last part describes the insect olfactory system and encoding of odour quality.

SUMMARY

The host-plant selection sequence of phytophagous insects can be divided into three steps: (i) habitat location, (ii) host location, and (iii) host acceptance. Chemoreception plays a main role during the process. Olfaction is typically the most important sensory modality during the first two steps, whereas contact chemoreception dominates the third. At all steps in the selection sequence, positive and negative external stimuli interact with each other and also with internal factors in the insect, and the balance between positive and negative stimuli can be tipped towards either acceptance or rejection of a particular habitat or host.

Non-host volatiles (NHV) have been shown to modulate host location behaviour in several insect orders. Few studies report effects at the habitat level, but in forest ecosystems, indications of anti-attractant effects at the habitat level has been found in a small number of conifer-inhabiting coleopterans and lepidopterans. In agricultural systems, intercropping studies have frequently found lower pest insect abundance in polycultures compared to monocultures. It has been hypothesized, and sometimes demonstrated, that repellent NHV from the intercrop is the main mechanism for the observed patterns of pest abundance. However, several other mechanisms have been suggested, all discussed here.

Positive and negative olfactory stimuli are perceived by olfactory hairs (sensilla), mainly located on the antennae. A brief overview of the insect olfactory system is presented and encoding of positive and negative stimuli by the peripheral and central nervous system is discussed.

INTRODUCTION

The sense of smell is regarded as the oldest of our senses, present in organisms of all phyla (Hildebrand and Shepherd, 1997). To a large extent, insects rely on olfaction in order to accomplish various tasks throughout their lives. Suitable food sources and places for oviposition are often located by use of volatile chemicals released from plants or prey items. Odours are also used by insects to detect the presence of conspecific and/or heterospecific individuals and most well-studied is probably the use of sexual pheromones in mate location. To be able to detect and discriminate among the many different odours that insects encounter, a large number of olfactory receptor proteins is required. Each type of receptor protein is expressed in a subset of neurons present in the sensilla on the insect antennae (Rützler and Zwiebel, 2005). Insects are able to detect a large number of odorants and the receptor proteins in insect antennae are extremely sensitive to the specific odours they perceive. For instance, sexual pheromones are typically released by females at a rate of a few nanograms (10^{-9}g) per hour. Still, conspecific males are attracted over distances of tens of meters.

Many insects feed on plants that are of economic importance to humans. Serious pest insects exist in the fields of agriculture, horticulture and forestry. Since the utilization of commonly used insecticides is becoming more restrictive and many of the most effective chemicals are already prohibited, the demand for alternative pest control strategies is increasing. The insects' extremely sensitive olfactory sense can be exploited by humans in several ways to reduce damage to economically important plants. For instance, pheromones are used in monitoring systems, mating disruption and mass-trapping for various kinds of pest insects (Agelopoulos et al., 1999; Harris and Foster, 1999). Moreover, the potential of utilizing attractive odours (i.e. pheromones and kairomones) in combination with repellent and/or deterrent volatiles released by non-host plants have been shown in several bark beetle species (Schlyter and Birgersson, 1999; Byers, 2004). In addition to the utilization of semiochemicals, plants of economic interest can also be planted and grown in ways that prevent pest insect outbreaks. Forest and agricultural monocultures experience pest insect outbreaks more frequently than mixed-species forests and other natural ecosystems (Andow, 1991; Jactel et al., 2005). Since forest ecosystems are difficult to manipulate due to their size, long generation time of trees as well as the several years it normally takes for an insect to reach pest status (Watt, 1992), most research has been done in agricultural systems. However, the mechanisms that explain the reduced pest abundance are not well understood. Often, the role of volatile chemicals has not been thoroughly investigated. Since the olfactory sense is of primary importance in the host location process of most insects, volatile chemicals from non-host plants are likely to reduce the host finding efficiency, which may, at least in part, explain the observed patterns of pest outbreaks.

In order to further develop the utilization of semiochemicals or mixed planting strategies in pest management, we must understand the mechanisms behind the insects' choice of habitat and host, and how biodiversity affects the insects' habitat- and host location ability. If the combination of host and non-host plants in polycultures impedes the habitat location ability of herbivorous insects, opportunities exist to grow plants in ways to keep pest insects away from economically important fields and forests. This paper will focus on habitat location mechanisms in phytophagous insects, with emphasis on olfactory chemoreception and the involvement of volatiles from non-host plants that modulate the response to attractive signals. In order to provide a complete picture, theories about host selection in general are also presented.

HOST-PLANT SELECTION SEQUENCE

Herbivorous insects do not choose plants randomly for feeding or oviposition. Instead, most insect species are highly selective in their choice of host plant. Not only are certain plant species selected, but also specific individuals and plant organs. In addition, host selection behaviour may change with the developmental phase of the insect, and different life stages often differ in their preferences and ability to utilize plant species as hosts (Schoonhoven et al., 2006). Host selection is a crucial event in the life of an insect and mistakes might have serious fitness consequences. For instance, newly hatched larvae of many insects are relatively immobile and unable to move away from unsuitable plants. Thus, the survival of these larvae to a large extent depends on their mothers' choice of plant (Renwick, 1989).

Suitable hosts are unequally distributed through space and time. At the landscape scale, insects must be able to find suitable habitats, which often are patchily distributed (Schooley and Wiens, 2003). Within the right habitat, insects have to search for the correct host species and also for a particular host individual. Factors such as nutritional quality, water content, toxic secondary metabolites, attack susceptibility, risk of predation and parasitism as well as the presence of competing individuals have to be taken into consideration before the insect chooses a particular host individual (Bernays and Graham, 1988; Renwick, 1989; Schlyter and Birgersson, 1999). In theory, the host selection process can be divided into three different steps (Saint-Germain et al., 2004) (Figure 1):

(i) habitat location
(ii) host location
(iii) host acceptance

Before discussing the different steps, it is useful to define some of the terms that are commonly used when describing host selection behaviour.

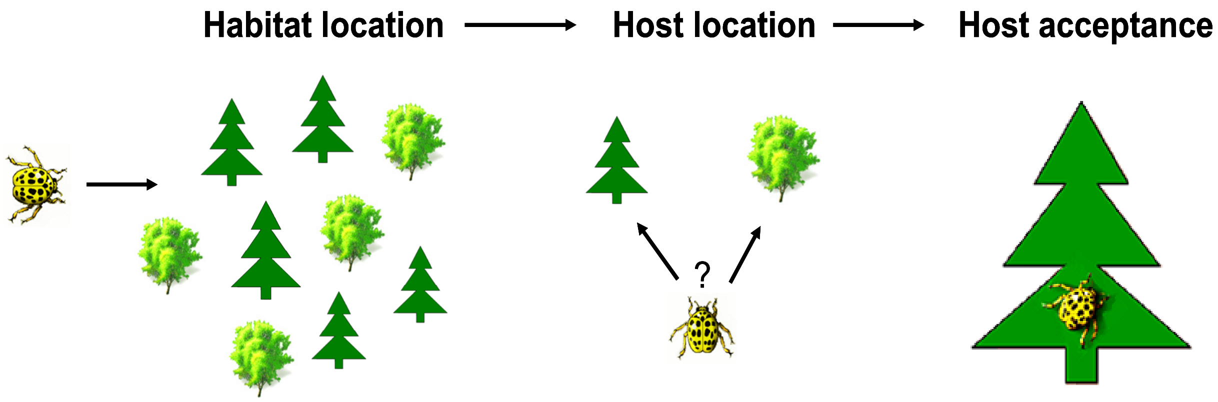


Fig. 1. Three steps in the host-plant selection sequence.

Terminology

Commonly used terms that explain behavioural and neural processes in host selection behaviour, are defined in Box 1.

Box 1

Searching. The term 'searching' means 'to look carefully in a place in an effort to find something'. Finding is the end result of searching (Schoonhoven et al., 2006).

Selection. In the strict sense, selection means to choose from alternatives. It thus implies a weighing of alternatives, such as two or more alternative food plants. However, it is often difficult to prove that the insect compare different alternatives, especially when contacts occur sequentially. In cases when alternatives have been compared before final acceptance occurs, the term 'selection behaviour' is appropriate (Schoonhoven et al., 2006).

Acceptance. Acceptance occurs when the insect oviposit or exhibit sustained feeding on the plant. The term 'acceptance' should only be used when selection has occurred, i. e. when the insect has chosen between alternatives. For instance, if an insect is released in the middle of a monoculture and is observed to initiate sustained feeding on a plant, it cannot be concluded that the insect selected the plant because there were no alternatives present. It can only be said that the plant was accepted by the insect (Schoonhoven et al., 2006).

Preference. The term 'preference' can only be applied when a set of different plants is available to the insect. If an insect consistently feeds relatively more on a particular plant compared to the plant's relative abundance, the insect is said to 'prefer' that plant over the others (Schoonhoven et al., 2006).

Recognition. This term is often used in connection with acceptance. 'Recognition' means that a particular stimulus or combination of stimuli originating in the external world matches a model in the insect's central nervous system (CNS) (Dethier, 1982). If the profile of incoming sensory information on plant cues matches the internal model, the plant is recognized as a host (Schoonhoven et al., 2006).

The terms defined in Box 1 refer to rather complex neural and behavioural processes. These processes are triggered in the presence of different kinds of external stimuli. Apart from visual stimuli, behaviour-modifying chemicals, collectively termed semiochemicals or infochemicals, are of primary importance (Schoonhoven et al., 2006). Semiochemicals are involved in interactions between individual organisms. They are subdivided into two major groups, *pheromones* and *allelochemics*, depending on whether the interaction is intra- or interspecific, respectively. The allelochemics are further subdivided into four different groups based on whether the receiver, the emitter, or both benefit in the interaction. The definitions of these groups have been modulated over time and are thus heterogeneous, sometimes causing confusion. *Kairomones* are chemicals that benefit the receiver but are nonadaptive to the emitter (Nordlund and Lewis, 1976). *Allomones* were first defined by Brown, (1968) as chemicals that are favourable to the emitter. The definition of an allomone has later been extended. According to Nordlund and Lewis, (1976), an allomone is a substance that trigger behavioural or physiological reactions in the receiving organism that are favourable to the emitter but not to the receiver. Included in this definition are toxins and nutrients. However, toxins and nutrients are themselves to the benefit or detriment to the interacting organisms and should thus be separated from the information conveying chemicals (infochemicals) (Dicke and Sabelis, 1988). I do not include toxins and nutrients in my definition of an allomone. The third group of semiochemicals is *synomones,* which are chemical substances beneficial for both the emitter and the receiver (Nordlund and Lewis, 1976). The fourth group is the *apneumones*, which are substances emitted by non-living material that are favourable to the receiving organism, but detrimental to an organism of another species that **may** be present in the nonliving material (e.g. substances emanating from food material that attract the predators or parasitoids of insects that are likely to be found in or on the food) (Thorpe and Jones, 1937; Nordlund and Lewis, 1976).

Single chemical substances can be used by insects as information conveying signals. However, the semiochemical signals that insects use are typically blends of several molecules. For instance, the compounds included in a pheromone should not themselves be classified as pheromones, rather pheromone components. In the same manner, I regard kairomones, allomones, synomones and apneumones as the **signal** that convey the information, rather than the individual chemical substances, that constitute the signal. A single chemical substance or chemical blend can be involved in interactions between more than two different species at the same time. Thus, substances (or blends) can be classified as more than one type of semiochemical, depending on which interaction that is considered. If an herbivorous insect is attracted to its host plant by chemicals emitted by the plant, and the chemicals also attract the herbivore's parasitoids, these chemicals act both as kairomones and synomones, in the respective interaction (Nordlund and Lewis, 1976). Another example is the secondary metabolites that are used by plants in the defence against herbivores. These chemicals typically repel insects, but might also be used as attractive signals by specialist insects adapted to consumption of the plant. Thus, the chemicals function both as allomones and kairomones, again depending on which pair of species that is being considered (Whittaker and Feeny, 1971).

In addition to the classification described above, semiochemicals are also classified according to the behavioural responses they elicit in insects. This terminology is presented in Table 1 and adopted from Dethier et al., (1960).

Tab.1. Definitions of chemicals in terms of the responses they elicit in insects (Dethier et al., 1960)

Attractant	A chemical that causes insects to make oriented movements towards its source
Repellent	A chemical that causes insects to make oriented movements away from its source
Arrestant	A chemical that may slow the linear progression of the insects by reducing speed of locomotion or by increasing turning rate
Feeding or ovipositional stimulant	A chemical that elicits feeding or oviposition in insects
Deterrent	A chemical that inhibits feeding or oviposition in a place where insects would, in its absence, feed or oviposit *

* For a detailed classification of deterrents and antifeedants in phytophagous insects, see Månsson, (2001; 2005)

Non-host volatiles – repellent synomones?

The term 'non-host volatiles' (NHV), is a collective term for volatile substances released by non-host plants. Consequently, there are millions of volatiles that can be regarded as NHV for a particular insect species. The term, in itself, says nothing about the responses the volatiles elicit in insects. However, when NHV are studied in relation to insects' host selection behaviour, we often find repellent and/or deterrent compounds, or compounds that in other ways modulate host finding, among the NHV. It should be noted that compounds that exist in large amounts in non-host plants and are regarded as NHV, may also be present in the host plants but in much lower amounts (Zhang and Schlyter, 2004). Non-host volatiles have been found to be repellent and/or deterrent for a number of insect species in various insect orders: e.g. Coleoptera (Schroeder, 1992; Mauchline et al., 2005), aphids (Homoptera: Aphididae) (Nottingham et al., 1991; Hardie et al., 1994; Pettersson et al., 1994; Agelopoulos et al., 1999), Lepidoptera (Khan et al., 2000; McNair et al., 2000; Liu et al., 2005), Diptera (Linn et al., 2005) and Hymenoptera (Gohole et al., 2003).

Applying the semiochemical terminology discussed above, NHV that modulate insect behaviour are best classified as synomones. The insect's host location ability is increased by avoidance of non-host plants. At the same time, the non-host plants benefit by avoiding attacks from phytophagous insects that are not adapted for consumption of that plant species. Whether the effect of NHV on the host seeking insect is repellent and/or deterrent or something else, is often difficult to determine. Usually, when the effect is studied, NHV are presented together with attractive signals, such as pheromones and/or kairomones. So in most cases, it can only be concluded that NHV have 'anti-attractant' effects, and repellency (i. e. insects make oriented movements away from the source) can typically not be demonstrated. However, the range of attraction (R_A) of pheromone baits for the European spruce bark beetle (*Ips typographus*) has been estimated to 10-30 m (Schlyter, 1992), whereas the active inhibitory range (AIR) for NHV has been estimated to 2 m or more (Zhang and Schlyter, 2003). Although R_A and AIR both depends on the absolute and relative amounts of positive and negative stimuli, it is likely that pheromones are active at larger distances than NHV. Thus, at large distances, a host seeking insect is attracted to a source of pheromone release, but upon perception of NHV at a closer distance, the insect might abort its progression towards the source and changes its flight direction away from the source. Therefore, active NHV can probably, in most cases, be classified as repellent signals.

The role of NHV in host selection behaviour have been studied extensively in various conifer bark beetle species (Coleoptera: Curculionidae: Scolytinae) (Figure 2) (reviewed by Zhang and Schlyter 2004). When the repellent effect of NHV on bark beetles' host selection behaviour is discussed, NHV are commonly subdivided into two groups depending on the site of release: (i) green leaf volatiles (GLV) and (ii) non-host bark volatiles. GLV are released in large amounts by broad-leaved angiosperm (Magnoliophyta) trees and herbaceous plants and are mostly aliphatic C_6 primary alcohols, aldehydes and acetates that are derived from the free fatty acids, linoleic and linolenic acid via C_6 aldehydes (Zhang et al., 1999a; Zhang and Schlyter, 2004). However, it has been found that GLV are also emitted from the bark of angiosperm trees (*Betula* spp. and *Populus* spp.) (Borden et al., 1998; Zhang et al., 2000). In contrast to the common presence in angiosperms, GLV are usually found only in trace amounts in coniferous trees. The dominant volatiles released by conifers are mainly monoterpenoids. For angiosperm-inhabiting insects, GLV in general can of course not be classified as non-host volatiles, but still, specific green leaf volatiles might be present or absent in a particular host plant species.

Both common and specific volatiles from the bark of non-host trees might play an important role in host selection by conifer-inhabiting bark beetles. Examples of repellent non-host bark volatiles that have been found in the bark of various species of angiosperm trees are C_8 alcohols, aromatic compounds and the spiroacetal *trans*-conophthorin (Guerrero et al., 1997; Zhang et al., 2000; Zhang and Schlyter, 2004).

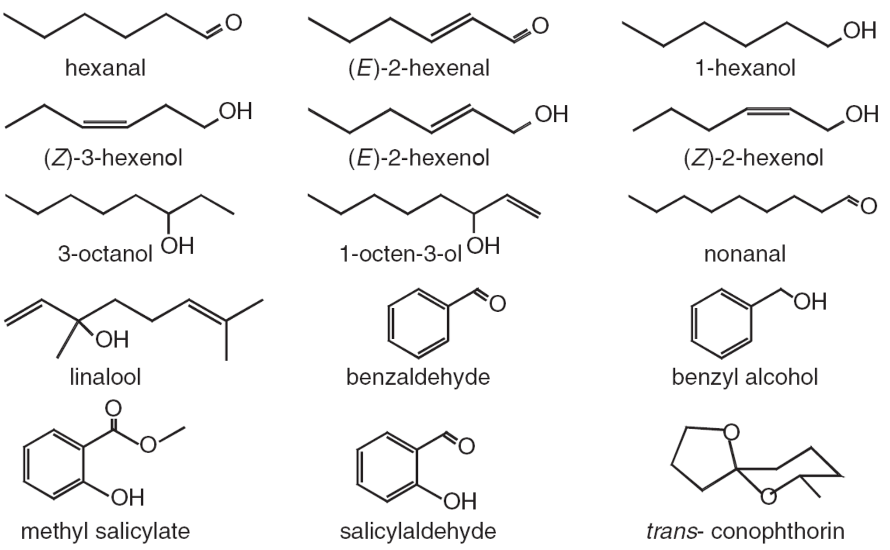


Fig. 2. Major non-host volatiles from bark or leaves of angiosperm trees that are behaviourally or antennally active in conifer-inhabiting bark beetles. Mistakes in the original figure were found and have been corrected (from Zhang and Schlyter, 2004; see http://www-vv.slu.se/fs/sch-pub.htm for corrected version).

Habitat location

Habitat scale and perceptual range

Before discussing general principles of habitat location, the word ‘habitat’ needs to be defined. Lawrence, (2000) defines habitat as “the environment within an organism is normally found. A habitat is characterized by the physical characteristics of the environment and/or the dominant vegetation or other stable biotic characteristics”. Thus, a habitat can be as general as a forest or more specific, such as the bark of a spruce tree. This is important to have in mind when habitat location is described as a step in the process of host selection. Some studies have focused on habitat location at the landscape level, but it is more common that habitat location mechanisms are studied on a smaller scale. Much research has been done on how parasitoids locate the habitat of their host insects. In these cases, the habitat is often regarded as the plants on which the hosts are likely to be found (i.e. not landscape level) (Nadel and van Alphen, 1987; Ngi-Song et al., 1996). In addition, habitat and host location in parasitoids are in principle different compared to phytophagous insects. The habitat a parasitoid searches for is the habitat of its host, typically an infested plant or non-living food material (Vinson, 1976). When the habitat is found, the parasitoid starts to search for a host (a living animal), which later on will serve as the habitat for the developing parasitoid larvae. In contrast, the hosts (plants) of phytophagous insects are the ones that on a larger scale may comprise the major part of the dominant biotype (habitat). In this paper, I will try to use habitat location for the landscape scale in order to more clearly separate it from host location.

General principles of habitat location at the landscape scale in phytophagous insects are not easily found in the literature. A main reason is probably because it is difficult to determine exactly when and at what distance from the host plant the host selection should be regarded as habitat location or host location. It is also possible that insects that are outside a suitable habitat may start to search for a host plant immediately and not first for a habitat. Thus, the mechanisms governing habitat location might be the same as the mechanisms behind long distance host location and the distinction between the habitat and host location level might be diffuse. There are also practical problems with the experimental design because experiments have to be done in the field at a large scale, which, depending on study species, might be difficult and time consuming to perform.

Despite the scarcity of literature on habitat location, it is obvious that some insects will have to disperse from over-crowded habitats, adults could emerge from overwintering pupae that is no longer inside the correct habitat, or an insect might be involuntarily transported long distances by wind or water etc. In these cases, insects must have the ability to locate and orient towards a suitable habitat in order to survive and reproduce. When insects move between suitable habitat patches, they have to cross a ‘matrix’ of unsuitable habitat. For these species, movement behaviour and the distance from which they can detect suitable habitat patches (the ‘perceptual range’ of the insects) are key determinants for individual fitness (Schooley and Wiens, 2003).

Individuals with a poor ability to detect suitable patches will spend more time searching in the matrix than individuals with a large perceptual range. This means that individuals with a poor perceptual range will exhibit a higher mortality risk and reduced mating opportunities. Therefore, natural selection would favour traits that increase the likelihood of finding a suitable habitat. The perceptual range of an individual is not constant, but varies depending on environmental conditions such as size of the target patch, matrix structure (e. g. landscape structure and vegetation) and direction of the target patch relative to prevailing winds (Schooley and Wiens, 2003).

The fact that insects are able to locate highly specific habitats was demonstrated in a study on the whitespotted sawyer (*Monochamus scutellatus*) (Coleoptera: Cerambycidae) (Saint-Germain et al., 2004). This species can only reproduce successfully on heavily stressed trees and is frequently found in recently burned forests. However, during the reproductive phase, adults of *Monochamus* species also need to feed on healthy trees. The results from the study showed that plots of burned forest that had a high percentage of healthy, unburned forest in the proximity were the most intensely colonized. This result suggested that large-scale habitat location mechanisms play an important role in the host selection process, but the sensory cues used in habitat location could, unfortunately, not be determined in their study (Saint-Germain et al., 2004).

Sensory cues for habitat location

In principle, there are two ways for an insect to locate a suitable habitat: (i) by random movements or (ii) by using information available for the insect’s sensory system. Here, focus will be on the latter. Both vision and olfaction can be used in long range location of host habitats and their relative importance varies between species (Schoonhoven et al., 2006). The importance of olfactory cues in habitat location can be exemplified in pine weevils that migrate through conifer forests in order to find suitable breeding habitats. The suitable habitat is patches of forests where dying roots are available, either as parts of trees or as fresh stumps. In Scandinavia, the migration is done by long distance flights guided by olfactory cues. The fact that olfaction is used is evidenced by the large number of weevils that are attracted to large sawmills that process conifer logs (Schlyter, 2004). Another example where olfactory guidance has been suggested as the mechanism for long distance habitat location, comes from a study on cactus bugs (*Chelinidea vittiger*) (Hemiptera: Coreidae), which are phytophagous habitat specialists that inhabit patches of low-growing cactus (*Opuntia* spp.) (Schooley and Wiens, 2003). Cactus bugs were released in unsuitable habitat at various distances from patches of *Opuntia* and the walking pathways towards the patches were observed. The results showed that there was a strong bias for upwind orientation, which suggests that cactus bugs rely on olfaction in order to locate suitable habitats. In addition, the walking pathways were highly directional. This type of movement pattern have been shown, by computer simulation models, to be the most effective search strategy when insects search for suitable habitats in the unsuitable matrix (Zollner and Lima, 1999). Olfaction has also proven to be important in habitat location of predators, for instance, heteropterans (Freund and Olmstead, 2000) and the sevenspotted ladybird *Coccinella septempunctata* (Coleoptera: Coccinellidae) (Ninkovic and Pettersson, 2003).

The importance of vision in habitat location has been demonstrated in the ladybeetle *Chilocorus nigritus* (Coleoptera: Coccinellidae) (Hattingh and Samways, 1995). *C. nigritus* is a predator, but the importance of visual cues in large-scale habitat location is probably not restricted to predators. In this study, the beetles were released inside a closed perspex tunnel that was placed inside a room with the walls painted with various landscape features, exposed to the beetles in different combinations. The position of the beetles inside the tunnel was then recorded over an extended period of time. It was found that *C. nigritus* preferred vertical stripes (simulating trees) over horizontal stripes. The beetles also preferred a horizon with an artificial tree line over a flat horizon (Hattingh and Samways, 1995). Although this study was done inside a lab, and no odours were present, it demonstrates that large-scale landscape features can be used by insects in habitat location.

Non-host volatiles in location of unsuitable habitat

Natural selection would favour insects that have evolved multiple mechanisms for finding their hosts and avoiding unsuitable hosts and non-host species, maximising the use of available information in the environment (Byers et al., 2000). Similarly, the ability to avoid non-host habitats would mean that the insects do not waste time and energy by searching for suitable hosts in areas where host plants are unlikely to be found. However, the role of NHV, or other repellent signals, has not been well-studied at the habitat or landscape level.

In conifer-inhabiting bark beetles, it has been suggested that the general GLV released from leaves of non-host angiosperm trees might serve as a signal of unsuitable habitat (Schlyter and Birgersson, 1999). Avoidance of high concentrations of GLV from non-host trees would allow bark beetles to avoid flying into habitats dominated by non-host trees (non-host habitat). However, this interesting hypothesis cannot be tested until concentrations of volatiles are measured in the forest and compared with physiological and behavioural thresholds (Zhang and Schlyter, 2004). Interestingly, Gilbert et al., (2005) found that infestation levels of the bark beetle *Tomicus piniperda* showed a negative relationship with the amount of edges shared by coniferous and broad-leaved forest patches. This result was interpreted as an effect of the non-host volatiles' disruptive potential on the host-finding process. Similarly, infestation levels of the European pine stem borer *Dioryctria sylvestrella* (Lepidoptera) were found to be reduced in the proximity of mixed-species stands of broad-leaved trees. *D. sylvestrella* is attracted to volatiles from the host tree, maritime pine (*Pinus pinaster*). The lower infestation levels close to broad-leaved stands could therefore have resulted from the 'masking' of the attractant by non-host volatiles (Jactel et al., 2002). However, the authors find this explanation unlikely since the effect was present at distances as large as 300-800 m from the edges of the broad-leaved stands.

The reasoning that NHV can signal unsuitable habitats is not restricted to conifer-inhabiting insects. For instance, the black bean aphid (*Aphis fabae*) is repelled by isothiocyanates and myrtenal, compounds that are present in non-host plants in the Brassicaceae family. It has been suggested that *A. fabae* uses these compounds to avoid a wide range of non-host plants and ecosystems where host plants are unlikely to be present (Agelopoulos et al., 1999). It is also possible that the monoterpenes that dominate coniferous habitats may be a general signal of unsuitable habitat for angiosperm-inhabiting insects, in the same way as GLV signals unsuitable habitat for conifer-inhabiting insects. Indeed, the ambrosia beetles *Trypodendron domesticum* and *Xyleborus* (*Anisandrus*) *dispar*, colonizing dead angiosperm (broad-leaved) trees, respond negatively to α-pinene, one of the major monoterpenes in coniferous trees (Nijholt and Schönherr, 1976; Schroeder and Lindelöw, 1989). However, a possible effect on the habitat level was not studied. In contrast to the general signals, it is more uncertain if specific NHV that can be found in only a few number of non-host species, may serve as repellent signals at the habitat level. Perhaps these signals are more likely to be used at the host location level, when the insects already are in a suitable habitat.

Related to the discussion about the importance of non-host volatiles in habitat location are the results obtained from various intercropping studies. By planting the main crop together with a different plant species (the intercrop), damage from pest insects have often been reduced compared to control plots where the main crop is grown as monoculture. In some studies, it has been proposed that volatiles from the non-host plant repel the pest insect (Khan et al., 2000), or 'mask' the odours from the host plant (Tahvanainen and Root, 1972; Thiery and Visser, 1986). The mechanisms that have been used to explain the results of intercropping studies will be discussed in detail later, under the heading "Proposed mechanisms".

Host location

Inside suitable habitats, a host searching insect must be able to locate a suitable plant species. Most phytophagous insects are specialists, meaning that they only feed on one or a few genera or on a single plant family or subfamily (Bernays and Graham, 1988). Several mechanisms have been proposed to explain the evolution of host specificity, such as reduced exposure to generalist predators, increased chances of mate location, morphological adaptations for hanging on to specific plant surfaces (Bernays and Graham, 1988), increased host finding efficiency (Bernays, 1999) and increased efficiency in detoxifying secondary metabolites (Dethier, 1982). Not only do insects select specific plant species, but also specific plant individuals that the insects find more suitable than others.

Visual cues

Insects might use visual cues to distinguish hosts from non-hosts. Three optical characteristics of plants may influence host selection behaviour: colour, size, and shape (Schoonhoven et al., 2006). For instance, diurnal butterflies have been shown to have preferences for specific flower colours and some dipterans are able to recognize the reflectance properties of their host-plant leaves. Insects belonging to other orders have also been shown to exhibit colour preferences and might also use differences in reflectance intensity between plant species or between leaves and organs within a plant. Tissues of high nutritional quality are often selected. These are often younger tissues, which display a relatively strong reflection in the yellow region. For details, see Schoonhoven et al., (2006).

Olfactory cues and negative signals

Chemical stimuli play a major role in the host location process. Orientation towards a plant and landing may depend on the presence of attractants and arrestants or the absence of repellents emanating from the plant (Figure 3). Relatively inconspicuous constituents are often just as important as the 'typical' chemicals of a plant (Renwick, 1989). For example, the Colorado potato beetle (*Leptinotarsa decemlineata*) is attracted to the specific composition of general GLV of its host (Visser and Avé, 1978). For many insects, negative signals seem to be as important as positive signals. This can be demonstrated by the fact that the attraction to aggregation pheromones (often synergized by kairomones) in more than 20 conifer bark beetle species is inhibited by general green leaf volatiles (Dickens et al., 1992; Schroeder, 1992; Borden et al., 1998; Byers et al., 1998; Zhang et al., 1999b; Byers et al., 2004; Zhang and Schlyter, 2004). In addition, more specific non-host bark volatiles, such as *trans*-conophthorin, 3-octanol, 1-octen-3-ol have also been shown to have inhibitory effects on the attractive bark beetle signals (Zhang and Schlyter, 2003). Thus, the decision to land on a certain plant can be influenced by the ratio between positive and negative signals, or the presence of specific attractants and/or absence of specific repellents.

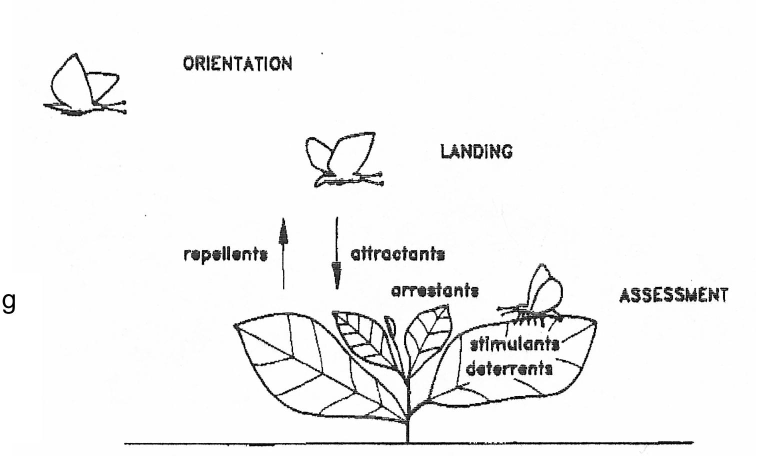


Fig. 3. A schematic drawing of the host selection process in phytophagous insects (from Renwick, 1989).

Factors such as the physiological state or motivation of the insect, environmental conditions, previous experience as well as the presence of enemies and competing individuals can influence the insect's choice to land on a certain plant. (Dethier, 1982; Renwick, 1989; Cunningham et al., 2001; Anton et al., 2007). For instance, overcrowding is avoided by ovipositing female *Rhagoletis* flies by deposition of pheromone on the fruit surface to prevent further oviposition on that fruit (Renwick, 1989). Another mechanism to avoid overcrowding is to utilize the aggregation pheromone of heterospecific, sympatric species as negative signals of host suitability. This has been suggested for bark beetles of the genus *Dendroctonus* that are interrupted by pheromone components from the *Ips* genus (Tømmerås et al., 1984). Bark beetles also use the compound verbenone as a signal of unsuitable hosts. Verbenone inhibits the attraction of bark beetles to their respective pheromone and is derived from α-pinene. α-Pinene is a major monoterpene hydrocarbon constituent of conifers and can be oxygenated by biological agents, such as bark beetles or fungi to form the corresponding ketone, verbenone (Schlyter and Birgersson, 1999). High amounts of verbenone released from a tree indicate that the tree is already colonized and avoidance of such trees is clearly beneficial for the fitness.

Schlyter and Birgersson, (1999) hypothesized that the three different kinds of negative signals (general green leaf volatiles, specific non-host bark volatiles and verbenone) that inhibit the attraction of several bark beetles to their respective pheromone might represent three different levels in the host location process (Figure 4). As discussed above, general GLV might represent the habitat level. In addition, the specific non-host bark volatiles might represent the species level, whereas verbenone is likely to be a signal of host unsuitability. Although there is no direct evidence, the hypothesis gained support by a study performed by Zhang and Schlyter, (2003) who investigated the inhibitory effects of non-host volatiles and verbenone on the European spruce bark beetle, *Ips typographus*. The results demonstrated a redundancy (def: one compound in a blend can be replaced by another compound without change in effect) between compounds within the same (hypothetical) level, while synergism (def: the combined effect of a blend is larger than the sum of the effects of its individual components) was found mostly between the negative signals between the levels.

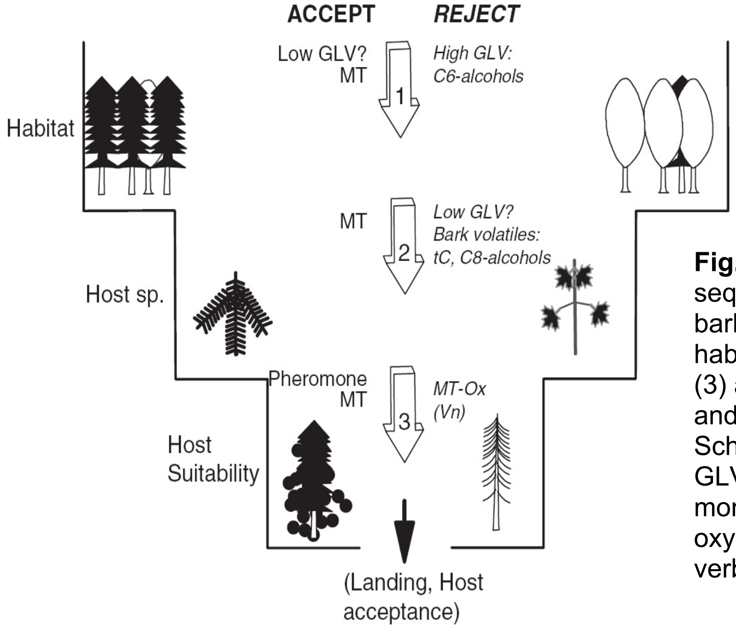


Fig. 4. A hypothetical choice sequence for a conifer-inhabiting bark beetle to find (1) the correct habitat, (2) the right host species and (3) a suitable individual (from Zhang and Schlyter, 2004; modified from Schlyter and Birgersson, 1999). GLV, green leaf volatiles; MT, monoterpene hydrocarbons; MT-Ox, oxygenated monoterpenes; Vn, verbenone; tC, *trans*-conophthorin.

Host acceptance

When an insect has alighted on a particular plant, the suitability of the plant is assessed. The final decision the either accept or reject a plant is often dependent on contact chemoreception and involves an interplay between less volatile stimulants and deterrents. The presence of feeding or oviposition stimulants might trigger feeding or oviposition, while the presence of deterrents can make the insect leave the plant. In few cases, hosts are accepted based on the most conspicuous compounds in the plant, but it is more common that acceptance depends on the presence of mixtures of relatively non-conspicuous compounds that act synergistically (Renwick, 1989). The contact recognition of a plant is often a complex sequence of behaviours that, in addition to chemoreception, also involves assessment of physical characteristics of the plant surface, such as glandular structures and leaf waxes. For instance, contact recognition in the turnip root fly, *Delia floralis*, involves extension of proboscis, walking and running over leaves and stems, and walking at the ground around the stem before oviposition occurs (Renwick, 1989).

Although, the host acceptance step is not the focus of this review, some terminology should be clarified to avoid confusion. A deterrent was previously defined as a ‘chemical that inhibits feeding or oviposition in a place where insects would, in its absence, feed or oviposit’. Hence, in the strict sense, the definition does not imply that the insect must have landed before deterrent chemicals come into play. However, the definition does not say that insects make oriented movements away from deterrent chemicals (as they do upon perception of repellents). Thus, it might be ‘inbuilt’ in the definition that deterrents have their effects after the insects have landed. Chemicals that, when perceived, reduce or prevent feeding, can also collectively be termed ‘antifeedants’. According to Schoonhoven et al., (2006), an antifeedant is the same as a feeding deterrent. However, many different definitions of antifeedants exist. Månsson, (2001) define antifeedants as volatile and non-volatile preingestive inhibitors (compounds that affect orientation, searching and host selection), a group of chemicals that include repellents, arrestants, suppressants and feeding deterrents. For a detailed description, I recommend Månsson, (2001; 2005). Antifeedants have the potential to be used in pest insect control and candidate antifeedant compounds must possess several essential properties (Table 2). However, the properties are fulfilled by few if any of the compounds analyzed so far (Schoonhoven et al., 2006).

Tab. 2. Criteria for antifeedants in crop protection (Månsson, 2001; Schoonhoven et al., 2006).

- No or very low toxicity to vertebrates
- No or very low toxicity to plants
- Active at very low concentrations
- Effective to many pest insect species
- Harmless to beneficial arthropods (natural enemies, pollinators)
- Be absorbable by the plant and translocated through the plant
- Compatible with other pest management methods
- Limited persistence in the environment
- Have low cost and constant supply
- Not result in habituation or resistance
- Be stable during storage
- Be easily applicable
- Not affect taste, smell or appearance of the product
- Not yield toxic metabolites

Short summary of host selection

At this point, it may be helpful to briefly summarize the host selection part of the present review. Basically, at all three steps in the host location process, positive and negative external stimuli interact with each other and also with internal factors in the insect (assuming that host selection is a non-random process). At all levels, the balance between positive and negative stimuli can be tipped towards either acceptance or rejection of a particular habitat or host.

THE ‘STABILITY-DIVERSITY HYPOTHESIS’

An ongoing debate in ecology is whether biodiversity leads to ecosystem stability. Before 1970 it was generally believed that more diverse communities had enhanced ecosystem stability (McCann, 2000). It was proposed that the amount of choice of the energy in going through a food web measures the stability of the system. Hence, more species in an ecosystem would mean that the energy has more alternative ways through the food web and the ecosystem would then be less affected by disturbances (MacArthur, 1955). However, mathematical and statistical models have challenged the theory by showing that diversity tends to destabilize community dynamics (May, 1973). In addition, Doak et al., (1998) stressed that because of statistical reasons, “stability will essentially always rise with species diversity because of statistical averaging of the fluctuations in species abundance”. This is based on a single principle: if community biomass is the sum of the biomasses of many species, then variation in total biomass (the stability measure) will decrease with increased diversity just because of ‘averaging’ of the individual species’ random variations in biomass. This averaging will operate without species interactions and might play a substantial role in explaining the stability-diversity correlations (Doak et al., 1998).

Although the suggested positive correlation between stability and diversity has been criticised from theoretical modelling studies, support for the theory also exist. An early proponent (Elton, 1958) of the theory was inspired by the apparently lower frequency of insect pests outbreaks in complex tropical forests than in simpler communities such as boreal forests. In addition, many studies that have focused on ecosystem stability in agroecosystems, have frequently found that crops grown as monocultures have more pest problems, compared to polycultures. A review of

150 studies showed that diverse agroecosystems had lower pest populations than monocultures in 62 % of the cases (Risch et al., 1983). Until recently, the effects of biodiversity on the stability of forest pest populations have not shown consistent evidence and there are few direct comparisons that have shown the relationship with tree species diversity (Watt, 1992). However, a meta-analysis derived from 54 independent studies showed that in most cases (39), lower tree species diversity resulted in greater insect pest abundance, density or damage (Jactel et al., 2005). Pure stands were compared with mixed stands by calculation of Hedges's *d* effect size. Positive *d* indicates higher insect densities or damage in pure stands as compared to mixed stands, whereas negative *d* indicates the opposite (Figure 5). The results were also analysed with respect to insect taxa. In all taxa except Homoptera, the mean effect size was positive and significant. Of special interest are the large positive mean effect sizes obtained for Lepidoptera and Coleoptera, because forest pest insects in these orders are known to cause most forest damage worldwide (Jactel et al., 2005).

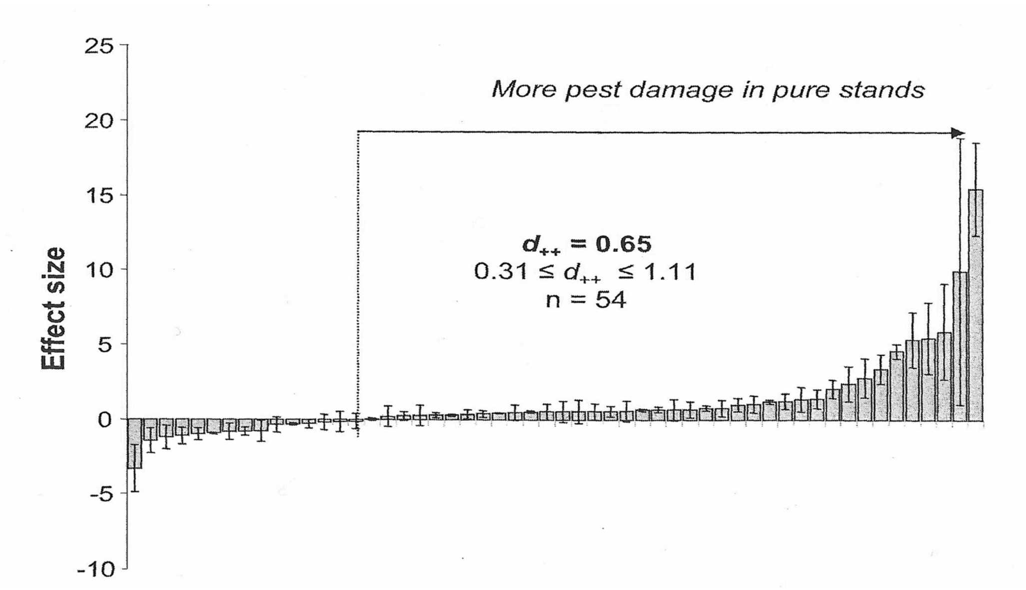


Fig. 5. Hedges's *d* effect size and variance of individual studies on the response of pest abundance or damage to pure vs. mixed stands. In most cases the effect is positive, indicating that lower tree species diversity results in greater insect abundance, density, or damage. Values of d_{++}, the grand mean effect size, are given with the bootstrap confidence interval (from Jactel et al., 2005).

The 'semiochemical-diversity hypothesis'

Based on the findings of the inhibitory effects of non-host volatiles on conifer-inhabiting bark beetles, Zhang and Schlyter, (2003; 2004) hypothesized that as mixed forests have greater semiochemical diversity, they may disrupt host finding and reduce the possibility of outbreaks of conifer bark beetles. This hypothesis was named the **'semiochemical-diversity hypothesis'** and would provide new support for the general 'stability-diversity hypothesis'. However, a test of the hypothesis at the habitat and landscape level will need both long-term and large-scale experiments and observations (Zhang and Schlyter, 2003). Nevertheless, the lower abundance of conifer insect pests near stands of broad-leaved trees (Jactel et al., 2002; Gilbert et al., 2005), might be support for this hypothesis.

EFFECTS OF BIODIVERSITY ON PEST POPULATIONS

It has been known for a long time that growing several crops on the same piece of land often results in yield increases because of the reduced abundance and damage from pest insects. In the tropics, crops are often grown as polycultures and the percentage of cropped land devoted to polycultures is in some places more than 90 %. In contrast, the intensive agriculture in the Western world is dominated by monocultural planting strategies, where only one or a few cultivars are grown over large acreages (Schoonhoven et al., 2006). The word *intercropping* is used to describe systems where more than one crop is grown in one area simultaneously, in such a way that the crops interact agronomically. Intercrops can be grown simultaneously with no distinct arrangement (mixed cropping), as distinct rows (row intercropping), as wider strips (strip intercropping), or one species can serve as a trap crop, which attracts the insects away from the main crop (trap-cropping systems) (Schoonhoven et al., 2006).

Many studies have investigated the effect of increased vegetational diversity in agro-ecosystems, and in most cases, insect herbivores have been found to be less abundant in polycultures compared to monocultures (Risch et al., 1983; Andow, 1991) (Table 3, Figure 6). However, it should be noted that intercropping practices also can increase the abundance of pest insects. Especially polyphagous insects can benefit from increased vegetational diversity (Andow, 1991; Jactel et al., 2005) (Table 3). Despite the high prevalence of intercropping studies, information about the exact mechanisms behind the lower pest abundance in polycultures is often lacking. Typically, the mechanisms that generate the results are not critically tested and possible mechanisms are often only proposed, not determined.

Tab. 3. Relative abundance of arthropod species in polycultures compared to monocultures (Andow, 1991).

	% more abundant	% less abundant	% variable	% no difference	Total no. of species
Herbivores	15	52	20	13	287
Monophagous	8	59	19	14	220
Polyphagous	40	28	24	8	67

Proposed mechanisms

Several mechanisms have been proposed to explain the relatively lower abundance of pest insects in intercropped fields. Some of the mechanisms that explain results from a particular study cannot be regarded as general hypotheses. Examples of such mechanisms can be changes in microclimate parameters (e.g. temperature, humidity and light intensity) that are unfavourable to the pest insect or the pest insect might feed on the intercrop or material from the intercrop etc (Sekamatte et al., 2003). However, some hypotheses exist, which can be regarded as more general theories (explained below). These mechanisms are applicable also to forest-inhabiting insects. In addition, the mechanisms are not mutually exclusive, and it is likely that several mechanisms contribute to reduce pest insect abundance in polycultures. Table 4 presents examples of studies where different mechanisms have been proposed to explain the observed decreases in pest insect abundance and/or damage. Studies where mechanisms have been elucidated in the lab are also shown.

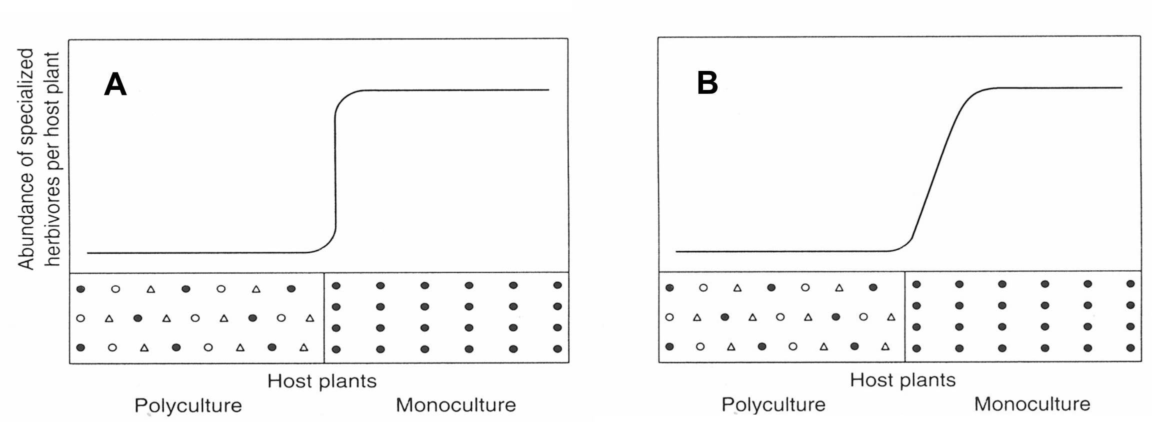


Fig. 6. Effect of polyculture vs. monoculture on the abundance of specialized herbivores per host plant. **A)** An abrupt change in herbivore abundance at the border between poly- and monoculture (from Schoonhoven et al., 2006). **B)** My modification of the figure from Schoonhoven et al., (2006), demonstrating a realistic edge effect. The species diversity in the polyculture affects herbivore abundance in the monoculture close to the border (supported from Gilbert et al., (2005); Jactel et al., (2002); Jactel et al., unpublished). Filled circles = host plants; open circles and triangles = non-host plants.

The 'resource concentration hypothesis'. The theory behind this hypothesis is that herbivores, especially those with a narrow host range, are more likely to find hosts that are concentrated (i.e. that occur in dense or pure stands). Insects that arrive in a clump of suitable host plants will tend to remain in that area. Thus, these patches will have a 'trapping effect' that depends on several factors, such as stand size and purity and the host requirements of the herbivores in the region (Root, 1973). The absolute number of available hosts might be important for species whose population dynamics are resource dependent. Therefore, the 'resource concentration hypothesis' might apply for bark beetle species like *Ips typographus* and *Ips sexdentatus*, which typically develop severe outbreaks the year following a storm (Jactel et al., 2005).

Physical barrier to host location. Insects might be unable to find their hosts because they are physically hidden by non-host plants (Watt, 1992). This hypothesis has been used to describe situations where the non-host plants have been larger or taller than the host plants (Finch and Collier, 2000). In forests, non-host angiosperm trees can reduce host tree discovery by conifer-inhabiting insects (Jactel et al., 2005) and the opposite might be true for angiosperm-inhabiting insects.

Visual camouflage. Insects might have difficult to distinguish host plants against a background of non-host vegetation. Since the predominant colour of most plants is green, hosts become less apparent (visually camouflaged) amongst the foliage of non-host plants (Finch and Collier, 2000). This mechanism can also be applied to forest insects. For instance, females of the pine processionary moth (*Thaumetopoea pityocampa*) use the tree silhouette standing out against a clear background to locate its host tree (Jactel et al., 2005).

Masking of host plant odours. Host plants are believed to be protected against olfactory guided herbivores by the release of 'odour-masking' substances from non-host plants. In complex communities there exist an 'associational resistance' to herbivores (Tahvanainen and Root, 1972). This resistance is not present in monocultures and might explain the higher abundance of pest insects in simplified communities. Yamasaki et al., (1997) define a 'masking' substance as "an agent inhibiting the locomotory movements toward the attractant source". A functional explanation of how 'odour-masking' works have been proposed for the Colorado potato beetle

(*L. decemlineata*) (Visser and Avé, 1978; Thiery and Visser, 1986). The beetle is attracted to the specific GLV composition of its host, potato. However, when potato odour is combined with the odour from wild tomato, the beetles are no longer attracted to the host odour (but still not repelled). The proposed explanation is that the relative proportion of individual GLV components is disturbed, and the beetles do not recognize the odour as a host signal.

Repellent chemicals. The odours given off by a non-host plant repel the searching insect. Aromatic plants have been suggested to be particularly repellent for host seeking insects (Uvah and Coaker, 1984). As previously discussed, non-host volatiles have been shown to repel several insect species in various orders, including many bark beetle species. The 'repellent chemicals hypothesis' and the 'odour-masking hypothesis' can both be incorporated into the 'semiochemical-diversity hypothesis' proposed by Zhang and Schlyter, (2003). It is possible that the 'associational resistance' (Tahvanainen and Root, 1972; Hambäck et al., 2000) that is present in mixed habitats is largely the result of inhibitory non-host volatiles.

Altering the profiles of host plant odours. This mechanism relies upon plants being able to take up root exudates from adjacent plants, which may alter the volatile profile of the host plant. The altered profile would then make the insects unable to recognize their host (Finch and Collier, 2000).

The 'enemies hypothesis'. Natural enemies (i.e. predators and parasitoids) of pest insects are thought to be more efficient in diverse environments because of the greater diversity of prey/hosts and microhabitats. Because of the wide variety of herbivores that become available at different times or in different microhabitats, natural enemies can reach larger population sizes (Root, 1973). The availability of alternative prey and hosts is likely to mostly benefit generalist enemies. But, it has been shown that a better supply of pollen, nectar and honeydew might increase the effectiveness also of specialized predators and parasitoids. In addition, diversified communities provide better habitats for natural enemies because they have a larger variation in microclimates and microhabitats and thus provide better shelter to escape adverse conditions (Jactel et al., 2005). Indeed, a literature survey have shown that 68 (53 %) of a total of 130 natural enemy species had higher population densities in polycultures compared to monocultures, whereas in only 9 % of the cases, lower population densities were observed (Andow, 1991). However, the relationship between diversity and the abundance of natural enemies is complex and it is often difficult to predict how a particular enemy species responds to increased diversity. The response of an individual enemy species is determined by its ecological requirements and is also influenced by the response of its prey or host. For instance, a higher abundance of natural enemies in pure stands has been explained by the accompanying higher abundance of prey in pure stands (Root, 1973). It is also important to note that increased vegetational diversity also can have negative effects on natural enemies. A parasitoid (*Dentichasmias busseolae*) of the spotted stemborer (*Chilo partellus*) were shown to be repelled by the non-host plants (molasses grass) that were used as intercrops to reduce damage to the main crop (maize) (Gohole et al., 2003). In theory, more diverse habitats can also reduce the effectiveness of generalist natural enemies to control a particular pest insect if the enemy species is preferably feeding on other non-pest herbivore species (Jactel et al., 2005).

Appropriate / inappropriate landings. This theory is presented by Finch and Collier, (2000). According to the theory, it is the amount of green non-host material that is responsible for the reduced damage in polycultures. Volatile chemicals emanating from plants are signals to flying insects that they are passing over suitable host plants. This induces insects to land, but since specialist phytophagous insects cannot distinguish between hosts and non-hosts when both are green (Finch and Collier, 2000), insects make a lot of inappropriate landings when different crops are grown together compared to monocultures where all landings are appropriate. Even if an insect lands on a host plant, the stimulants that are perceived by contact chemoreceptors might not be sufficient to arrest the insect. For instance, female cabbage root flies (*Delia radicum*) have to make several 'spiral flights' and land several times on a host plant to receive sufficient stimulation for host plant acceptance. In polycultures, the risk of making an inappropriate landing in the sequence of spiral flights is high, and if it happens, the overall process will then be repeated. Whether insects will remain in an area after they have made inappropriate landings, mainly depends on whether the stimuli released by host plants are sufficiently stimulating to prevent the insects from moving elsewhere (Finch and Kienegger, 1997). In principle, the theory involves a three-link chain of events in which (1) the initial link is governed by host-plant volatiles, (2) the central link (i.e. the decision to land) by visual stimuli, and (3) the final link by contact chemoreception (Finch et al., 2003). Although the theory is developed mainly based on observations on *Delia* flies, the authors claim that it can be regarded as general and it should work for both specialist and generalist insects.

Tab. 4. Some examples of intercropping studies (or studies related to intercropping) where increased biodiversity has shown to reduce (or have the possibility to reduce) pest insect damage and/or abundance.

Reference(s)	Pest insect(s)	Main crop(s) (or hosts)	Intercrop(s) (or non-hosts)	Proposed mechanism(s)	Comment(s)
(Sekamatte et al., 2003)	Termites (*Microtermes* spp.)	Maize	Soyabean Groundnut Common beans	Natural enemies Termites fed on legume litter Physical obstruction	More ants (enemies) in intercropped plots. No evidence of physical obstruction.
(Theunissen et al., 1995)	Mainly: Cabbage moth (*Mamestra brassicae*) Cabbage aphid (*Brevicoryne brassicae*) Cabbage root fly (*Delia brassicae*)	White cabbage	White clover Subterranean clover	Natural enemies Resource concentration Competition with intercrop reduced quality of crop	Many parasitized aphids in intercropped plots. Heads of intercropped cabbage were more compact.
(Uvah and Coaker, 1984)	Carrot fly (*Psila rosae*) Thrips (*Thrips tabaci*)	Carrot (carrot fly) Onion (thrips)	Onion (carrot fly) Carrot (thrips)	Carrot fly: Natural enemies 'Odour-masking' and/or repellent chemicals Thrips: unclear, but perhaps reduced 'apparency' from high carrot densities	Mixing carrots and onions produced a mutually beneficial 'associational resistance'. Carrot fly: Natural enemies alone unlikely. Younger onions more effective than older onions. Responds behaviourally to host compounds.

Tab. 4. cont.

(Skovgård and Päts, 1997)	Lepidopteran stemborers (*Chilo partellus, C. orichalcociliellus* and *Sesamia calamistis*)	Maize	Cowpea	None	Mechanisms not discussed, but a previous study has shown increased parasitism.
(Khan et al., 2000)	Lepidopteran stemborers (*C. partellus* and *Busseola fusca*)	Maize Sorghum	Napier grass and Sudan grass used as trap crops. Molasses grass and legumes (Fabaceae) used as intercrops.	Attractive compounds identified in trap crops Unique and repellent compounds identified in intercrops Natural enemies	One of few studies where the role of volatile chemicals has been studied, both electrophysiologically and behaviourally.
(Nottingham et al., 1991)	Black bean aphid (*Aphis fabae*) Cabbage aphid (*B. brassicae*)	Bean and spindle (black bean aphid) Brussels sprouts (cabbage aphid)	Brussels sprouts (black bean aphid) Bean (cabbage aphid) Winter savory, summer savory, tansy, basil, thyme and sage (both aphid species)	'Odour-masking' Repellent chemicals	Tests done in olfactometer. Tansy repellent to cabbage aphids. Winter savory and thyme 'masked' attraction of black bean aphid to host plant. Isothiocyanates repelled black bean aphids.
(Root, 1973)	Several, including: Crucifer flea beetle (*Phyllotreta cruciferae*) Cabbage butterfly (*Pieris rapae*) Cabbage aphid (*B. brassicae*)	Collards (*Brassica oleracea*)	Several (natural vegetation)	Resource concentration	'Natural enemies hypothesis' also discussed but not supported by the results.
(Tahvanainen and Root, 1972)	Crucifer flea beetle (*P. cruciferae*)	Collards (*B. oleracea*)	Several including: Ragweed Tomato	'Odour-masking' or repellent chemicals	Evidence that non-host volatiles interrupt host finding. 'Associational resistance' reduces outbreaks in diverse vegetations. Natural enemies had no effect on pest population.
(Mauchline et al., 2005)	Pollen beetle (*Meligethes aeneus*)	Oilseed rape	Essential oils from non-host plants: Lavender Peppermint Eucalyptus Geranium	'Odour-masking' or repellent chemicals	Study performed in olfactometer. Repellent chemicals more likely than 'odour-masking'. Lavender most repellent. Potential to develop 'push-pull' control strategy.
(Thiery and Visser, 1986; 1987)	Colorado potato beetle (*Leptinotarsa decemlineata*)	Potato	Wild tomato	'Odour-masking'	Tests done in wind tunnel. Non-host chemicals were not repellent. Potential use in intercropping systems.

Tab. 4. cont.

(Finch and Kienegger, 1997)	Eight pest insect species on brassica crops	Cabbage Cauliflower Brussels sprouts Chinese cabbage	Subterranean clover	Physical obstruction Visual camouflage Appropriate / inappropriate landings	Authors believe mainly in the 'appropriate / inappropriate landings theory'. Chemical involvement unlikely, because many non-host plants with different volatile profiles and paper models have shown to have disruptive effects.
(Nottingham, 1987)	Cabbage root fly (*Delia radicum*) Carrot fly (*P. rosae*)	Cabbage (cabbage root fly) Carrot (carrot fly)	Onion Sage	'Odour-masking' or repellent chemicals	Experiment performed in wind tunnel. Chemicals from onions made host odours less attractive for both insect species.
(Finch et al., 2003)	Cabbage root fly (*D. radicum*) Onion fly (*Delia antiqua*)	Cauliflower (cabbage root fly) Onion (onion fly)	Several including: Low growing bedding plants Weeds Aromatic plants 'Companion plants' Vegetable plants	Appropriate / inappropriate landings	The amount of green material is the important factor. Flies spent more time on non-hosts. Volatiles from non-hosts seem unimportant. Discussion mainly about results on the cabbage root fly.
(Morley et al., 2005)	Cabbage root fly (*D. radicum*)	Cabbage	Clover Artificial clover and cabbage (green cardboard)	Appropriate / inappropriate landings	Flies landed on clover plants and stayed much longer time compared to cabbage. Volatiles from non-hosts seem unimportant.

Case studies

Although many studies have suggested that volatile chemicals from non-host plants may (in part) explain the observed results, it has seldom been critically tested. However, Khan et al., (2000) investigated the role of volatile chemicals from host and non-hosts, mainly on the lepidopteran stem borer *Busseola fusca* (Noctuidae), a species that can cause serious damage to maize and sorghum. Both electrophysiological recordings (GC-EAD) and behavioural tests were done. The objective of the study was to identify repellent intercrops as well as attractive trap crops to incorporate in a 'push-pull' strategy against the stem borers. Napier grass and Sudan grass were found to attract more stem borers than maize did, and were thus chosen to be used as trap crops. In contrast, molasses grass and some legumes (*Desmodium* spp.), when grown as intercrops, reduced stem borer damage. Subsequent GC-EAD analyses demonstrated six antennally active compounds in the trap crops (octanal, nonanal, naphthalene, 4-allylanisol, eugenol and linalool). Each of these was also shown to be behaviourally attractive. The most effective intercrop, molasses grass, contained five antennally active compounds that were absent in the trap crops ((*E*)-β-ocimene, α-terpinolene, β-caryophyllene, humulene and (*E*)-4,8-dimethyl-1,3,7-nonatriene). These compounds were subsequently shown to be repellent to the stemborers (Khan et al., 2000). This study clearly demonstrates that repellent chemicals released by non-host plants can be one of the mechanisms behind the reduced damage caused by increased biodiversity in agriculture.

Not all authors agree that repellent volatiles from non-host plants can explain the reduced damage observed in intercropped plots. In an attempt to make a general theory that would explain the reduced damage frequently observed in polycultures, the 'appropriate/inappropriate landings theory' (explained in detail above) was launched (Finch and Collier, 2000). According to the theory, the role of volatile chemicals is only to indicate for a flying insect that it is passing over suitable host plants, which might stimulate the insect to land. However, the role of repellent chemicals from non-hosts is not appreciated and it is only the amount of green surfaces that surrounds the host plants that disrupts host-plant finding (Finch et al., 2003). The theory has been developed based on detailed analyses on the behaviour of (mainly) the cabbage root fly (*D. radicum*). A detailed study of the host selection and egg laying behaviour of the cabbage root fly and the onion fly (*Delia antiqua*) was done to support the theory (Finch et al., 2003). The host plant used in the experiment was cauliflower (*Brassica oleracea* var. *botrytis*) and 24 different non-host plants were used, including low growing bedding plants, weeds, aromatic plants, 'companion plants' (*Tagetes* spp.) and vegetable plants. Plants with grey and reddish foliage and blue flowers were included among the 24 species.

Because of a more extensive dataset obtained from the cabbage root fly, the results are mainly discussed with respect to this species. The study showed that only four of the non-host plant species failed to reduce the number of eggs laid by the cabbage root fly. These were all relatively low growing. It was also shown that cultivars with reddish foliage were less disruptive than the comparable cultivars with green foliage. Similarly, plants with grey foliage failed to reduce the number of eggs laid by either the cabbage root fly or the onion fly and the plant with blue flowers failed to reduce the number of eggs laid by the cabbage root fly. The results also indicated that 'odour-masking' or repellent chemicals were unimportant since the cabbage root fly landed readily on the leaves of all plants tested and aromatic plants (proposed to be particularly repellent (Uvah and Coaker, 1984)) were not more disruptive than other plants. Finally, the results showed that flies tended to become inactive when they landed on non-host plants and stayed 2-5 times longer on non-host plants. The latter result contradicts the general theory that herbivores typically leave non-host plants more rapidly than host plants (Andow, 1991; Potting et al., 2005). Taken together, the results from this study indicate that the 'appropriate/inappropriate landings theory' explains the observed effects of increased biodiversity on the behaviour of the cabbage root fly (Finch et al., 2003). However it should be noted that Nottingham, (1987) demonstrated that odours from onion affected the orientation of cabbage root flies towards host odour (cabbage) in wind tunnel experiments. While cabbage odour alone stimulated upwind movement, the combination of cabbage odour and onion odour did not stimulate upwind movement more than odourless control. Unfortunately, Finch et al., (2003) did not include onion in their experiments with the cabbage root fly.

One general theory?

The question rises whether it is possible to develop a general theory that explains the lower abundance of pest insects in diversified agroecosystems? The answer is: probably not. Herbivorous insects differ widely in their behavioural ecology, such as colonization pattern, movement and host-plant finding behaviour, and studies have shown that different herbivores respond differently to diversification (Potting et al., 2005). The ability of the insects to make controlled movements towards host plants and the sensory capabilities (perceptual range) of the insects are crucial factors that influence the response to diversification. Small insects, such as whiteflies, aphids and thrips have a very limited ability to control their flight direction and their dispersal is typically governed by passive, random aerial dispersal. For these species, plant recognition usually occurs after the insect has landed. On the other hand, larger insects, such as beetles, moths, and butterflies are strong fliers with ability for directional flight, like upwind towards an odour source. These larger taxa are able to recognize specific habitats and host plants in flight and can use visual or olfactory cues to orient towards host plants. Therefore, the potential to avoid unsuitable habitats, (i.e. intercropped plots) and orient towards more suitable ones (i.e. monocultures) depends to a large extent on which insect taxa that are considered (Potting et al., 2005).

According to Finch and Collier, (2000), the 'appropriate/inappropriate landings theory' can be regarded as general because it involves elements of the other hypotheses. However, I argue that the theory has been supported from studies on too few species for it to be regarded as general. Moreover, there are several studies, in addition to the study on stemborers (Khan et al., 2000), that indicate that volatiles released by non-host plants have disruptive effects on the attraction to host plants. For instance, an intercropping study involving carrots and onions showed that younger (smaller) onions reduced the number of eggs laid on carrots by the carrot fly (*P. rosae*) more than did older (larger) onions (Uvah and Coaker, 1984); 'masking' of host plant odours was clearly demonstrated for the Colorado potato beetle (*L. decemlineata*) (Visser and Avé, 1978; Thiery and Visser, 1986; 1987); and compounds that were repellent to the pollen beetle (*M. aeneus*) were found in several aromatic non-host plants (Mauchline et al., 2005). Furthermore, the repellent effect of NHV has been demonstrated in several other insect species, especially bark beetles (Zhang and Schlyter, 2004) and host selection has been found to be highly affected by the presence of NHV. I suggest that insects that are able to detect and respond to volatiles from non-host plants use them as negative signals to avoid unsuitable hosts and habitats. Of course, other mechanisms probably operate simultaneously to contribute the observed reductions in damage and abundance that might result from diversification. The most straightforward way to investigate the potential effect of repellent or 'odour masking' stimuli form non-hosts is to include electrophysiological recordings and study the behavioural responses to the antennally active compounds present in non-host plants.

Intercropping: effects on habitat or host location?

It is difficult to determine whether increased plant diversity in agroecosystems affects the habitat location or host location level or both. Most studies that have proposed repellent chemicals or 'odour-masking' chemicals as mechanisms to explain the observed lower damage or abundance of pest insects in polycultures, have not determined whether the insects avoid the more diverse habitat or if they enter the habitat but have problems with finding the correct host. For instance, Tahvanainen and Root, (1972) found that the efficiency of host finding and colonization were enhanced by the conditions in the monocultures. Fewer *Phyllotreta cruciferae* were found on collard plants in diverse plots compared to monocultures, but the numbers of *P. cruciferae* present on non-host plants in the mixed habitats were not recorded. This makes it difficult to determine if the pest insects avoided the habitat as a whole or if they just had problems with host finding in the diverse habitats. However, Uvah and Coaker, (1984) recorded the number of female carrot flies that entered the monocultures as well as the intercropped plots and found that the number of females entering the monocultures was greater (144) than the number entering intercropped plots (88). This indicates that the insects' habitat location ability is impeded by the presence of non-host plants (onions) in the diversified ecosystem. Moreover, the 'push-pull' strategy developed to reduce damage by lepidopteran stem borers (Khan et al., 2000) can probably also be related to the habitat location level.

Repellent intercrops were used in combination with attractive trap crops to direct the stem borers away from the 'main crop habitat' and towards the 'trap crop habitat'.

A last example is from a study on the predatory ('natural enemy') sevenspotted ladybird (*Coccinella septempunctata*) (Ninkovic and Pettersson, 2003). Olfactory experiments showed that the ladybird was more attracted to mixed odours of barley and weeds than to barley odour alone. It was hypothesised that the ladybird responds to particular habitat odours before it searches for particular targets, such as attacked plants. If natural enemies are able to respond to habitat odours, herbivorous insects probably also have the ability. Indeed, insects that are able to utilize volatile chemicals emanating from non-host plants as negative signals probably have the possibility to use the signals in order to facilitate both the habitat location and host location steps of the host selection process.

SENSORY MECHANISMS AND OLFACTORY CODING

Overview of the insect olfactory system

As previously discussed, insects rely heavily upon olfaction when searching for hosts, oviposition sites and mating partners. Odours are perceived by olfactory receptor neurons (ORNs) that are located in the sensilla (singular: sensillum) (Figure 7) mainly on the antennae. An olfactory sensillum consists of a multiporous cuticular structure, neurons and accessory cells. The cell bodies of the neurons are typically located beneath the sensillum and the filament-like dendrites protrude into the sensillum and are bathed in the receptor lymph. The cell membrane of the dendrites contains receptor proteins to which odour molecules bind (Mustaparta, 2002). Typically, there are two to five neurons in each sensillum, but in locusts up to 50 neurons can innervate a single sensillum (Schoonhoven et al., 2006). Sensilla are classified according to their morphological form and several types exist (Schneider, 1964). As examples, *sensilla trichodea* ('sensory hairs' typically associated with perception of pheromones) and *sensilla basiconica* ('sensory pegs or cones' typically associated with plant odours) can be mentioned (Mustaparta, 2002).

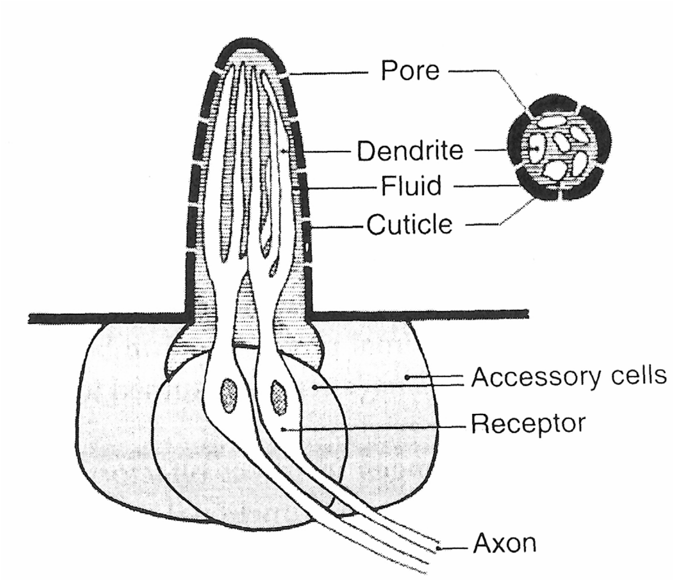


Fig. 7. Schematic drawing of longitudinal and transverse sections of an insect olfactory sensillum innervated by two ORNs (from Schoonhoven et al., 2006).

The axons from the ORNs form the antennal nerve and run without synapses to the primary olfactory centre of the brain, the antennal lobe (AL) (Schoonhoven et al., 2006) (Figure 8). Here, the nerve divides into fascicles and form glomerular structures together with the dendrites of the AL neurones. In the glomeruli, the primary processing of odour information occurs. The number of glomeruli is constant within a species and is thought to be related to the number of different olfactory receptor proteins (Mustaparta, 2002). Plant odours are processed by ordinary glomeruli, whereas pheromone information is processed in the specialized macroglomerular complex (MGC). The neurones of the AL consist of local interneurones with synapses within the AL, and projection neurons that convey odour information to higher brain centra in the protocerebrum (Hallem and Carlson, 2004). The odour information is conveyed from the AL to two major olfactory centra in the protocerebrum, the calyces of the mushroom bodies and the lateral horn of protocerebrum. The mushroom bodies are involved in associative learning, whereas the lateral horn is thought to mediate innate responses to odours (Lin et al., 2007). Descending neurones from the lateral protocerebrum make connections with motor neurons in the suboesophagial ganglion, tritocerebrum, and thoracic ganglia (Mustaparta, 2002).

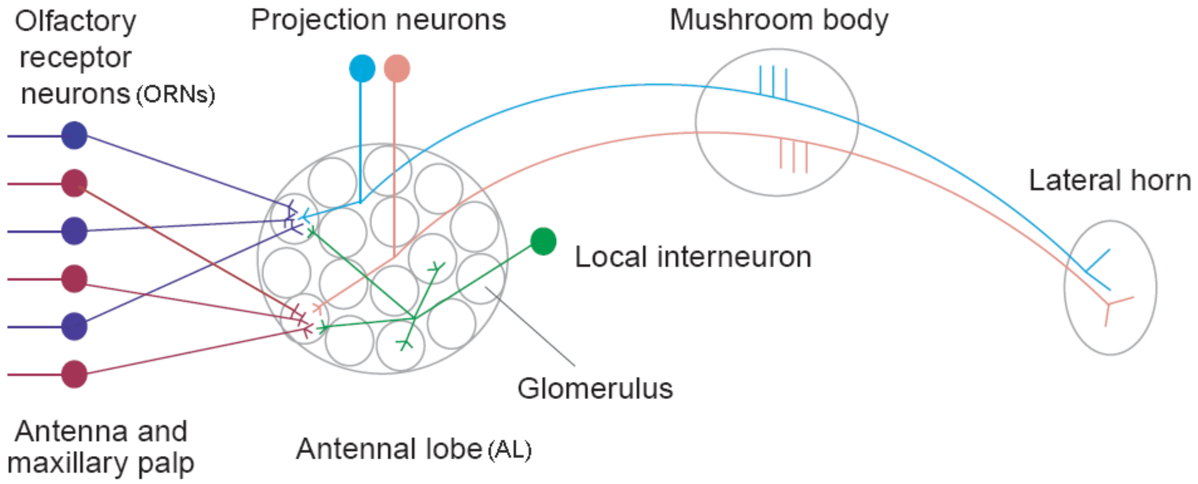


Fig. 8. Overview of the insect olfactory system (exemplified from *Drosophila melanogaster*) (modified from Hallem and Carlson (2004)).

Encoding of odour quality

When odour molecules enter the sensillum lumen, they bind to water-soluble odorant-binding proteins (OBPs) that carry the molecules to the olfactory receptor proteins. Either the odour molecule or the complex of OBP and odour molecule then binds to the olfactory receptor proteins in the membrane of the ORN. Via signal transduction (involving cAMP and IP3), ion channels are opened, leading to depolarization of the dendritic membrane. If the generated depolarized receptor potential exceeds a threshold, action potentials that travel to the glomeruli of the AL, are generated (Schoonhoven et al., 2006). Responses can be both excitatory (increased firing rate) and inhibitory (decreased firing rate) (Hallem and Carlson, 2004). Inhibitory responses have been reported (Mustaparta, 1975; Dickens et al., 1984), but it seems like excitatory responses are more common (Mustaparta et al., 1980; Tømmerås and Mustaparta, 1989; Wibe and Mustaparta, 1996; Hansson et al., 1999; Røstelien et al., 2000; Larsson et al., 2001; Stensmyr et al., 2001). By increasing odour intensity, the firing frequency of the responding ORNs increases (assuming response is excitatory), but odour intensity might also be encoded by recruitment of less sensitive ORNs (Mustaparta, 2002).

With few exceptions (Goldman et al., 2005), one ORN expresses only one type of receptor protein, and ORNs with the same type of receptor project in one or a few glomeruli (Mustaparta, 2002). Since several ORNs may express the same type of receptor protein, there is a high degree of convergence in the AL (Hallem and Carlson, 2004). Therefore, a projection neuron or a local interneuron may reach its threshold for depolarization at a lower concentration than that needed to depolarize a given receptor cell. This convergence is thought to increase the signal-noise ratio between action potentials generated by odour molecules and spontaneous background firing activity from the ORNs (Schoonhoven et al., 2006). Since odours typically consist of a blend of compounds, a given odour generates a specific spatial activation pattern ('fingerprint') of glomeruli in the AL (Hansson et al., 2003). Before the information continues into protocerebrum, the signal between active and quiescent glomeruli is sharpened by means of lateral inhibition from local interneurones (Mustaparta, 2002). However, the local circuitry in the AL and the response characteristics of local interneurones are complex (Ng et al., 2002; Wilson and Laurent, 2005), and recent results have demonstrated that lateral excitation seems to be a common mode of communication among glomeruli (Shang et al., 2007).

Specialist and generalist receptor neurons

Two main categories of receptor neurons have been distinguished, 'specialist' and 'generalist' receptor types. A specialist receptor responds only to one or a few structurally related compounds, whereas a generalist receptor responds to many, structurally unrelated compounds (Schoonhoven et al., 2006). Receptors that respond to sexual pheromones have for a long time been known to be highly specialized. On the other hand, receptors that respond to plant volatiles were previously thought to be of the generalist type, but several more recent studies have shown that plant odour receptors also are highly specific (Hardie et al., 1994; Blight et al., 1995; Wibe and Mustaparta, 1996; Wibe et al., 1997; Røstelien et al., 2000; Larsson et al., 2001; Bichão et al., 2005), and specific responses have been recorded to compounds as general as GLV (Hansson et al., 1999; Larsson et al., 2001; Barata et al., 2002). It is now believed that generalist receptor neurons are relatively rare, but some neurones might still be more selective than others. The reason why the view has changed is explained by the fact that often in the past, too high stimulus concentrations have been used and/or the key stimulus for a specialized receptor neuron was not known (Schoonhoven et al., 2006).

Information about odours can be mediated in two ways. The term 'labelled-line' is related to specialist receptors and describes situations where information about one odorant is mediated by one type of receptor neurone. The opposite term, 'across-fibre pattern' is used when many ORN types mediate information about one odorant (i.e. ORNs are less specific). In some species, ORNs have been shown to have some overlap in response spectra to compounds within the same chemical group, but no overlap between neurons that respond to chemicals of different groups. In these species, plant odours have been interpreted as being encoded by a combination of labelled-line and across-fibre patterns (Wibe et al., 1997; Barata et al., 2002). Although the two coding modes sometimes have been described as mutually exclusive, they are probably the two extremes of a continuum (Schoonhoven et al., 2006).

Encoding of repellent NHV

Two main techniques are used when odours are analysed electrophysiologically: (i) coupled gas chromatographic-electroantennographic detection (GC-EAD) (Arn et al., 1975) and (ii) recordings form single sensilla (single-sensillum recordings (SSR) or single-cell recordings (SCR)). In GC-EAD, the simultaneous occurring receptor potentials from all activated olfactory neurons are measured and recorded as an electroantennogram (EAG). The technique is used to investigate if specific odorants are perceived by the antennae, i.e. if the insect is able to smell the odorants. For instance, GC-EAD has been used to detect electrophysiologically active NHV in several bark beetle species (Borden et al., 1998; Zhang et al., 1999b; Barata et al., 2000; Schlyter et al., 2000; Zhang et al., 2000; 2001; Byers et al., 2004). However, GC-EAD tells us nothing about how the NHV are perceived by specific olfactory receptor neurons. Receptor neuron specificity must be studied by recordings from single olfactory cells. In SCR, the pattern of action potentials (spike activity) in a single olfactory neuron is measured by inserting a microelectrode into a sensillum (Schoonhoven et al., 2006). Relatively few studies have focused on peripheral perception and encoding of repellent NHV, but some studies on aphids and coleopterans can be found. It should be noted that it is important to include both EAG and SC recordings in the same study. Studies have shown that compounds not eliciting EAG responses can be detected by SCR (Blight et al., 1995; Jönsson and Anderson, 1999; Bichão et al., 2005), and some compounds have been found to give EAG responses, but no single cells have been identified (Tømmerås, 1985; Bichão et al., 2005).

Aphids. Nottingham et al., (1991) studied single sensillum responses of the black bean aphid (*A. fabae*) and the cabbage aphid (*B. brassicae*) to host and non-host compounds. Both species were found to have receptors sensitive to several isothiocyanates, compounds primarily found in cruciferous plants. Thus, isothiocyanates are host compounds for the cabbage aphid but are non-host compounds for the black-bean aphid. Behavioural tests showed that the isothiocyanates attracted cabbage aphids, but repelled black bean aphids. The recorded electrophysiological responses were excitatory for both species.

In addition, black bean aphids posses olfactory receptor neurones that respond specifically to two plant-defence related compounds, methyl salicylate and (−)-(1*R*,5*S*)-myrtenal. These compounds repel and inhibit attraction of black bean aphids to the host, broad bean (*Vicia faba*). The repellent NHV were suggested to be indicators of unsuitable hosts or non-host plants (Hardie et al., 1994). Electrophysiological and behavioural responses to methyl salicylate have also been demonstrated in the bird-cherry-oat aphid (*R. padi*). Methyl salicylate was hypothesised to facilitate the alternation between winter and summer hosts (Pettersson et al., 1994). In all cases, ORNs responded by increased firing activity.

Eucalyptus woodborer. The eucalyptus woodborer (*Phoracantha semipunctata*) (Coleoptera: Cerambycidae) is relatively well-studied with respect to SC responses to host and non-host volatiles (Barata et al., 2002; Lopes et al., 2002). By coupling gas chromatography with SCR (GC-SCR), responses to volatiles from host (*Eucalyptus globulus*) and non-host plants (*Pinus pinaster* and *Olea europeae*) were analysed. ORNs responded by increased firing rate to volatiles from all three species. Of the responding ORNs, 48 responded to volatiles from the host, whereas eight responded *exclusively* to volatiles from non-hosts (Barata et al., 2002). Only four compounds from non-host species elicited responses and only one of these (α-cubebene) was identified. Interestingly, the ORNs that responded to non-host compounds seemed to be highly specific, indicating that the compounds are biologically relevant. Behavioural experiments were not conducted, but the non-host volatiles were suggested to function as inhibitory signals in host location (Barata et al., 2002). Behavioural effects of NHV have, on the other hand, been studied in coniferophagous cerambycids, and showed repellent effects of angiosperm bark volatiles (Morewood et al., 2003) and common green leaf volatiles (Suckling et al., 2001). Furthermore, all ORNs in the eucalyptus woodborer that responded exclusively to compounds from non-hosts were found together with a second ORN that responded to host compounds or to compounds common to host and one of the two non-host species (Lopes et al., 2002). This observation was not discussed, but co-localization could perhaps be interpreted as a mechanism to sharpen the contrast between positive and negative stimuli.

Most ORNs (78 %) responded specifically to one or two, major or minor, compounds from host or non-host. Depending on response specificity, ORNs were grouped into one out of three groups: those that responded to monoterpenes, sesquiterpenes and non-terpenoids, respectively. Within the groups, ORNs could further be divided into subgroups of relatively high specificity. There was no overlap in response spectra between the three main groups, but some overlap within each group. This suggests that plant odour information is mediated to the brain both via labelled-line channels for specific odorants and across-fibre patterns for other compounds. Similar results have been obtained for the pine weevil *Hylobius abietes* (Wibe and Mustaparta, 1996; Wibe et al., 1997) and suggest that plant odours are discriminated by a "fingerprint" mechanism, i.e. the relative activity of many ORNs mediate the code to the brain about plant odour quality (Barata et al., 2002). In addition, studies on the pine weevil has found selective ORN responses to carvone and limonene (Wibe et al., 1997), compounds with antifeedant and anti-attractant properties, respectively (Nordlander, 1990; Schlyter et al., 2004). These results are similar to the results obtained for the cerambycids.

Conifer-inhabiting bark beetles. In conifer-inhabiting bark beetles, not much research has been done that reports SC recordings with non-host volatiles. However, there are several studies in which SC recordings on pheromones and host volatiles have been performed. Cells specialized to either pheromone compounds or host plant compounds have been found (Dickens et al., 1984; Tømmerås, 1985). Moreover, ORNs that selectively respond to specific enantiomers have also been discovered (Mustaparta et al., 1980; 1984). It has also been shown that the predatory beetle *Thanasimus formicarius* is attracted to and have specialized olfactory receptors for several bark beetle pheromone compounds and volatiles in spruce bark (Hansen, 1983; Tømmerås, 1985). However, only a few studies on conifer bark beetles have demonstrated electrophysiological responses of single olfactory neurons to volatiles present exclusively in non-host trees. Only in one (Guerrero et al., 1997) have specific non-host compounds been identified. Guerrero et al., (1997) report a cell type in the pine shoot beetle (*Tomicus destruens*) that was tuned to benzyl alcohol, a compound not present in the host tree *Pinus pinea*. At high concentrations, benzyl alcohol was shown to repel *T. destruens*. In the ambrosia beetle (*Trypodendron lineatum*), two cells that exclusively responded to birch bark vapour have been found (Tømmerås and Mustaparta, 1989), and in the European spruce bark beetle (*Ips typographus*), eleven cells were found (eight of these responded also to the pheromone compound *exo*-brevicomin) (Tømmerås and Mustaparta, 1987). In the two studies, the specific non-host compounds were not identified. Table 5 presents SCR studies on the most well-studied coniferous bark beetle species.

Tab. 5. Examples of conifer-inhabiting bark beetle species (Coleoptera: Curculionidae: Scolytinae) that have been shown by SCR to respond to odours of various origins.

Species	Beetle-produced compounds	Host compounds	Non-host compounds	Tested compounds without responses	References
Ips typographus	(+)-ipsdienol (–)-ipsdienol (–)-ipsenol *exo*-brevicomin (–)-*cis*-verbenol (+)-*trans*-verbenol 2-methyl-3-buten-2-ol (–)-verbenone amitinol phenylethanol	myrcene campher pino-camphone	pine bark extract birch bark extract	(+)-*cis*-verbenol (+)-ipsenol (+)-verbenone (–)-*trans*-verbenol *endo*-brevicomin frontalin (+)-lineatin (–)-α-pinene [a] (+)-α-pinene	(Mustaparta et al., 1984; Tømmerås et al., 1984; Tømmerås, 1985; Tømmerås and Mustaparta, 1987)
Ips pini	(+)-ipsdienol (–)-ipsdienol ipsenol *cis*-verbenol *trans*-verbenol verbenone	linalool camphor myrcene		α-pinene 1-octanol	(Mustaparta et al., 1977; 1979; 1980; 1984)
Dendroctonus pseudosugae	(+)-frontalin (–)-frontalin 3-methyl-2-cyclohexenone 3-methyl-2-cyclohexenol 1-methyl-2-cyclohexenol *trans*-verbenol *cis*-verbenol verbenone ipsenol	α-pinene limonene		*endo*-brevicomin camphene ipsdienol	(Dickens et al., 1984; 1985)
Trypodendron lineatum	(+)-lineatin phenylethanol	ethanol methanol butanol α-pinene [b] β-pinene [b] spruce bark extract	pine bark extract birch bark extract	(+)-ipsdienol (–)-ipsdienol (+)-ipsenol (–)-ipsenol 2-methyl-3-buten-2-ol (+)-verbenone (–)-verbenone *cis*-verbenol *trans*-verbenol *exo*-brevicomin *endo*-brevicomin amitinol frontalin propanol	(Tømmerås and Mustaparta, 1989)
Tomicus destruens		compounds in pine extract (data unpublished)	benzyl alcohol (other compounds unpublished)		(Guerrero et al., 1997)

[a] (–)-α-pinene was shown to elicit EAG response, but no single cell was found (Tømmerås, 1985)
[b] Response to a GC-fraction containing α- and β-pinene.

The SCR studies on conifer-inhabiting bark beetles are mainly from the 1970s and 1980s. At that time, not much was known about inhibitory volatiles from non-host trees, which may explain the lack of literature. Today, the number of identified NHV is relatively large and the techniques have improved. Therefore, NHV with known repellent effect could easily be tested on single olfactory sensilla. It would be interesting to investigate if the observed redundancy and synergism reported for *I. typographus* (Zhang and Schlyter, 2003) are reflected in the specificity of the olfactory receptor neurons on the antennae. It is possible that compounds with redundant effects are perceived by the same type of olfactory receptor proteins, whereas synergizing compounds are likely to be perceived by different receptor types. It should also be studied whether integration of positive and negative stimuli occurs in the antennae or in the CNS and if information is conveyed via labelled-lines or across-fibre patterns or both. In most studies on the various species discussed here, the integration of odour stimuli seems to occur in the CNS since compounds most often do not interact at the receptor level (Mustaparta et al., 1977; 1979; 1980; Wibe et al., 1998; Barata et al., 2002). However, a study on the Douglas-fir beetle (*Dendroctonus pseudosugae*) demonstrated that the two pheromone components, 3-methyl-2-cyclohexenone and 3-methyl-2-cyclohexenol stimulated their respective cells while causing a decrease in spike activity, below the spontaneous rate, for the cell specific for the other substance (Dickens et al., 1984). In addition, inhibitory responses have also been observed in the pine weevil (*H. abietes*). Inhibition was mainly observed in cells that were excited by many compounds (Mustaparta, 1975).

CONCLUSIONS AND FUTURE DIRECTIONS

The host selection process of phytophagous insects can be divided into three steps: habitat location, host location and host acceptance. At all steps, acceptance or rejection of a particular site is influenced by positive and negative stimuli that interact with internal factors in the insect. While host location and host acceptance are relatively well-studied, less literature can be found where the habitat level has been studied. Even fewer studies have focused on the role of repellent chemicals from non-hosts at the habitat level.

However, after reviewing the literature, it can be concluded that olfactory guided insects are able to locate highly specific habitats. In addition, the repellent effect of volatile compounds from non-host plants is most intensively studied in conifer-inhabiting bark beetles, but has been demonstrated in several other insect groups. For sure, repellent NHV are influencing host location, but if they are active at the habitat level is not as clear. Still, the hypothesis that NHV might signal unsuitable habitat is supported by intercropping studies that have shown an olfactory based disruptive effect of non-host plants and a lower prevalence of pest insects in the intercropped habitat. Additional support comes from the studies on coniferous pests that showed a lower abundance near edges of broadleaved stands of trees. The fact that compounds from non-host plants are biologically relevant is also supported from electrophysiological studies that have found olfactory receptors, narrowly tuned to compounds exclusively present in non-host plants.

In order to elucidate the role of negative stimuli at the habitat or landscape level, large-scale and long-term field experiments have to be performed. The hypothesis that the negative stimuli of various origins might represent three different levels in the host location process of conifer-inhabiting bark beetles (Schlyter and Birgersson, 1999), should definitely be tested. The hypothesis was supported by an observed redundancy between compounds within the same hypothetical level and synergism between compounds between different levels (Zhang and Schlyter, 2003). However, a critical test cannot be conducted until concentrations of volatiles are measured in habitat air and compared with physiological and behavioural thresholds (Zhang and Schlyter, 2004). Additional problems are that forest ecosystems are large and trees have long generation times, which make them difficult to manipulate. Therefore, a test of the role of repellent NHV in habitat location is probably more easily performed in agricultural ecosystems. Since several mechanisms are likely to operate, and not all species are influenced by volatiles from non-host plants (as evidenced by some intercropping studies), it is important to choose a study species that is known to behaviourally respond to NHV. In addition, intercropping studies typically lack electrophysiological recordings and/or behavioural studies on antennally active compounds. The most straightforward way to analyse the role of chemicals in diversified ecosystems is to include electrophysiological recordings and behavioural tests. Only then can the role of volatiles from non-host plants be determined. I argue that in order to obtain a better understanding of host selection in insects, mechanisms that govern the observed lower pest abundance or damage in polycultures, need to be determined, not only proposed.

Information is also lacking on how repellent NHV are perceived by the insect antennae. Since a large number of NHV has been identified in conifer-inhabiting bark beetles, SC recordings should be done on these species. It is of interest to investigate if the observed redundancy and synergism between different compounds (Zhang and Schlyter, 2003) are reflected in the selectivity of the olfactory receptor neurons. Questions that need to be answered are whether repellent NHV are perceived by specialist or generalist ORNs (i.e. if information is encoded by labelled-line or across-fibre patterns) and if integration of positive and negative signals occurs at the peripheral level or in the central nervous system of the insect. So, by directing research towards small scale electrophysiological recordings as well as large-scale field experiments at the habitat level, a broader understanding of the host selection process in phytophagous insects would be obtained. This information will be useful in semiochemical mediated pest management and in the development of planting strategies to avoid or reduce insect damage.

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