

CHAPTER 6

Host-plant selection: how to find a host plant

6.1 Terminology	136
6.2 Host-plant selection: a catenary process	137
6.3 Searching mechanisms	138
6.4 Orientation to host plants	143
6.4.1 Optical versus chemical cues	143
6.4.2 Visual responses to host-plant characteristics	145
6.4.3 Olfactory responses to host plants	149
6.4.4 Flying moths and walking beetles: two cases of olfactory orientation	149
6.5 Chemosensory basis of host-plant odour detection	152
6.5.1 Morphology of olfactory sensilla	152
6.5.2 Olfactory transduction	153
6.5.3 Olfactory electrophysiology and sensitivity	154
6.5.4 Olfactory specificity and coding	157
6.6 Host-plant searching in nature	158
6.7 Conclusions	160
6.8 References	160

One of the most notable features of herbivorous insects that has emerged from the previous chapters is that most species are very selective feeders and meticulously choose the plants on which they deposit their eggs. Recent research on several species has shown that they select not only certain plant species but also specific plant organs. At the outset of this chapter on selection behaviour it is important to note that the host-plant range of a certain insect species does not necessarily include all plant species that appear under laboratory testing conditions behaviourally acceptable or nutritionally adequate; under natural circumstances it is often more restricted. Also, host selection behaviour may change with the developmental phase of the insect, and different life stages often differ in their host-plant preference or their ability to use a plant species as a host. Despite the fact that neonate

insect larvae have a small body size and consequently possess limited energy reserves, they are capable of leaving the plant on which they hatched if they judge it unsuitable.

There are several situations that make it necessary for a herbivorous insect to search for a host plant. For instance, eclosion of adults from pupae that overwintered in the soil may occur far from potential food or oviposition plants if these are annuals. Arrival in a novel habitat after migration or dispersal, and local exhaustion of food plants, are other examples of such circumstances. In natural habitats, host plants commonly grow together with non-host plants in mixed and complex vegetations. For host-plant specialists, the ability to find and recognize host plants in these habitats is crucial, and this ability constitutes the focus of this and the next chapter.

6.1 Terminology

It is useful first to define terms that are generally used to describe or categorize host-plant selection behaviour.

Searching

Whenever an insect is remote from a potential foodplant, it needs to search for and find that plant. To locate a host plant, the insect needs to move towards it and contact it, or at least to arrive and stay in the proximity of it in order to examine its characteristics further. The observation that the insect contacts the plant, however, gives no information on the mechanism used in establishing this contact. The term 'searching' means 'to look carefully in a place in an effort to find something'. 'Finding' (sometimes unfortunately used as a synonym¹⁰⁴) may rather be the end result of searching—hence the subtitle of this chapter. As searching has a connotation of directionality, it is important to note that the movement pattern of an insect may vary from random, resulting in contact by chance, to oriented and strongly directed movements (see below).

Selection

In the strict sense of the word, 'to select' means to choose from among alternatives. In order to do this, it is necessary that differential sensory perception of alternative food plants occurs. Selection thus implies a weighing of alternatives. From a methodological point of view, it is difficult to prove that comparison of alternatives is being made during selection behaviour, especially if contacts with potential hosts occur sequentially. Sequential contacting of different host-plant species occurs more frequently than simultaneous contacting and this implies that a short-term memory must be invoked to enable comparisons over time. In cases in which alternatives have been assessed before final acceptance occurs, either at a distance by approaching and turning away again or by actual contact-testing, the term 'selection behaviour' is appropriate.

Acceptance

Acceptance of a plant is said to occur when either sustained feeding or oviposition occurs.

'Acceptance' is a term devoid of the assumptions implied by the term 'selection'. For example, when a beetle is released in the middle of a monoculture of beans and is observed to initiate sustained feeding after climbing a bean plant, it cannot be concluded that the beetle selected the bean plant as a host plant, as no alternatives were available. It can only be said that the bean plant has been accepted by the insect. Acceptance is affected by motivation, the general willingness to feed or oviposit, which itself results from the integration of internal physiological state parameters (e.g. level of satiation, maturation state of eggs) of the insect. Acceptance is a term distinct from acceptability, which is a plant trait and defined as the likelihood that a particular plant species is selected for feeding or oviposition.

Preference

When, in dual or multiple choice assays, an insect consistently feeds or oviposits more often on one of the alternative plants, it is said to 'prefer' that plant over the others. This may also be observed under field conditions when the degree of feeding or oviposition on a certain plant species is higher than would be predicted from its relative abundance. Clearly, preference is a relative concept and applicable only to the set of plant species or genotypes that were actually available to the insect.

Recognition

This term is often used in connection with acceptance. It means 'to know again' and implicitly refers to a neural process. It implies that there is an internal standard or 'image' of the plant(s) sought for. This image is present in one or another form in the central nervous system (CNS) of the insect. The profile of incoming sensory information on plant cues is compared with this stored image and, when it matches sufficiently, the plant is recognized as a host. The putative image is genetically fixed, but can be modified by experience to a fair extent (see Chapter 8).

From the above, it appears that the terms searching, selection, preference, and recognition implicitly refer to complex behavioural processes, the neural mechanisms of which are being elucidated (see

below) but as yet are only partly understood. The proper use of these terms is important to avoid confusion between ecologists describing patterns of association and behaviourists addressing mechanisms.¹⁴⁹ Here we use preference as an insect trait that is not influenced by plant density, plant dispersion, or plant quality, unless the insect is learning (see Chapter 8).

It is also important at this point to relate the behavioural terms defined above to the classification of behaviour-modifying chemicals. These chemicals are collectively termed semiochemicals¹¹⁶ or infochemicals.⁵⁰ For this purpose we adopt the terminology proposed by Dethier *et al.*,⁴⁸ which is summarized in Table 6.1. Corresponding terms in semiochemical and infochemical terminology are: kairomone, for attractant and feeding and oviposition stimulants; allomone, for repellent and deterrent. Flower volatiles that attract pollinators (see Chapter 12) are examples of synomones.

The difference between semiochemical and infochemical terminology is that, whereas in semiochemical terminology the origin of the produced chemical determines its designation as a kairomone, allomone, or synomone, in infochemical terminology the adaptive value of the use of the information that the chemical carries is the central issue.

6.2 Host-plant selection: a catenary process

Insects are often said to show ‘programmed behaviour’ and stereotyped, predictable sequences of behavioural acts—so-called *reaction chains*.⁸ This means that more or less distinct behavioural elements follow one another in a fixed order. The insect shows appropriate reactions to a succession of stimuli (Fig. 6.1).

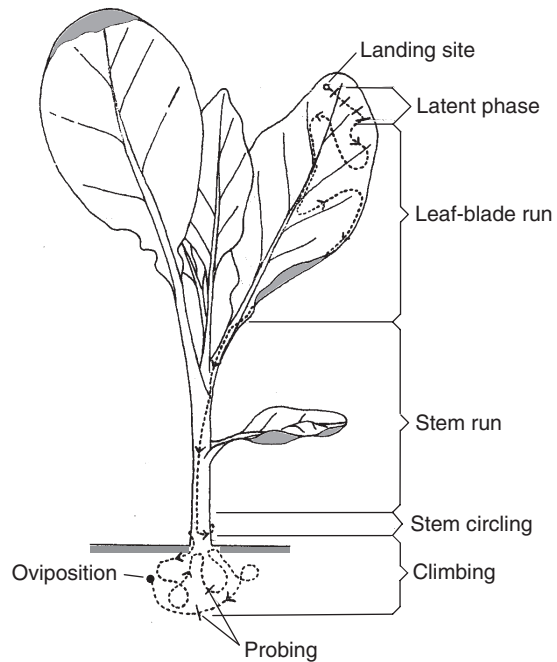


Figure 6.1 Complex behaviour patterns involve a sequence of stimulation and response steps, as exemplified by oviposition behaviour in the cabbage root fly *Delia radicum*. An airborne gravid female fly may land in response to yellow-green wavelengths (500–600 nm), as reflected by green foliage. During the ‘latent phase’ she walks along the leaf, pausing now and then to groom or to make short flights. During the next phase, the ‘leaf-blade run’, she walks continuously, often along the leaf edge and frequently changing direction. With taste hairs on her tarsi she assesses the suitability of the plant. If she contacts the appropriate chemical stimuli, she moves on to a midrib of a leaf or a stem, which is quickly followed (‘stem run’). At the stem base she moves around it sideways (‘stem circling’), keeping her head downwards. During the ‘climbing phase’ she walks around close to the cabbage stem and occasionally climbs up the stem a few centimetres. She then starts ‘probing’ the soil with her ovipositor, probably testing soil particle size and water content. When again the adequate stimuli are perceived, she finally lays her eggs in the soil close to the stem. (From Zohren, 1968.)¹⁸⁹

AQ: Please check the word ‘issue’ used in the para “The difference... issue.”

Table 6.1 Chemical designations in terms of insect responses (from Dethier *et al.*, 1960)⁴⁸

<i>Attractant</i>	A chemical that causes insects to make oriented movements towards its source
<i>Repellent</i>	A chemical that causes insects to make oriented movements away from its source
<i>Arrestant</i>	A chemical that may slow the linear progression of an insect by reducing actual speed of locomotion or by increasing turning rate
<i>Feeding or ovipositional ostimulant</i>	A chemical that elicits feeding or oviposition in insects (‘feeding stimulant’ is synonymous with ‘phagostimulant’)
<i>Deterrent</i>	A chemical that inhibits feeding or oviposition when present in a place where insects would, in its absence, feed or oviposit

When the outcome of a sensory evaluation is rejection of a particular plant or plant part as a food or oviposition site, the herbivore 'jumps back' to one of the earlier steps in the reaction sequence. Modification of selection behaviour as a result of previous experience (see Chapter 8) leads to faster decision-making or to changes in preference, but the sequence remains the same. As we will see from the examples presented below, such sequences of behavioural phases and of elements within each phase can be quite long and elaborate.

In the process of host-plant selection two main consecutive phases may be distinguished, delimited by the intermittent decision to stay in contact with the plant: (1) searching and (2) contact-testing. The first phase may end with the event of finding; the second phase ends with acceptance or rejection. Acceptance is a crucial behavioural decision as it results in ingestion of plant material or deposition of eggs, with possible negative consequences for fitness. A host-plant selection sequence is schematically depicted in Figure 6.2A.

Going through the sequence, the number and intensity of the cues that the plant offers to the insect increase, thereby also potentially increasing the intensity and modalities of sensory information that the insect can collect about the plant. A standardized host-plant selection sequence can be described as follows:

1. The insect has no physical contact with a plant and either rests or moves about randomly, walking or flying.
2. It perceives plant-derived cues, optical and/or olfactory.
3. It responds to these cues in such a way that the distance between its body and the plant decreases.
4. The plant is found, i.e. it is contacted by either touching or climbing it, or by landing on it.
5. The plant surface is examined by contact-testing (e.g. palpation of leaf surface).
6. The plant may be damaged and the content of tissues released by nibbling or test-biting (in the case of biting-chewing species), probing (piercing-sucking species), or puncturing with the ovipositor.
7. The plant is accepted (as evidenced by one or more eggs being laid or continued feeding) or is rejected, resulting in the insect's departure.

During each of these steps the insect may decide to turn away from the plant before contacting it, or to leave it after contact. When it arrives in a patch of potential host plants, it may exhibit repetition of the same sequence with respect to different plant individuals of the same or other species. In the end it may return to and select the plant that was examined first but was left after that initial contact.

In this and the next chapters, host-plant selection behaviour will be discussed using this sequential framework. The focus will be on the different plant cues affecting selection behaviour and the sensory apparatus via which these are perceived and affect selection behaviour. The crucial decision to accept or to reject a plant is based not only on sensory information of plant cues but also on the insect's physiological status (satiety, sexual maturity, egg maturation, etc.¹³). The integration of these two variables, together with information on previous experiences stored in the insect's memory, occurs in the CNS.⁴⁵ For the purpose of this chapter we will assume that the internal status is such that the insect is not engaged in migration or dispersal activity and that its motivation for feeding or oviposition is high.

It should be noted that not all herbivores follow the standardized sequence described above and summarized in Figure 6.2A. Some take short-cuts and others show more complicated sequences. Some well studied examples have been schematized in Figure 6.2B-E.

6.3 Searching mechanisms

To understand the ways in which herbivorous insects search, it is necessary to present a description of searching behaviour as well as a discussion of the possible causal mechanisms involved.

The sequence of behavioural steps that is passed through during searching differs among insect species and developmental phases, and depends on the cues available. The whole range, varying from random search to highly directed search patterns, has been observed. In the field, random search has been described for various insects, such as polyphagous caterpillars,⁴⁶ immature and mature polyphagous locusts,^{2,108} and adult oligophagous Colorado potato beetles (*Leptinotarsa decemlineata*).⁸³

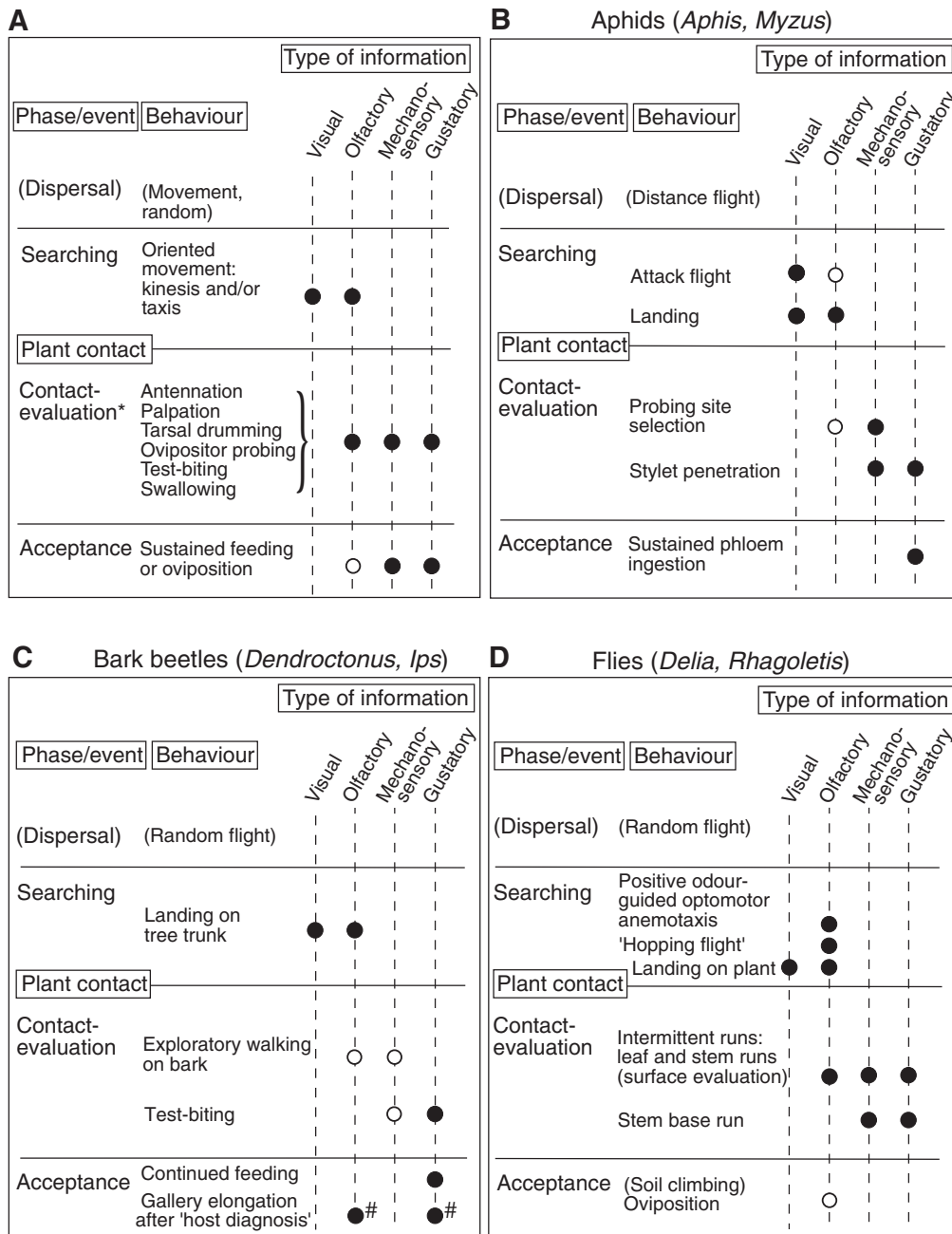


Figure 6.2 (A) Generalized sequence of host-plant selection behaviour of herbivorous insects. *Left column*: behavioural phase or event. *Middle column*: common behavioural elements occurring within a behavioural phase. *Right column*: main plant-derived stimuli affecting the behaviour. Black dot indicates well documented plant cue for several species; white dot indicates suggested or probable; asterisk (*) denotes examples of behavioural elements displayed by many species; not all elements occur in a particular species and not necessarily in this sequence. In parentheses at the top, dispersal is indicated as a preceding behavioural phase with its behavioural elements (which do not belong to the host selection sequence). (B–E) Host selection behaviour sequences of representatives of the four major herbivorous orders, following the scheme of (A), with specific elements and terms. (B) Alate aphids (*Myzus*, *Aphis* spp.). (C) Adult bark beetles (*Dendroctonus*, *Ips* spp.). #Progressive colonization by gallery elongation occurs when repellents or deterrents are absent. (D) Adult herbivorous flies (*Delia*, *Rhagoletis* spp.). For optomotor anemotaxis, visual cues are ground pattern movements, mechanosensory cues are air streams; both not plant-derived. (E) Adult nocturnal moths (*Helicoverpa* spp., *Manduca sexta*); optomotor anemotaxis, as (D). (Compiled from various sources.)

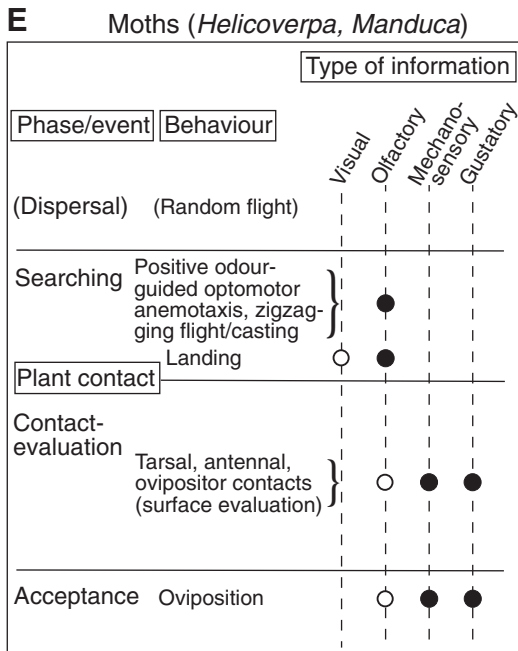


Figure 6.2 (Continued)

In these cases, the frequency, rate, and direction of movement appear unrelated to the acceptability of plants within their perceptual range, that is, the range in which host plant-derived cues are detectable by the sensory system. The generation of random movements can be explained by the functioning of so-called 'central motor programmes' located in the CNS. When an insect becomes motivated to search for food, for example because blood trehalose levels fall below a certain level (an internal-state parameter), these programmes are activated and as a result the insect may start a random walk. Only internally stored (e.g. in memory) and proprioceptive information is used.¹⁷⁹ This searching type may be the best possible, either when environmental cues provide no directionality or when the sensory capacity of the insect is insufficient to obtain the required stimuli. During searching, scanning movements may be performed that serve to increase the probability that a resource is detected along the path, mainly because the path is widened. This is seen in caterpillars moving on the

ground in search of host plants. The caterpillars raise their heads and first thoracic segments, and sway these from one side to the other.

During random searching, several types of orientation response may be performed upon stimulation by plant-derived cues. These responses may be either non-directed or directed. The non-directional changes in random movement are classified as *kineses*.^{89,145} The insect may change its linear speed of movement (orthokinesis) or it may change the rate or frequency of turning (klinokinesis). The intensity of the external stimulus (light intensity, plant odours, humidity, etc.) and the spatial or temporal differences in it determine the strength of these responses. One (unilateral) receptor is sufficient to sense the stimulus intensity by temporal comparisons of incoming sensory information by the CNS. These kinetic responses often lead to area-restricted search (an intensified search in a small area) and arrestment. They are most prominent close to a host plant or upon contact (Figs. 6.3 and 6.4), when the rate of linear movement often decreases and turning rates increase.¹⁰⁷

Directed movement becomes possible when the host plant emits signals that, either alone or in combination with a second cue, allow directionality to be perceived by the sensory system of the searching insect. Movements in this case are directed by sensory information on external cues but may still be under the influence of central motor programmes (see below). When a distinct directionality towards the food plant results from the analysis of movement patterns, such oriented movements relative to an external source of stimulation are termed *taxes*, and may be towards the source (positive) or away from the source (negative). Orientation to visual or chemical cues, or to their combination, is common to many insects. Over short distances, within a few centimetres, in relatively undisturbed, still air, insects may respond to plant odour gradients by positive chemotaxis. This may be achieved either by temporal comparisons of information coming from the olfactory receptors (klinotaxis) or by comparing sensory input coming simultaneously from a bilateral pair of (olfactory) receptors and trying

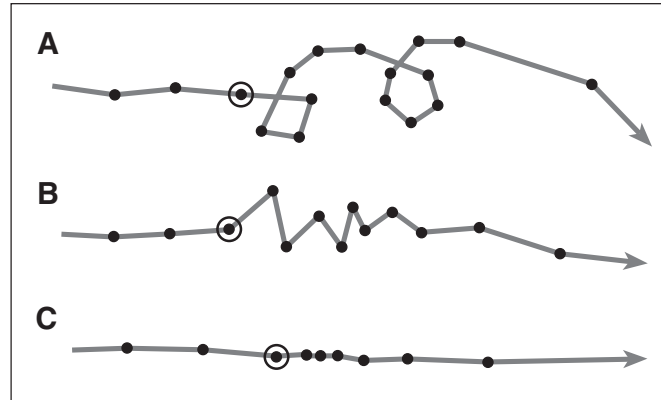


Figure 6.3 Searching patterns used where resources are aggregated. In these cases it may be advantageous for an insect to search an area more thoroughly once it has already encountered a host plant. This strategy increases its chance of finding another host plant. Mechanisms used for restricting the area of search include: **(A)** periodic increases in turning tendency, generating looping or circling; **(B)** alternation in turning direction, generating zigzags; **(C)** adjustments in lengths of moves between stops. Dots indicate landings; circled dots represent landings on host plants followed by egg-laying. (From Bell, 1991.)¹⁷

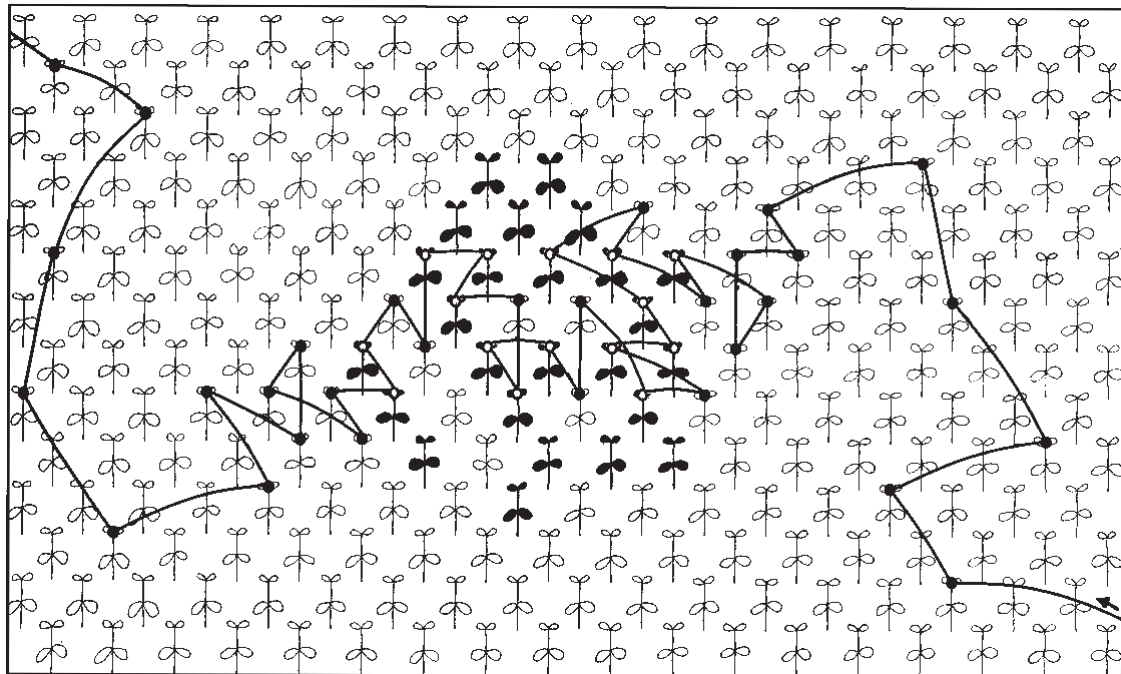


Figure 6.4 Schematized search behaviour in egg-laying females of *Cidaria albulata*, a specialist herbivore on *Rhinanthus* spp. The moths fly shorter distances between alightings and show more turning flight near a host-plant stand, thereby increasing the chance of alighting on a host plant. Turning of flight path and alighting (at least the latter) are stimulated by host-plant odour. Total number of plants, 252; no. of *Rhinanthus* plants, 25 (10%). Total no. of alightings, 45; number of alightings on *Rhinanthus*, 15 (33%). (From Douwes, 1968.)⁵⁵

to obtain equal stimulation of both sides (tropotaxis; symmetrical orientation). A third type of orientation is menotaxis, the maintenance of a constant angle with stimulus direction by preserving a non-symmetrical distribution of sensory stimulation.

Two special cases of menotaxis, *anemotaxis* and *photomenotaxis*, need special attention because they have been found to operate in herbivorous insects. Anemotaxis and photomenotaxis mean oriented movement by maintaining a set angle to the prevailing wind direction or light direction, respectively. Wind or light direction, perceived as air flow by mechanoreceptors or as photon flow by photoreceptors, may be sampled successively at the left

and right sides of the body by serial counterturning movements. Wind direction is detected mechanically by walking insects but mainly visually in the case of flying insects. Anemotactic behaviour, influenced by plant odours, is seen in a number of herbivorous insects under laboratory conditions. In contrast to what might be expected, odorous cues do not exhibit a gradient, required for chemotaxis, at distances greater than a few centimetres (see Section 6.4.4). The movement of air in the outside world is mostly turbulent.¹¹¹ Odour trails comprise complex plumes actually consisting of discontinuous packets of odour molecules that are moving downwind in random direction. A concentration gradient is absent (Fig. 6.5). The best way

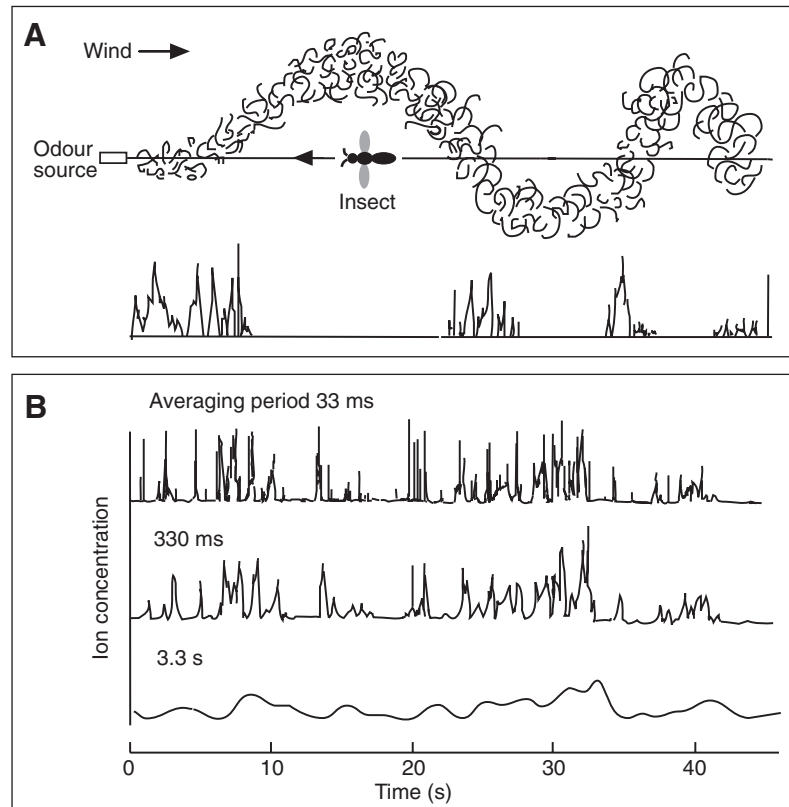


Figure 6.5 (A) Schematic drawing of an undulating and meandering odour plume and an odour signal encountered over time when an insect moves upwind in a straight line to a small odour source. (B) Signal amplitudes generated by a stationary ion probe located in an odour plume when different averaging periods are used. Packets of odour, resulting from air turbulence, pass the odour receiver. Upon increasing the averaging period, differences in signal amplitude decrease, leading to a decreased resolution of concentration differences by olfactory receptors. However, even at an average time of 3.3 s, the signal is still intermittent and the major bursts of the original can clearly be distinguished. (From Murlis, 1986.)¹⁰⁹

to minimize the mean time to discovery of the odour source is to explore actively the area surrounding the packet, by performing transverse movements perpendicular to the mean air flow, to increase the rate at which packets of odour are encountered, and locating the midline of the plume. The odour packets are most likely to originate from a cone-shaped space with the top of the cone pointing upwind. The cone-shaped volume is best explored using a zigzag motion until another packet is encountered. This search strategy utilizes simple behavioural rules for movement, combined with knowledge of mean air speed and direction.¹¹ The resulting movement patterns, casting and zigzagging, match the predictions from theory remarkably well (see Section 6.4.4).

Photomenotaxis, or light compass orientation, is a main mechanism for insects walking on the ground.¹⁴⁵ Although it is difficult to demonstrate anemotaxis in the field, because of lack of control over wind direction and the ubiquitous occurrence of air turbulence, which prevents a consistent directionality and is prominent especially in the boundary layer over the soil surface, the use of photomenotaxis can be investigated relatively simply. One method is Santschi's 'mirror test',¹⁴⁵ and a second method to demonstrate photomenotaxis is the 'turntable test'.⁸³

Although the descriptions of movement types and the way in which plant-derived cues may be used are useful to demonstrate the existence of different searching strategies, the number of documented cases for which the orientation mechanism has been fully analysed is small. Especially under field conditions, combinations of mechanisms, rather than a single one, operate under natural circumstances (see Section 6.6). Alternative or additional classifications of searching patterns can be found in the literature.^{16,177,179} Models of searching behaviour indicate that, contrary to what one might expect, random walking can be a very effective search strategy and that the rate of random movement is an important factor in determining the success of non-random search.¹⁰⁷ Directed orientation is often viewed as adaptive, as it improves the efficiency of search, that is, it produces a higher success ratio per unit of time and energy invested in searching behaviour.

6.4 Orientation to host plants

6.4.1 Optical versus chemical cues

Two important types of stimuli that could be used as directionality cues by herbivorous insects are optical and odorous characteristics of plants. The relative importance of the two varies between species, as becomes particularly noticeable when diurnal and nocturnal species are compared. The two types of stimulus are often used in an integrated way (see Section 6.5).

The nature of optical and chemical plant-derived cues differs in some important aspects. Light can be characterized by its intensity, spectral composition, and polarization. The unit of light energy, the photon, moves self-propelled at the speed of light. The spectral reflectance pattern of a plant is not substantially altered by air movements and is relatively constant at varying distances from the plant. In contrast, volatile compounds emanating from plants move slowly. In still air they move by diffusion and in all dimensions, but in moving air their concentration in space is highly variable (see below). Odour concentrations rise sharply when the plant is approached. Absolutely still air and complete absence of turbulence are very rare, if not completely lacking, under natural circumstances, and wind speeds are mostly greater than the linear speed of diffusion of organic molecules. In moving air (the normal situation), volatiles are carried away from the source with the prevailing direction of air flow and will be dispersed downwind as packets of odour (see Section 6.3).

In the literature the concept of an odour-filled space has been used that, based on Sutton's model of diffusion, has a semi-ellipsoidal shape in moving air. More recently, however, by the use of ion detectors with a short response time, it has become clear that the odour occurs in a stochastic fashion as packets or filaments of molecules in a meandering plume (Fig. 6.5). Outside the plume boundary, which can be visualized by the use of smoke, no odour packets occur. When moving upwind, the insect may contact spatially separated packets of odour molecules at concentrations only slightly lower than those found close to the plant. Most information on the spatial distribution of odorous molecules comes from studies on the distribution

patterns of sex pheromones, which are released from the insect body, virtually a point source. Chapman has stressed the fact that point sources produce odour plumes different from those emanating from big plants or plant patches; clearly, the form of the food source may shape the plume.³³

In summary, when considering abiotic factors, optical plant characteristics are relatively constant with respect to their distribution and largely independent of temperature and wind speed, but of course they depend on light intensity. Odours emanating from plants have a spatially highly variable distribution and concentration, which depends on wind speed, temperature, and to some extent on light intensity. Moreover, the quality and quantity of emitted plant volatiles may vary depending on the plant's physiological state and on whether it is under attack by herbivores (see Fig. 4.7).^{21,160}

Apart from these abiotic factors, the main issues to be considered regarding the relative usability of optical and odorous cues are their specificity and their 'active space', 'effective zone', or 'effective attraction radius'.²⁶

Quite often it has been assumed implicitly that optical cues cannot be used to recognize host plants, for the reason that 'all plants are green' (i.e. the dominant reflectance-transmittance hue is 500–580 nm). In apparent contrast, several plant species have been found to emit volatile chemicals or chemical blends that appear to be taxon specific, either qualitatively (unique compounds) or quantitatively (characteristic ratios).¹⁷⁷ This has probably led to the greater attention paid in the literature to odours as guiding factors in host-plant searching, especially in the case of specialized herbivores. In contrast to the low variability of spectral composition of light reflected by foliage, however, intensity of reflected light may differ more pronouncedly between species, because of the presence of wax crystals or trichomes on the leaf surface, or because of biotic (age, nutrient status) and abiotic (density, incident light intensity, background) factors.

The maximum distance over which plant cues can guide an insect to its host plant is another important factor related to the concept of *active space*. Active space is defined as the space within which the intensity of a stimulus or cue is above

Table 6.2 Distances over which odorous or optical plant cues have been shown to elicit positive taxis-type responses from herbivorous insect species

Insect species	Distance (m)	Reference
Odorous cues		
<i>Leptinotarsa decemlineata</i>	0.6	83
	6	49
<i>Ceutorhynchus assimilis</i>	20	58
<i>Delia radicum</i>	24	63
<i>Dendroctonus</i> spp.	30	181
<i>Pegomya betae</i>	50	138
<i>Delia antiqua</i>	100	85
Optical cues		
<i>Delia brassicae</i>	2	128
<i>Empoasca devastans</i>	3.6	142
<i>Leptinotarsa decemlineata</i>	8	171
<i>Rhagoletis pomonella</i>	10	3

the threshold for a behavioural response. In the absence of visual cues, behavioural responses to plant odours have been demonstrated at distances of 5–30 m for several oligophagous species, with a maximum of 100 m reported for the onion fly *Delia antiqua* (Table 6.2). The fact that some insects can be lured to scented traps suggests that volatile plant compounds may under field conditions attract herbivorous insects, sometimes over large distances. Tephritid fruit flies and diabroticite root-worm beetles can be attracted in large numbers to traps baited with specific blossom aroma components. This applies also to some polyphagous species, such as corn earworms⁷⁷ and Japanese beetles. The latter may be attracted in open areas to such traps from a distance of up to 400 m. In these cases, volatile-baited traps appear to be an effective and sensitive tool for monitoring insect densities.¹⁰²

The significance of values on linear distances and conclusions about active spaces under natural conditions depend heavily on both the biomass and the complexity of the vegetation, factors that have not been varied extensively in field studies on insect host-plant searching. The integrity (unmixed character) of the stimulus produced by an individual host plant or a patch of host plants in a mixed plant stand is thought to be preserved over relatively short distances only,¹⁶² although in some instances odours may remain attractive despite

mixing with other plant volatiles. Thus, gravid beet flies (*Pegomya betae*) are attracted by the odour of young beet leaves over distances of up to 50 m, even if these odours have passed non-host plants.¹³⁸ Optical contrasts in a mixed plant stand may be perceived over distances of a few metres, especially in flying insects. At present, few firm data exist on the size of active spaces based on either optical or odorous signals, and the conclusion that the active space of odorous signals is greater than that of optical cues^{19,128} seems premature. Indeed, under field conditions they always occur together and it will be shown below (see Section 6.6) that insects use combinations of signals, which may enable them to overcome the disadvantage inherent in relying solely on either one.

6.4.2 Visual responses to host-plant characteristics

Three optical characteristics of plants may influence host selection behaviour: spectral quality, dimensions (size), and pattern (shape).¹²⁸ The spectral

sensitivity of insect compound eyes ranges from 350 to 650 nm (near-ultraviolet to red) and thus includes shorter wavelengths than that of the human eye (Fig. 6.6). The ommatidium, the basic photoreceptor and image-formation unit of the insect compound eye, is of a fixed-focus type. This results in maximum acuity at very close range, whereas at greater distances perception of shape is poor. For a more detailed discussion of characteristics of photoreceptors and the sophisticated visual system of insects, the reader is referred to other texts.^{24,153} Although the size of plants or plant parts and their shapes show considerable variation between and within plant species, this variation presumably aids plant selection only at close distances.

To illustrate the extent to which visual discrimination is used in host-plant selection, examples of insect responses to optical host-plant cues, such as shape and colour will be presented.

(a) Lepidoptera

The responsiveness of day-foraging butterflies to colours has been relatively well studied. When

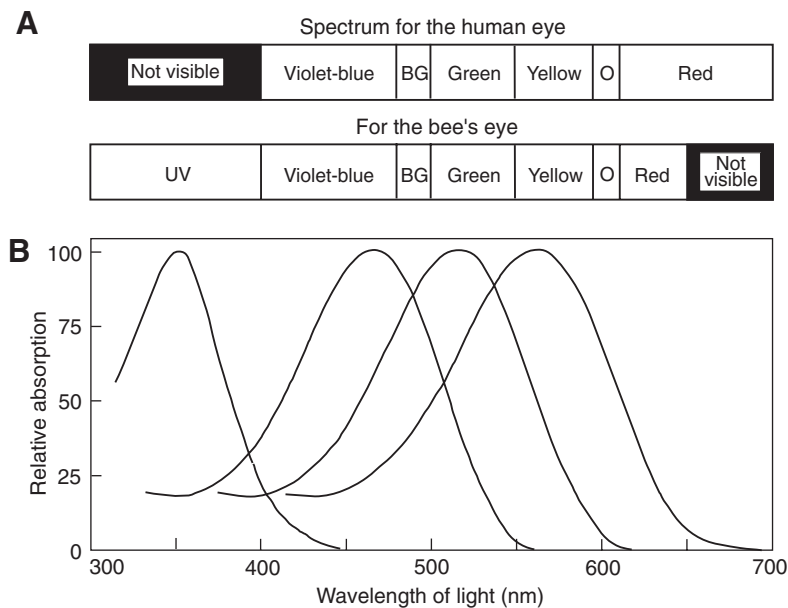


Figure 6.6 (A) Comparison of the wavelength spectra (nm) perceived by humans and honeybees. (Data from Chittka and Waser 1997.)³⁵ (B) Spectral sensitivity curves of a tetrachromatic insect eye (*Spodoptera* sp.). The absorption of each pigment is expressed as a percentage of the maximum for that pigment. (From Langer *et al.*, 1979.)⁹⁷

artificial leaves of green paper are offered to gravid cabbage white butterflies (*Pieris brassicae* and *P. rapae*), naive individuals show landing responses, albeit at much lower frequencies than in response to cabbage leaves. Immediately upon alighting on the substrate they start to 'drum' it for a few seconds, even though specific host-plant chemicals are absent. For *P. brassicae*, true colour vision and wavelength-specific behaviour have been demonstrated (Fig. 6.7), and *P. rapae* clearly showed landing preferences for differently coloured artificial substrates. In both *P. brassicae* and *P. rapae*, associative learning (see Chapter 8) in response to different shades of green has been demonstrated.^{169,174} These butterflies switch their colour preference for landing responses from the green colour of leaves to the yellow, blue, and violet colours of flowers, depending on their motivation for oviposition or nectar feeding, respectively. In the papilionid butterfly *Battus philenor*, discrimination of leaf shape has been demonstrated, and this butterfly uses leaf shape as an

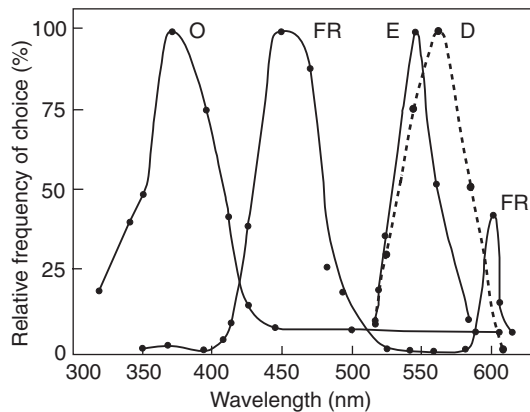


Figure 6.7 Relative effectiveness of different wavelengths in eliciting behavioural responses from *Pieris brassicae* butterflies. The y-axis gives the relative frequency of choice (%), normalized to the maximally visited wavelength (=100%). A so-called open-space reaction (O, lack of response to plants and tendency to increase flight altitude) is induced by wavelengths in the ultraviolet range; a feeding reaction (FR, extension of the proboscis) is maximally induced by blue and to a lesser extent by yellow, and egg-laying (E) and drumming (D) by slightly different wavelengths in the green part of the spectrum. (From Scherer and Kolb, 1987.)¹⁴³

associatively learned signal for preferential landing on host plants.¹²¹ The pierid butterfly *Eurema hecabe* prefers artificial leaves having longer contours, corresponding with the compound leaf shapes of its fabaceous hosts.⁷⁹ The butterfly *Papilio aegaeus*, a specialist of rutaceous plants, responds to the false colours that arise from polarization of reflected light. Its photoreceptors combine sensitivity to colour with sensitivity to polarization, whereas in other insects such as the honeybee these occur in separate ommatidia. Leaf surface traits, such as glossy or glaucous appearance, affect the polarization of reflected light, as do variations in the vertical/horizontal plane of leaf orientation. Perception of false leaf colours might thus guide oviposition site selection.⁸⁸ The nocturnal moth *Mamestra brassicae* prefers to land on medium-sized yellow-coloured artificial substrates that are offered in a vertical position. The combination of an optical target with host-plant odour increases landing probability.¹³⁵

Despite the fact that single rhabdome stemmata of caterpillars are very simple organs compared with the compound eye of the adult butterfly, caterpillars are able to discriminate object sizes and colours, enabling them to orient towards plant silhouettes after dropping to the ground.^{101,132,142}

(b) Diptera

In the case of herbivorous flies among the families Tephritidae (fruit flies) and Anthomyiidae (root maggots), the use of visual cues has been amply demonstrated.¹²⁷ For a flying *Rhagoletis pomonella* female in search of oviposition sites (i.e. apple fruits), the sequence of visually oriented behaviour can be described as a series of consecutive steps. At a distance of about 10 m, a single tree is perceived as a silhouette contrasting against the background. Perception of colour is unlikely at this stage, especially when the insect is facing direct sunlight, as is the perception of details of shape, because of its limited visual acuity. When the fly is at a distance of a few metres or less from the plant and finds itself either in front, under, or above the tree crown, spectral quality and intensity of the reflected light are the main cues evoking alightment on, for instance, foliage, fruits, or trunk. At still closer range (1 m or less), as a third step, detailed

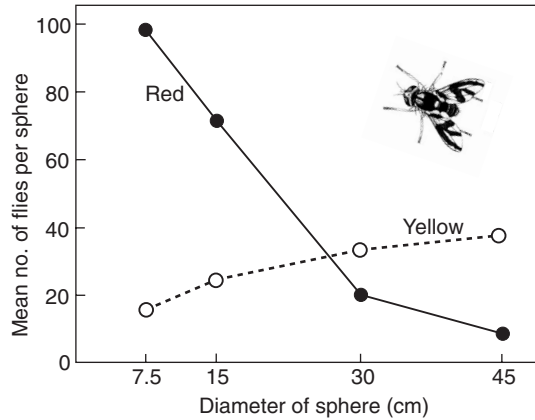


Figure 6.8 Visual responses of apple maggot flies (*Rhagoletis pomonella*) to red and yellow odourless sticky spheres of increasing diameter under orchard conditions. Visual preferences were measured on the basis of catches of flies on the spheres. A red sphere of 7.5 cm in diameter matches the size and colour of a ripe apple. The higher number of flies caught on larger yellow spheres is interpreted as a response to a supernormal substitute stimulus for the green of leaves, on which the flies search for aphid honeydew as a source of energy. (From Prokopy, 1968.)¹²⁶

discrimination on the basis of size or shape becomes possible (Fig. 6.8).

In the cabbage root fly *Delia radicum*, visually based landing responses occur when the flies are offered artificial leaves that have been painted with colours mimicking host-plant leaf reflectance profiles (Fig. 6.9). When spectrally matched artificial leaves of three different host plants were offered simultaneously with the real leaves, no landing preferences were found. The flies shifted their preferences with plant age. The overriding preference for radish in the mature plant stage was much less pronounced in the young plant stage and this correlated with smaller differences in reflectance properties between the three host plants. During the post-alighting phases of host selection, leaf shape does not seem to influence oviposition, but artificial leaves possessing a stem are clearly preferred over those lacking one (Fig. 6.10).

When the flies were allowed to choose between different sizes of artificial leaf, the one that was four times as big was also landed on four times as often and received 2.5 times as many eggs.^{130,133} Colour preferences of a polyphagous and an oligophagous species of tephritid *Bactrocera* fruitflies were clearly

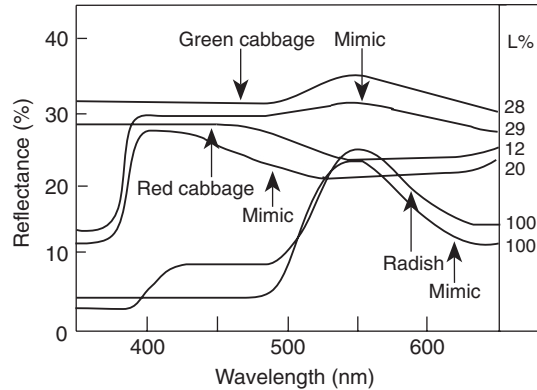


Figure 6.9 Reflectance properties of leaves of different cruciferous host plants and landing responses of cabbage root flies (*Delia radicum*) to real leaves or artificial mimics of these. Landing responses (L%) are expressed as the percentage of landings relative to radish, the plant on which the flies landed most frequently in a multiple choice test. Alternative host plants were green cabbage and red cabbage. In direct comparisons of real leaves and their mimics, flies landed with equal frequencies on both. Vertical axis gives the percentage of reflectance of incident light. (Redrawn from Prokopy *et al.*, 1983a.)¹²⁹

different. The polyphagous species *B. tryoni* preferred blue artificial spheres reflecting ultraviolet light (UV) over spheres lacking this reflectance.⁵⁶ This UV sensitivity is functional, as ripe natural host fruits have heavier waxblooms causing stronger UV reflection. Clearly plant colour, shape, and size play important roles in the host selection behaviour of these herbivorous flies, which belong to the best studied species in this respect. Visually guided behaviour is also influenced by odour perception (see Section 6.6).

(c) Homoptera

Attraction to the colour of foliage has been studied extensively in aphids and whiteflies.^{37,91,106} These small insects can generate only small motoric forces, and at wind speeds exceeding 1 m/s they are unable to maintain their airspeed against the wind direction. They are able, however, to exert active control over their groundspeed.⁸¹ Alate (i.e. the winged morph) aphids can still exert control over their transport by active taking off and alighting. The main factor that elicits an alighting response is the perception of plant colours. Thus *Brevicoryne brassicae* and *Myzus persicae* alight in the field

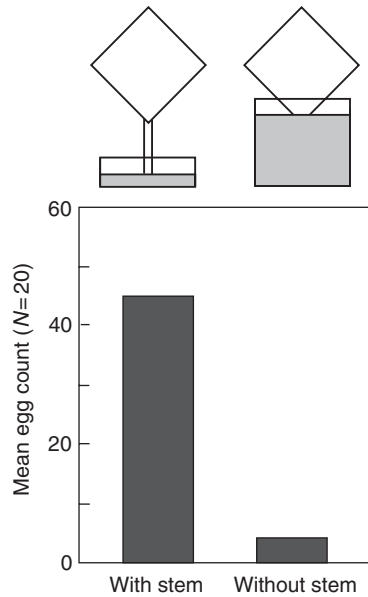


Figure 6.10 Effect of the presence of a stem as a morphological feature of artificial leaves on oviposition preference of cabbage root flies (*Delia radicum*). Artificial leaves (13 × 13-cm pieces of green paper dipped in paraffin and sprayed with a surface extract of cabbage leaves) of each type were offered together in the same test arena. (From Roessingh and Städler, 1990.)¹³³

preferentially on leaves reflecting a greater proportion of long-wave energy, with little or no regard for the taxonomic status of the plants. As sugar beet leaves have a higher 'long/short-wave ratio' than cabbage leaves (Fig. 6.11), more cabbage aphids alight on sugar beet leaves than on cabbage, although the former is not one of its hosts. 'Long/short-reflectance ratios' change with leaf age and water status. The colour attraction of these 'yellow-sensitive' aphid species serves to bias their landings towards plants of the appropriate physiological type rather than to recognize their host-plant species.⁹¹

Likewise, *Aphis fabae*, which alights three times as commonly on beet *Beta vulgaris* plants as on reed (*Phragmites communis*), has a preference for saturated yellow, which more closely resembles the reflectance profile of *Beta* leaves (Fig. 6.12). The mealy plum aphid *Hyalopterus pruni* displays so-called host alternation (see Section 8.4.1) between its summer host *Phragmites* and its winter host *Prunus* spp. Alates, which search for *Phragmites* in

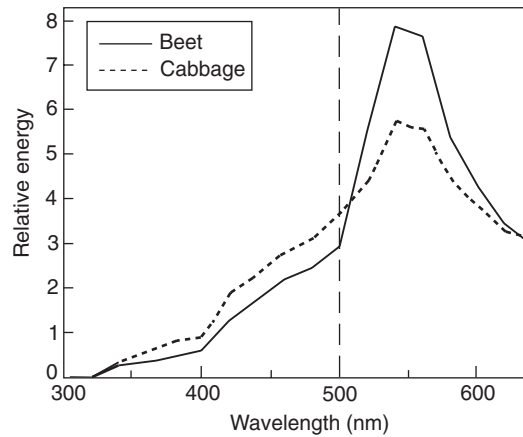


Figure 6.11 Relative energy curves of light reflected from the upper surfaces of mature leaves of sugar beet and cabbage in July under direct sunlight. The ratio between the areas under the curve to the right and left of the dashed line at 500 nm (the 'long/short ratio') is 3.2 for beet and 2.1 for cabbage. (From Kennedy *et al.*, 1961.)⁹¹

the spring, alight twice as often on reed plants than on adjacent non-host beet plants.¹⁰⁶ Discrimination between these two plant species is done in this case on the basis of a lower degree of saturation of the yellow reflectance of the *Phragmites* blades compared with that of *Beta* leaves. Thus, the visually based response to colours and reflectance intensity is species specific. Whiteflies avoid settling in the presence of short-wavelength illumination (400 nm), but will alight on green light (550 nm).³⁷ As with butterflies and flies, plant-surface wax loads may also affect visually guided host-plant selection behaviour in aphids. Early in the season, alates of the pea aphid *Acyrtosiphon pisum* are found at lower density on an isoline of pea *Pisum sativum* with reduced surface wax than on peas with a standard surface wax bloom.¹⁸⁴

Not only lepidopteran, dipteran, and homopteran insects, but also species belonging to other orders, use differences in reflectance intensity between plant species, or between leaves or organs within a plant, as a visual selection criterion for more nutritious tissues. These are often younger tissues, which display a relatively strong reflection in the yellow region. In fact, most diurnal insects are attracted to yellow. In many cases yellow surfaces act as a 'supernormal' stimulus, because

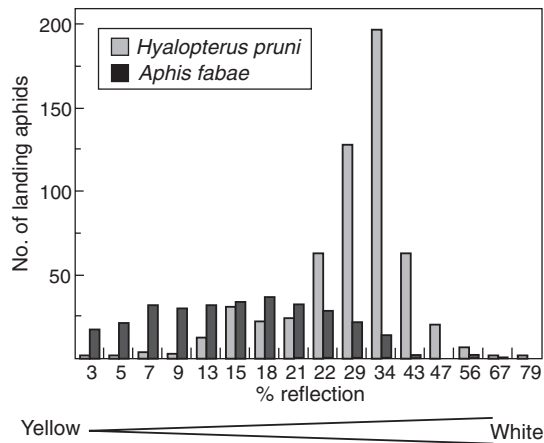


Figure 6.12 Visual landing preferences of two aphid species (*Hyalopterus pruni*, the mealy plum aphid, and *Aphis fabae*, the black bean aphid). Preference was measured as the number of alate aphids that landed on each of 16 plates, which together constituted a graded series from yellow to white colours with increasing reflection in the short wavelength band (decreasing saturation from left to right). (From Moericke, 1969.)¹⁰⁶

they emit peak energy in the same bandwidth as foliage, but at greater intensity.

Although there is a large body of information on the mechanisms of insect photoreception, our knowledge of the visual performance of herbivorous species in the field is limited relative to what is known about olfactory performance, discussed in the following sections.

6.4.3 Olfactory responses to host plants

When attempting to test the separate role of visual stimuli, test insects are exposed to objects with controlled optical characteristics, which are odourless. Conversely, to assess the effect of odours alone on orientation to host plants, the visual surroundings in which the odour tests are carried out should be homogeneous. For experiments in the laboratory, several set-ups have been developed that allow quantitative studies of orientation responses to odours (see Appendix C2).⁶¹ As discussed above (see Section 6.4.1), control over an odorous stimulus in terms of concentration and distribution is usually less exact than is often assumed. We will discuss in more detail two examples of orientation mechanisms to odours as

demonstrated under laboratory circumstances, one of a flying insect and one of a walking insect.

6.4.4 Flying moths and walking beetles: two cases of olfactory orientation

When a flying female tobacco hornworm moth (*Manduca sexta*) is searching for a host plant, she displays positive anemotaxis, that is, she flies upwind using the prevailing direction of air flow as a cue. Mechanoreceptors located on her antennae and serving as anemoreceptors provide this directional information (either by klinotaxis or tropotaxis; see Section 6.3). Her flight path can be described as a regular zigzag (a series of counterturns) of limited amplitude.

How does the odour emitted by the tobacco plant come into play? First, the host-plant odour may have acted as an activator (arousing agent) for flight to occur, by inducing the moth to take off from a resting or walking condition. Once in flight, she may pick up an odour plume emanating from one or a group of host plants, and her subsequent flight path is then determined mainly by trying to prevent loss of the odour plume. When, over a certain minimum time interval, olfactory receptor cells do not detect odour, a so-called 'casting' response ensues. The moth reduces speed and increases the amplitude of the counterturns, thereby flying more across wind and regressing in a downwind direction. When, during casting, odour molecules are picked up again by the olfactory sensilla, upwind zigzagging is resumed. This sequence of behavioural acts may be reiterated until final approach of the host plant. Closer to the odour source the intervals between counterturns decrease. This host-searching mechanism is designated as odour-conditioned (or odour-modulated) positive anemotaxis.

The female's host-plant searching behaviour is in fact very similar to the odour-modulated upwind flight of male moths in search of a female.¹⁰ In the latter case the odorous signal is a sex pheromone emitted by the female. A present view of the mechanisms steering this behaviour maintains that the serial counterturning is controlled by a motor programme in the CNS that is set in motion by olfactory activity, but afterwards is continued automatically (self-steered).¹⁸⁷ The switch from zigzagging to

casting, however, is controlled by olfactory information: absence of activity changes in the odour receptors over a certain minimum timespan causes casting behaviour. Upwind progress is made possible by optomotor feedback, that is, the flow of visual images of the surroundings, mainly the ground, controls the motor response via a feedback loop.

The female is able to maintain the parameters of its flight path (ground speed, track angle) and counterturning frequency close to some apparently preferred values over a range of wind speeds. Odour-conditioned anemotactic flight enables directed flight to an odour source and is basically different from the relatively straightforward chemotactic orientation to odour gradients. It has probably evolved because, as we have seen, such gradients do not exist over any distance in the field. Behavioural mechanisms employed in sex pheromone-guided mate-finding in male insects have been relatively well studied,⁵⁹ including temporal and spatial aspects.⁹⁴ However, information is still scanty for orientation mechanisms to plant odours under field circumstances.^{100,187} One of the best studied cases of the ability of a walking insect to orient to host-plant odours is the Colorado potato beetle *Leptinotarsa decemlineata*.¹⁷⁷ This specialist on solanaceous plants has a strong preference for the cultivated potato *Solanum tuberosum*, on which it is one of the most devastating insect pests. During the first 7 days of adult life the beetles need to feed in order to develop their flight muscles fully and, as a consequence, host-plant location is done by walking. To quantify their walking behaviour, a 'locomotion compensator' in combination with a wind tunnel has been used. This instrument allows detailed and automated recording of walking tracks without the insect contacting any obstacles (see Appendix C2).

When clean air is blown over a hungry beetle, it shows a menotactic response to the wind (anemotaxis), maintaining a relatively constant angle to the wind direction (Fig. 6.13). The walking track shows circling by making turns of 360°. When the air-stream carries the odour of intact potato plants, the straightness of the path increases dramatically. Now that circling is absent, average walking speed is increased and the beetles spend more time walking upwind. This response can be classified as

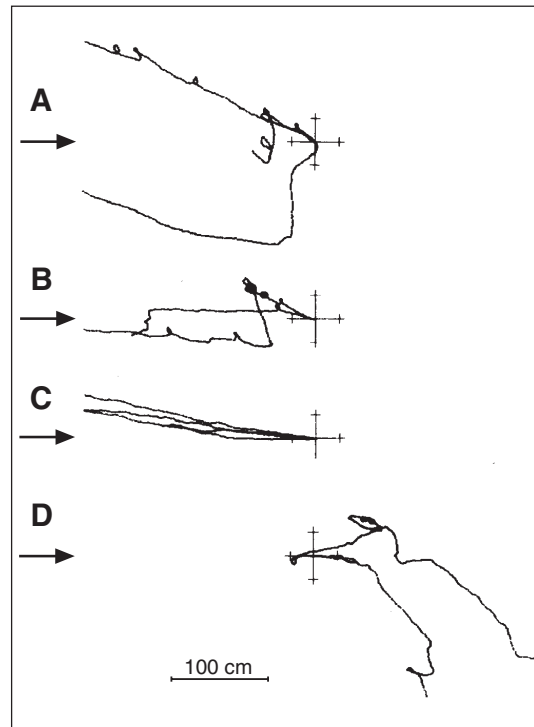


Figure 6.13 Walking tracks of an individual female Colorado potato beetle (*Leptinotarsa decemlineata*) during four consecutive periods (A–D) of 10 min. The stimulus situations were: (A) clean air stream; (B) air stream carrying the odour of cabbage (*Brassica oleracea*) plants; (C) air stream carrying the odour of potato (*Solanum tuberosum*) plants (the favourite host plant of the beetle); (D) air stream carrying a mixture of odours emanating from cabbage and potato. Arrows indicate the direction of the air stream. The plotter reset the position of the beetle to the origin (centre of cross) after a certain maximum distance had been travelled. Total distance travelled and track straightness are significantly higher for (C) than for the other three situations, which do not differ from one another. (From Thiéry and Visser, 1986.)¹⁶²

positive (i.e. upwind) odour-conditioned anemotaxis. When the odour of non-hosts, for instance cabbage plants, is offered, the track parameters are similar to those recorded for clean air. When the odour of potato plants is combined with that of cabbage plants, the orientation response to potato is neutralized and the walking tracks of the beetles cannot be distinguished from those performed in clean air (Fig. 6.13).

Somewhat unexpectedly, similar effects were found when the odour of another solanaceous plant, wild tomato (*Lycopersicon hirsutum*

Table 6.3 Selected cases of adult herbivores belonging to four major insect orders that display behavioural responses to plant odours; the insect's host-plant specificity, type of odour source, test environment, and availability of sensory data are indicated

Order and Species	Specialization category ¹	Odour source ²	Type of test environment ³	Sensory data ⁴	Reference
Hemiptera					
<i>Phorodon humuli</i>	M	G	L/F	SCR	28
<i>Cryptomyzus korschelti</i>	O	HP	L		180
<i>Cavariella aegopodii</i>	O	G	F(T)		34
<i>Lipaphis erysimi</i>	O	S	L	SCR	118
<i>Brevicoryne brassicae</i>	O	S	L(F)	SCR	118, 123
<i>Rhopalosiphum padi</i>	O	G	L(F)		122
<i>Aphis fabae</i>	P	HP	L(F)	SCR	90, 118
<i>Aphis gossypii</i>	P	HP	F		125
Coleoptera					
<i>Leptinotarsa decemlineata</i>	O	HP/G	L(F)	EAG/SCR	98, 162, 176
<i>Anthonomus grandis</i>	O	G	L/F	EAG/SCR	52, 53, 54
<i>Ips typographus</i>	O	G	L/F	SCR	105, 168
<i>Phyllotreta</i> spp.	O	S	L/F		124
<i>Ceutorhynchus assimilis</i>	O	S/HP	L/F	SCR	22, 58
<i>Popillia japonica</i>	P	G	F		1
<i>Listroderes obliquus</i>	P	G/S*	L		99
<i>Oreina cacaliae</i>	O	HP/HPE	L		86
<i>Phyllopertha diversa</i>		G	L	SCR	74
<i>Hylobius abietis</i>	O	HPE	L	SCR	186
Diptera					
<i>Psila rosae</i>	M	S	L/F	EAG	70, 71, 117
<i>Delia antiqua</i>	O	S	L/F	EAG/SCR	70, 80, 85
<i>Delia radicum</i>	O	S	L/F	EAG	40, 70, 117
<i>Rhagoletis pomonella</i>	O	G	L/F	EAG	60, 65, 114
<i>Dacus dorsalis</i>	P	G	L/F	EAG	102
Lepidoptera					
<i>Heliothis subflexa</i>	M	HPE	L		165
<i>Acrolepiopsis assectella</i>	M	S	L		161
<i>Plutella xylostella</i>	O	HPE	L	EAG	120
<i>Manduca sexta</i>	O	G/HP/HPE	L	EAG	164, 100
<i>Papilio polyxenes</i>	O	G	L	EAG	15
<i>Heliothis virescens</i>	P	HPE	L	SCR	82, 137, 166
<i>Trichoplusia ni</i>	P	HP	L		96
<i>Ostrinia nubilalis</i>	P	HP/G	L	EAG	29, 170
<i>Spodoptera littoralis</i>	P	HP/G	L	SCR	84, 141
<i>Mamestra brassicae</i>	P	HP/HPE/S/G	L	EAG	134, 136
<i>Cydia pomonella</i>	O	G/S	L/F	EAG	6, 38, 76

M, monophagous; O, oligophagous; P, polyphagous; HP, intact (host) plants; HPE, host-plant extract; G, generally occurring green-leaf volatiles; S, volatile(s) specific to the host plant taxon; L, behavioural test in the laboratory, in an olfactometer or a wind tunnel; F, field test, either trap catches (F(T)) or direct observations; (F-), behavioural responses to the odour source attractive under laboratory conditions could not be demonstrated under field conditions; EAG data on sensory perception of volatiles from the odour source available on the electroantennogram (EAG); SCR data on sensory perception of volatiles from the odour source available at single-cell level.

* The specific volatiles were isothiocyanates, which are characteristic for Cruciferae, one of the preferred host-plant families.

f. glabratum), was offered. This is an unsuitable plant for the beetle. Despite the taxonomic relatedness of tomato to potato, mixtures of their volatiles were not attractive to the beetles. The phenomenon that the presence of tomato odour prevents the beetles from orienting to their host plants has been termed 'odour masking'.¹⁶³ It has been suggested that this phenomenon plays a role in reducing population levels of herbivorous insects in mixed cropping systems (see Chapter 13).

Positive odour-conditioned optomotor anemotaxis and olfactory-induced visual orientation are presently considered to be the main mechanisms used during host-plant searching in herbivorous insects, in both specialized and polyphagous species.^{154,177} In addition, there is evidence that chemotaxis occurs within ranges of a few centimetres from the host plant, as has been demonstrated for several caterpillars and various root-feeding insects.^{93,115} Table 6.3 presents a selected summary of data on behavioural responses to plant odours in adults of herbivorous species belonging to four major orders. In each order, food specialists have been found to respond to identified odours specific to their host plant.

Generalist herbivores have been shown to exploit plant volatiles as signals conveying information on plant condition, thereby serving to optimize host-plant selection. The polyphagous *Myzus persicae* is more strongly attracted to and arrested by potato plants that are infected by potato leafroll virus, which have a higher host-plant quality than uninfected plants.⁵⁷ However, the generalist moth *Heliothis virescens* avoids ovipositing on plants damaged by conspecific caterpillars. Damaged plants emit specific volatiles only during the dark phase and these strongly repel nocturnally active female moths in search of an oviposition site.⁴² Not only herbivorous insects, but also many of their arthropod natural enemy species, exploit plant volatiles as infochemicals (see Chapter 10).^{51,157}

6.5 Chemosensory basis of host-plant odour detection

Insects rely heavily upon chemoreception when searching for food, oviposition sites, and mating partners, as well as for social communication.

In this context it is often stated that 'insects live in a chemical world'. Chemoreception refers to the classical senses of smell (olfaction, organs for detecting volatile chemical stimuli) and taste (gustation, or 'contact chemoreception' for the detection of dissolved or solid chemicals; see Chapter 7). The distinction between the two is not absolute, as insect taste sensilla have occasionally been found to respond also to odours,¹⁵⁶ and members of a gustatory receptor protein family³⁶ are expressed in the antenna and have olfactory functions.¹⁸³

6.5.1 Morphology of olfactory sensilla

Olfactory chemoreceptor cells are associated with so-called *sensilla* (singular: *sensillum*), organs consisting of neurons, accessory cells, and a cuticular structure (Fig. 6.14).

The cell bodies (perikarya) of the neurons are closely associated to the externally visible cuticular structure. The dendrites are usually located in specialized cuticular structures, which are classified on the basis of external form. They include hair-like varieties (*sensilla trichodea*), pegs and cones (*sensilla basiconica*, often involved in plant odour perception), pegs or cones sunk in shallow depressions (*sensilla coeloconica*), and pore-plate organs (*sensilla placodea*). Typically there are two to five neurons in olfactory sensilla,^{32,87,112} but in locusts up to 50 neurons may innervate one sensillum basiconicum. In pore-plate sensilla of the honeybee *Apis mellifera* up to 30 neurons innervate one sensillum placodeum.⁶⁹ Chemosensory neurons are mostly bipolar and their axons run to the CNS via peripheral nerves without intermittent synapses. The dendrite, a filament-like extension of the neuron that protrudes into the sensillum cavity, is specialized to respond to the chemical stimulus with a graded potential called the receptor potential. When this potential reaches a value above a certain threshold, it gives rise to a train of action potentials.

There are some important structural differences between olfactory and gustatory sensilla. Olfactory sensilla are multiporous, the entire sensillum wall or plate is perforated by up to thousands of minute pores (diameter about 10–50 nm), and dendrites are often branched.¹⁵⁸ In contrast, gustatory sensilla are

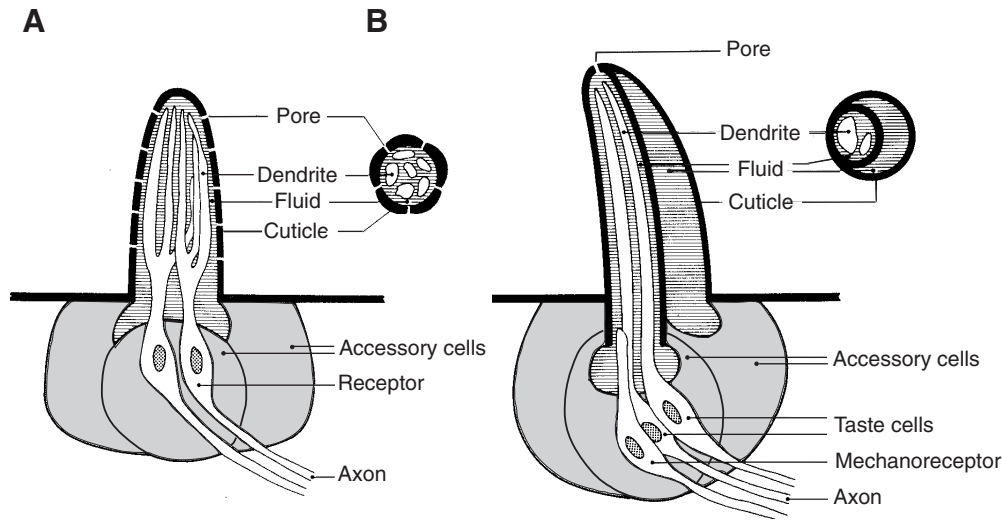


Figure 6.14 Schematic drawing of longitudinal and transverse sections of (A) an insect olfactory hair and (B) an insect taste hair. The olfactory hair is innervated by two bipolar chemoreceptor neurons; the taste hair is innervated by two chemoreceptors and one mechanoreceptor. (Courtesy of Dr. F.W. Maes, Groningen State University, The Netherlands.)

uniporous, the pore (diameter 200–400 nm) mostly being located at the very tip of a peg-, hair-, or papilla-like sensillum (Fig. 6.14). In both cases the dendritic tips are close to the pores, but are protected from desiccation by receptor lymph, which is secreted into the sensillum lumen by the tormogen and trichogen cells at the sensillum base. Olfactory sensilla are predominantly present on antennae, but may also occur on maxillary and labial palpi and on the ovipositor. The number of olfactory sensilla and the olfactory receptor cells associated with them is quite variable between species. Larvae of holometabolous insects have only small numbers of olfactory cells (e.g. less than 10 neurons for beetle larvae and about 100 for fly maggots and caterpillars^{183,188}). For female adults, this number amounts up to a few hundreds in Hemiptera, whereas for Lepidoptera it varies between 6500 and 177 000 (in female *Manduca sexta*) per antenna.³² The sensilla that house olfactory receptor cells may be multimodal, that is, they may also contain thermo-, hygro-, and mechanoreceptors.^{47,147}

6.5.2 Olfactory transduction

The transduction process—the process by which quality and quantity of the chemical stimulus is

converted into a receptor potential and eventually into action potentials—involves a sequence of steps. The recent past has brought considerable progress in the understanding of the molecular basis of olfactory transduction. A current model is depicted in Figure 6.15. The initial event is the diffusion of volatile stimulus molecules into the sensillum lumen via the pore(s) in the sensillum wall binding of these molecules to small (14 kDa) water-soluble odorant-binding proteins (OBPs), which carry the volatile stimulus molecules (ligands) to the olfactory receptor (OR) molecules present in the dendritic membrane. Either the stimulus molecule or the complex of OBP and stimulus molecule then binds to these membrane receptors. ORs in insects are G protein-coupled (GPC) seven-transmembrane proteins acting through activation of second messengers such as cyclic adenosine monophosphate (cAMP) or inositol 1,4,5-triphosphate (IP₃) involved in the opening of ion channels in the dendritic membrane. Opening of ion channels leads to depolarization of the dendritic membrane. When the magnitude of the depolarizing receptor potential exceeds a threshold, this results into generation of action potentials that travel over the axonal membrane to the glomeruli in the antennal lobe of the CNS (see below). The activity of stimulus molecules is most probably

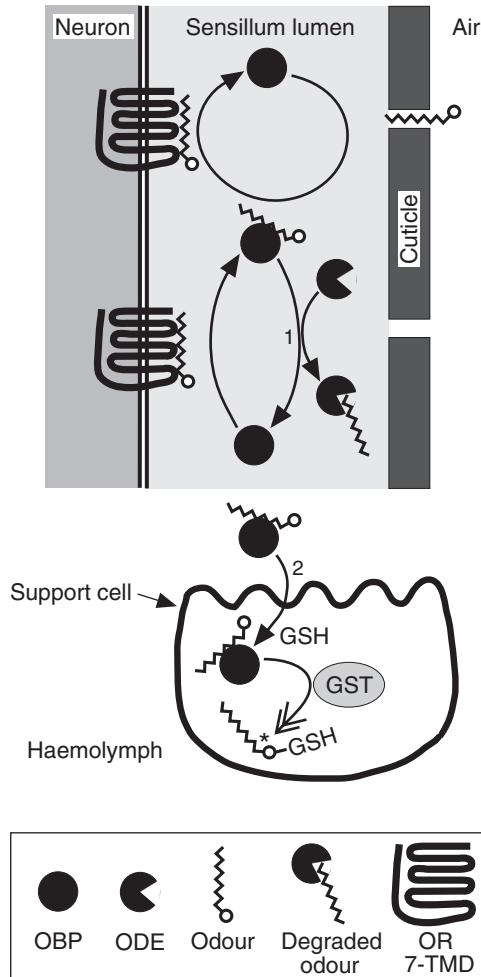


Figure 6.15 Generalized biochemical pathway of odour reception. Hydrophobic odour molecules enter the aqueous sensillum lumen via pores present in the cuticular hair wall. Hydrophilic odour binding proteins (OBPs) supposedly bind and transport odour molecules to receptor proteins (odour receptors (ORs), crossing the receptor neuronal membrane seven times) located in the neuronal membranes. Odour degrading enzymes (ODEs) (pathway 1) in the sensillum lumen supposedly degrade these odour molecules. The cytoplasm of support cells, which surround the nerve cell body, contains xenobiotic inactivating enzymes, such as glutathione-S-transferase (GST), which may also serve to inactivate odour molecules (pathway 2). GSH, glutathione. (Modified from Vogt, 2003.)¹⁸²

terminated by odour-degrading enzymes present in the sensillar lymph.¹⁸²

The fruitfly *Drosophila melanogaster* serves as the current model insect species for unravelling the molecular genetic basis of odour detection, as

the complete genome sequence has been known since 2000. This insect has 1300 olfactory neurons connected to 43 glomeruli in the antennal lobe. At present, between 25 and 60 candidate OBP genes and 61 candidate seven-transmembrane GPC-OR genes have been reported.^{182,183} Although they share particular base sequences, the sequences are diverse, showing only 17–26% sequence conservation and no apparent sequence homology with OR genes in other animal phyla. The numbers of genes implied in *D. melanogaster* are assumed to be similar for other insect species.

Present challenges in insect olfactory transduction are elucidating the functional role of OBPs in olfactory specificity and characterization of the ligand specificity of ORs involved in plant odour recognition.¹⁹⁰ Making use of genomic information on *D. melanogaster* and DNA sequence homology in OR genes of other species, the role of individual OR genes in plant odour recognition can be studied by gene-silencing techniques.⁶⁴

6.5.3 Olfactory electrophysiology and sensitivity

Basically two electrophysiological techniques are employed in studying sensitivity and specificity of the olfactory system in insects. A reflection of simultaneously occurring receptor potentials generated in the entire population of antennal olfactory neurons can be recorded as the so-called electroantennogram (EAG) (Appendix C3). The second method is to record from individual sensilla (so-called single-sensillum or single-cell recording), yielding patterns of action potentials, also called spike activity. This is the actual information-carrying signal that is processed in the CNS. Both methods have their advantages and limitations. The EAG reflects the response of the entire olfactory neuron population but has limited sensitivity. The SCR offers high sensitivity of detection of olfactory activity but in practice allows recording only from a small sample of the entire antennal neuron population.¹⁸⁵

Like most sensory cells, chemoreceptors are especially responsive to changes in stimulus intensity (i.e. changes in the concentrations of chemicals). Two reaction types occur: excitation, an

increase in the rate at which action potentials are produced upon stimulation with an odour; and inhibition, a decrease in firing rate relative to the unstimulated condition, in which spontaneous spiking occurs (Fig. 6.16).

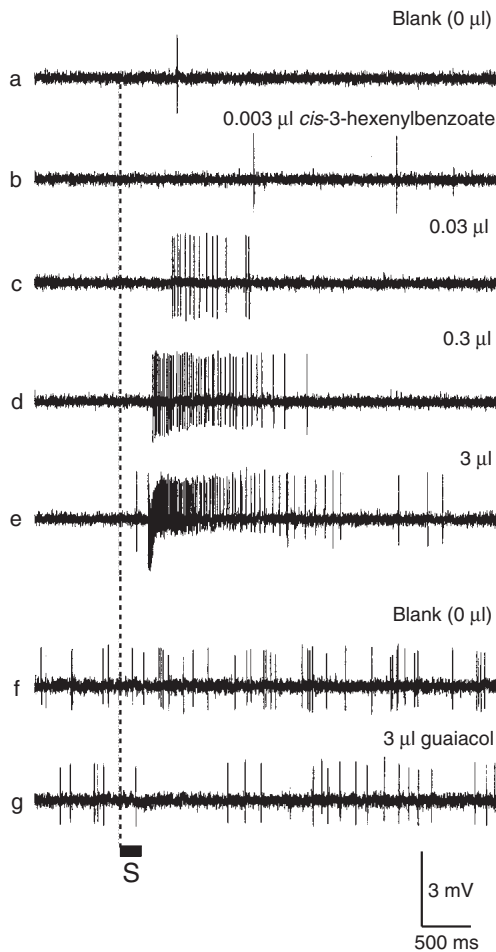


Figure 6.16 Electrophysiological recordings from two different type-A trichoid sensilla on the antenna of a female hawk moth (*Manduca sexta*), showing excitatory (b–e) and inhibitory (g) responses. The hairs were stimulated with the gaseous phase from olfactometer syringes containing filter paper charged with 30 μ l of mineral oil solution containing the odorants mentioned. (a–e) Responses of one olfactory receptor neuron (ORN) in a sensillum to: (a) mineral oil alone (blank); (b) 0.003 μ l; (c) 0.03 μ l; (d) 0.3 μ l, and (e) 3 μ l *cis*-3-hexenylbenzoate, an aromatic ester. (f–g) Responses of one ORN in a different sensillum to: (f) mineral oil alone (blank); (g) 3 μ l guaiacol, an aromatic alcohol. Stimulus bar (S) = 200 ms. (From Shields and Hildebrand, 2001.)¹⁴⁸

Olfactory cells have been shown to handle up to 33 odour pulses per second,^{14,110} allowing them to resolve the temporal pattern of odour bursts in a plume (see Fig. 6.5).

Concentration–response relationships generally show a sigmoidal shape at the level of EAGs as well as single-cell recordings (Figs. 6.17 and 6.18). Upon increasing the odour concentration by one order of magnitude, EAG amplitude and frequency of action potentials typically become 1.5–3 times higher until saturating concentrations are reached, above which no further increase occurs. The discrimination of concentration differences is optimal in the range between threshold and saturating concentrations (i.e. the rising phase of the dose–response curves) (Figs. 6.17 and 6.18). This, in principle, enables the insect to sense odour gradients, on the basis of which it may perform tropotactic behaviour (see Section 6.4.3). Different from gustatory receptors, olfactory receptors may function as flux detectors, which track the abundance of molecules over time, rather than concentration detectors.¹⁶⁷

Sensitivity of detection is enhanced enormously by the neural phenomenon of *convergence*. The

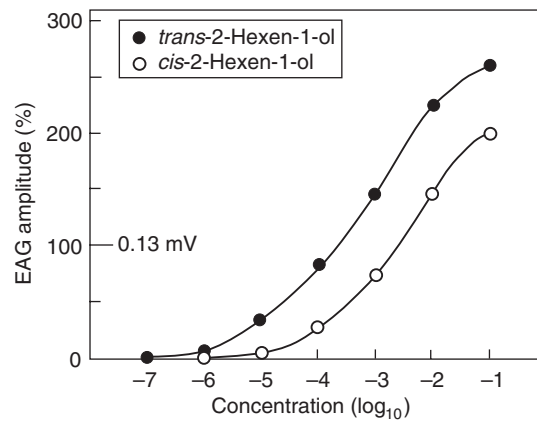


Figure 6.17 Relationship between concentration of two green-leaf volatiles and electroantennogram (EAG) response intensity evoked in the antennae of female Colorado potato beetles. Concentration is expressed as the dilution (v/v) in paraffin oil. EAG response is expressed relative to the response to a standard dose (10^{-3} or 1 ml/ml) of another green-leaf volatile, *cis*-3-hexen-1-ol. The *trans* compound evokes responses at concentrations about 10 times lower than those of the *cis* compound. (From Visser, 1976.)¹⁷⁶

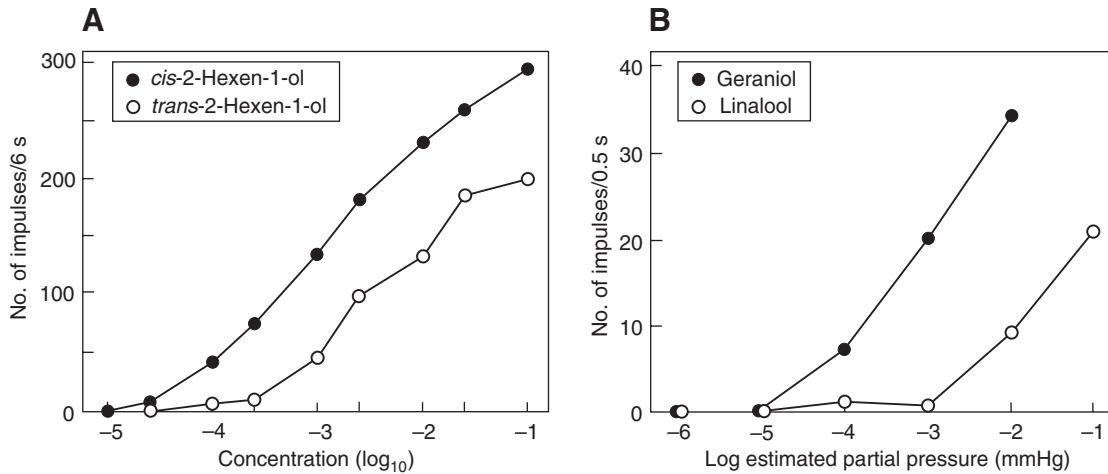


Figure 6.18 Relationship between the concentration of plant volatiles and the responses of single olfactory receptor neurons in two insect species. **(A)** Dose–response relationships for a single olfactory neuron innervating a sensillum basicanicum on the antenna of a female Colorado potato beetle when stimulated with two green-leaf volatiles. Concentration is expressed as the dilution (v/v) in paraffin oil at the source. (From Ma and Visser, 1978.)⁹⁸ **(B)** Dose–response relationships for three different olfactory cells narrowly tuned to terpenoid odorants in the antenna of female *Manduca sexta* moths. Vapour pressures of the odorants have been taken into consideration. (From Shields and Hildebrand, 2001.)¹⁴⁸ Note the scale differences in the vertical axes.

axons running from olfactory receptors cells make synaptic contacts with a limited number of first-order interneurons in the antennal lobe of the deutocerebrum, that is, they converge.⁷⁸ A local interneuron receives inputs from many receptor cells simultaneously and its threshold for depolarization may therefore be reached at a lower concentration than that necessary to depolarize a given antennal receptor cell. Convergence improves the signal-to-noise ratio, noise being the spontaneous background activity of the peripheral olfactory system. For example, 100–1000-fold lower concentrations are needed to measure responses in deutocerebral interneurons to antennal stimulation with green-leaf volatiles in the Colorado potato beetle, compared with thresholds of its antennal receptors.⁴¹ Axons of the olfactory neurons make synaptic contacts in spherical neuropils in the antennal lobe, called glomeruli. A glomerulus is a small convoluted mass of synaptic contacts between olfactory neurons, local interneurons, and projection neurons (Fig. 6.19).⁷ In several moth and butterfly species, between 60 and 70 glomeruli are present, in the honeybee 166, and in locusts 1000 glomeruli-like structures have been documented.

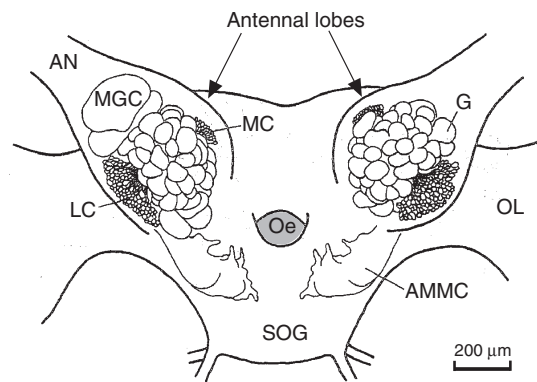


Figure 6.19 Frontal view of the brain of a male sphinx moth (*Manduca sexta*), showing the two neuropils of the deutocerebrum, the antennal lobes, and the antennal mechanosensory and motor centres (AMMC). The macroglomerular complex (MGC) is present only in males. Most cell bodies of antennal lobe interneurons are concentrated in two cell groups, a medial (MC) and a lateral (LC) cluster. AN, antennal nerve; G, glomerulus; SOG, suboesophageal ganglion; Oe, oesophageal canal; OL, optic lobe. (From Anton and Homberg, 1999.)⁷

When the number of projection neurons that arborize in the glomeruli and that send their axons to other brain centres, such as the mushroom

bodies, are compared with the number of antennal olfactory cells, a convergence ratio can be calculated, higher values of which are presumably associated with higher sensitivity. For *Locusta migratoria* this ratio is 150, for the honeybee *Apis mellifera* 650, and for the sphinx hawkmoth *Manduca sexta* 330. Antennal lobe output neurons in the brain of *M. sexta* were found to code fine-scale temporal variation in odour intensity in the millisecond domain.¹⁷⁵

6.5.4 Olfactory specificity and coding

How do olfactory receptors encode the multitude of volatile chemical stimuli present in the outside world into a message that will increase the chance of finding a host plant? Single-cell recording is required to analyse olfactory specificity. Individual plant chemicals and their mixtures can be tested for their effect in evoking changes in chemosensory activity, either exciting or inhibiting olfactory neuron activity. The olfactory system functions as a filter because olfactory receptor neurons are sensitive to only a limited array of volatile chemicals occurring in the environment. For both olfactory and gustatory neurons (see Chapter 7), classically two main categories have been distinguished: 'specialist' and 'generalist' receptor neurons. By definition, a specialist cell responds to only a small number of structurally related compounds, whereas a generalist neuron responds to a wide array of structurally unrelated compounds. Among insect olfactory receptors, sex pheromone receptors are the classical example of specialist receptor.¹⁴⁴

Over the past decade our view of olfactory neuron specificity in response to plant odours has gradually changed. A growing number of studies on insect herbivores have revealed a hitherto undiscovered degree of specificity of olfactory neurons responding to generally occurring plant volatiles such as green-leaf volatiles and terpenoids in beetles and moths.^{5,74,159} On the other hand, olfactory neurons specifically tuned to host-plant specific volatiles have also been found in, for instance, coleopterans,²² lepidopterous larvae,¹⁷⁸ and aphids.¹¹⁸ It now seems that generalist receptor neurons are relatively rare. This change of

view has been explained by the fact that often, in the past, too-high stimulus concentrations (relative to concentrations prevailing naturally in the environment) were used and, second, by a lack of knowledge of the key stimuli for the specialized olfactory neurons.⁷⁴

Recent findings indicate that oligophagous as well as polyphagous species have olfactory receptor neurons with high sensitivity and selectivity to chemicals that are common in many plant species as well as to chemicals more specific for certain plant groups.¹¹³ Thus, the majority (80%) of olfactory receptor neurons of polyphagous heliothine moths show selective and sensitive responses to the generally occurring sesquiterpenoid (–)-germacrene D, and this compound stimulates oviposition. However, it is unknown what message the airborne concentrations of this particular compound tells about a potential oviposition host plant in the context of all other volatile compounds released simultaneously.

The application of molecular techniques in the analysis of olfactory neuron specificity has led to the current paradigm that one olfactory neuron expresses one receptor protein.⁷² An individual receptor protein may interact with structurally diverse volatile ligands. Some ligands activate only few receptors, whereas others activate several receptor types. A single receptor type may produce an excitatory or an inhibitory response, depending on the ligand. It is customary to designate the specificity of a neuron in terms of the molecule to which it shows the lowest threshold¹⁶⁷ and is said to be tuned to this type of (or class of) molecules.

Olfactory receptor neurons can be classified into different response types. Three response types were found in antennal receptors of the sphinx moth *Manduca sexta*¹⁴⁸ and the eucalyptus wood borer *Phoracantha semipunctata*,¹² five were distinguished for antennal receptors of the Colorado potato beetle⁹⁸ and the cabbage white butterfly,⁴³ 12 in the weevil *Pissodes notatus*,²⁰ and 16 in *Drosophila melanogaster*.³⁹ The number of response types found will depend on the panel of odorants tested and the size of the antennal neuron population sampled. An organizational feature of the peripheral olfactory system that has received increasing attention is co-compartmentation of

olfactory neurons with different specificity in the same sensillum. This has the advantage that the blend ratios between volatile compounds to which the neurons are tuned are perceived and transmitted in an accurate way.¹⁶⁷

Research into olfactory coding has been extended from classifying response types of antennal olfactory neurons to unravelling olfactory information processing in the antennal lobe and the protocerebrum.^{31,78,113} Optical imaging techniques that make use of confocal laser scanning microscopy and calcium-sensitive fluorescent dyes allow the real-time monitoring of activation patterns of glomeruli when single compounds or mixtures are offered to the antennal receptors.^{67,68,151} Based on results obtained with these sophisticated techniques, three-dimensional maps of glomeruli can be constructed^{18,95} that allow a spatial representation of odours at the level of identified glomeruli.^{18,66,140} It has been found that antennal olfactory neurons of the same functional type project their axons to the same glomerulus, and glomeruli thus function as separate processing units.^{31,113} Electrophysiological analyses of projection neurons that transmit olfactory information from a single glomerulus to the mushroom bodies and other protocerebral centres suggest that each glomerulus has a characteristic molecular receptive range⁹² and that more than one glomerulus can be involved in processing information on single plant compounds.^{31,140}

In the natural environment behaviourally relevant odour signals are always blends. The olfactory system has to encode information on plant odour quality,³¹ quantity (concentrations, ratios), and spatial distribution, and to translate it into adequate behavioural decisions.

'Labelled-line' codes have been inferred to operate in oligophagous species, in which the activity of narrowly tuned olfactory neurons may trigger kinetic responses or odour-induced anemotaxis, either positive or negative. 'Across-fibre pattern' codes, supposedly more common in generalist species, are operating through reading out the ratio of the simultaneous activity of a number of olfactory neurons with overlapping but not identical molecular receptive ranges. The cellular elements involved in the analysis of across-fibre patterning are local interneurons and projection neurons of

the antennal lobe. Although both coding modes are sometimes described as mutually exclusive, they more likely represent extremes of a continuum.¹⁵² As many plant species release a complex blend of generally occurring green-leaf volatiles and terpenoids into the atmosphere (see Chapter 4) that lack qualitative taxonomic specificity, neural coding of ratios of the quantities released becomes critical, as these ratios may contain information on the plant taxon.¹⁷⁷ Across-fibre or combinatorial codes are better suited for this purpose and require fewer receptors to accomplish this task.²³

At the behavioural level, generally occurring green-leaf volatiles may synergize with one another, and also with taxonomically specific volatiles or with pheromones.^{27,38,60} Likewise, at the olfactory receptor level, interactions have been shown to occur between host-plant odour components as well as between host-plant odours and pheromones.^{73,119,173,180}

Aspects of olfactory specificity, coding principles, and CNS processing of plant odour information are rapidly evolving areas of study. These studies focus on a number of model species: the honeybee *Apis mellifera*,⁶⁷ *Spodoptera* spp.,¹⁴⁰ *Helicoverpa* spp.,¹⁵¹ and *Manduca sexta*.¹⁴⁸

6.6 Host-plant searching in nature

When a herbivorous insect is searching for a host plant in the field, it meets a multitude of stimuli, which are distributed heterogeneously. Inherent to the field situation is a lack of control over both the stimulus situation and abiotic parameters that possibly influence behavioural responses. It is therefore difficult to assess the relative importance of the two main stimulus modalities, optical and odorous plant cues, under field conditions. For several insect species it has been shown that significant stimulus interactions occur. During searching for food or oviposition sites, the importance of different types of stimulus may change with distance to the plant. Stimulus interactions may be one of the causes of the discrepancies indicated in Table 6.3, for which behavioural responses to odours observed in the laboratory could not be confirmed in the field.

The Colorado potato beetle, for instance, is well able to perform directed orientation in response to

odours alone and uses odour-conditioned positive anemotaxis, as has been convincingly demonstrated in laboratory studies.^{162,176} Behavioural observations on host-plant searching in the field, however, have given variable results with respect to the role of odours in host-plant location. De Wilde found upwind menotactic responses in the field at distances less than 6 m from a plot of potato plants (of unstated size).⁴⁹ Jermy and co-workers, however, found only a low proportion of beetles moving upwind in the field, and even in these cases their walking tracks did not reveal directed movement towards potato plants.⁸³ The beetles showed photomenotaxis and a high directionality of movement based on light-compass orientation rather than on odour-induced anemotaxis. In the vicinity of potato plants, interruptions of straight paths occurred, accompanied by an increased rate of turning. Jermy and co-workers estimated that the maximum distance at which a walking beetle could detect a single potato plant was about 60 cm, based on either olfactory cues or visual cues, or a combination. However, only one of every two beetles that came within this radius of detection was attracted to the plant. Odour masking is likely to be one of the causes of the small radius of detection in a complex natural vegetation. It was concluded that, under natural conditions, where individual potato plants may be scattered between non-hosts, host-plant finding is a chance event when the beetle starts at a distance of more than 60 cm from a potato plant.⁸³ These findings fit well into the model of 'alternating random and non-random (kinetic arrestment-type) search strategies' formulated by Morris and Kareiva.¹⁰⁷

Of all herbivorous insects in which host-searching behaviour has been studied, the apple maggot fly *Rhagoletis pomonella* and the cabbage root fly *Delia radicum* are probably those analysed in most detail.^{3,4,62,139} The visually guided host-searching behaviour of the apple maggot fly was described above (see Section 6.4.2). These flies are highly responsive to particular visual stimuli, but only after they have been 'activated' by apple odour. They show preferences for either yellow or red, depending on the size of the object and their motivational state (see Section 6.2). Spherical red objects of a limited diameter are preferred when the fly is searching for oviposition sites. In order to

acquire carbohydrates, the flies feed on aphid honeydew, which is present on apple leaves. Larger yellow spheres are preferred over red ones when the motivation for carbohydrate ingestion is high. Yellow serves as a supernormal substitute stimulus for the green hue of apple leaves. Apple odour elicits upwind flight, and odour-induced anemotaxis allows the flies to locate an apple-bearing tree within a patch of trees devoid of apples by a series of tree-to-tree displacements. In the same way they can find a synthetic odour source outside an odourless patch. Once at a tree bearing apples, selection of individual fruits by size or colour is done mainly visually. However, when there are few fruits or when they are green instead of red and therefore lack contrast with the leaves, odorous cues are used to aid the selection process (Fig. 6.20).

As an alternative to seven existing hypotheses, a new hypothesis to explain how plant diversity affects host-plant selection behaviour was launched by Finch and Collier.⁶² It is based on a substantial amount of detailed behavioural observations on *Delia* flies and other insects associated with cruciferous plants. Finch and Collier propose that selection occurs in three phases, the first governed by

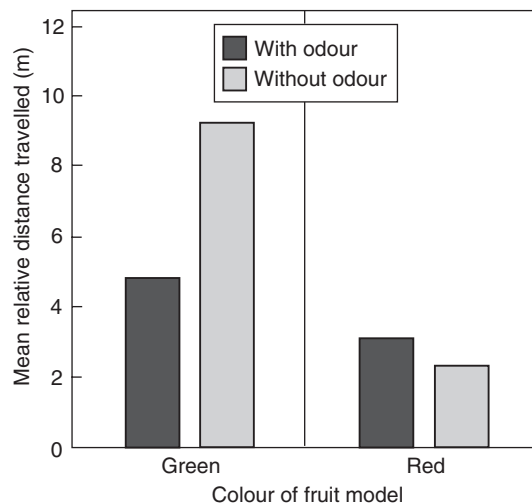


Figure 6.20 Demonstration of the interaction between olfactory and visual information in host selection behaviour of the apple maggot fly *Rhagoletis pomonella*; the effect of host fruit odour (a synthetic blend of six esters), released at 500 mg/h, on finding green or red fruit models in a tree carrying 16 models. (From Aluja and Prokopy, 1993.)³

volatile plant cues, the next by visual cues, and the final phase largely affected by non-volatile plant chemicals (see Chapter 7). The second phase has been largely overlooked and can be described in terms of indiscriminate landings on appropriate (host) plants and inappropriate (non-host) plants. In the first phase, olfaction of plant volatiles leads to arrestment and landing but provides no directional information (see Section 6.3). In the second phase, repeated contacting of the host plant is crucial to reinforce the stimulatory information that leads to entering the third phase, in which oviposition or feeding decisions are based largely, although not exclusively in the case of *Delia*,⁴⁰ on contact cues.

Field studies to date on host plant-searching behaviour have logically been focused on larger species, which, by virtue of their visual conspicuousness, can be directly observed and followed for some time while moving from plant to plant. As a result oviposition behaviour of butterflies has been studied in some detail.^{9,150} The picture that emerges from these studies is a predominant role of vision and associative learning involving optical and contact-chemosensory cues, promoting time and energy optimization of host selection behaviour.

In contrast to the situation mentioned above for fruit flies, host selection behaviour of bark beetles in forest ecosystems is governed largely by chemical cues. Highly intricate chemical communication systems are operating based on complicated interactions between host-tree odours, aggregation pheromones produced by the beetles or associated microorganisms, and interspecific inhibitory infochemicals.^{25,103,131}

6.7 Conclusions

Although our knowledge of the plant characteristics influencing host-plant searching and the ways in which insect herbivores detect and use them to their own advantage is increasing, the general picture is built upon information from a small number of relatively well studied species. Clearly, plant factors that affect insects over some distance are difficult to manipulate experimentally in the field. In many specialized herbivores no

evident orientation can be demonstrated when they are at some distance from their host plant, and it appears that in order to find a suitable plant they must literally bump into it. Searching then is essentially a random process, in which the chance of an encounter is determined largely by spatial factors.^{30,44,83} However, several specialized insect species have been observed under natural conditions to be perfectly able to integrate information from different cues, and studies have shown that the outcome of this integration, manifested as searching behaviour, is more complex than expected from a mere summation of responses across sensory modalities.^{17,33,75}

New insights in the molecular biology and neurophysiology of odour detection have evolved rapidly over the past decade and have significantly increased our understanding of the mechanisms involved. The challenge is to relate knowledge at the molecular and physiological levels to the behavioural and evolutionary significance of using odour information. Plant headspace volatile composition is complex in qualitative and quantitative respects, yet it is essential, when investigating which compounds convey relevant information about the suitability of a host plant, to know their naturally occurring concentrations. In fact, the minimal blend of identified volatiles causing attraction has been successfully formulated for relatively few species.^{102,155}

It can be expected that in the near future an integration of molecular biology, neurobiology, behaviour, and phytochemistry will considerably advance our understanding of host plant-finding mechanisms and the evolutionary selection pressures that mould them.¹¹³ In addition, it appears fruitful to pay explicit attention to the integration of optical and odorous plant cues.⁶²

6.8 References

1. Ahmad, S. (1982). Host location by the Japanese beetle: evidence for a key role for olfaction in a highly polyphagous insect. *Journal of Experimental Zoology*, **220**, 117–20.
2. Aikman, D. and Hewitt, G. (1972). An experimental investigation of the rate and form of dispersal in grasshoppers. *Journal of Applied Ecology*, **9**, 807–17.

3. Aluja, M. and Prokopy, R. (1993). Host odor and visual stimulus interactions during intratree host finding behavior of *Rhagoletis pomonella* flies. *Journal of Chemical Ecology*, **19**, 2671–96.
4. Aluja, M., Prokopy, R.J., Buonaccorsi, J.P., and Cardé, R.T. (1993). Wind tunnel assays of olfactory responses of female *Rhagoletis pomonella* flies to apple volatiles: effect of wind speed and odour release rate. *Entomologia Experimentalis et Applicata*, **68**, 99–108.
5. Anderson, P., Hansson, B.S., and Löfqvist, J. (1995). Plant-volatile receptor neurons on the antennae of female and male *Spodoptera littoralis*. *Physiological Entomology*, **20**, 189–98.
6. Ansebo, L., Coracini, M.D.A., Bengtsson, M., Liblikas, I., Ramírez, M., Borg-Karlson, A.-K., et al. (2004). Antennal and behavioural response of codling moth *Cydia pomonella* to plant volatiles. *Journal of Applied Entomology*, **128**, 488–93.
7. Anton, S. and Homberg, U. (1999). Antennal lobe structure. In *Insect olfaction* (ed. B.S. Hansson), pp. 97–124. Springer, Berlin.
8. Atkins, M.D. (1980). *Introduction to insect behavior*. Macmillan, New York.
9. Auckland, J.N., Debinski, D.M., and Clark, W.R. (2004). Survival, movement, and resource use of the butterfly *Parnassius clodius*. *Ecological Entomology*, **29**, 139–49.
10. Baker, T.C. (1988). Pheromones and flight behavior. In *Insect flight* (ed. G. Goldsworthy and C. Wheeler), pp. 231–55. CRC Press, Boca Raton, FL.
11. Balkovsky, E. and Shraiman, B.I. (2002). Olfactory search at high Reynolds numbers. *Proceedings of the National Academy of Sciences of the USA*, **99**, 12589–93.
12. Barata, E.N., Mustaparta, H., Pickett, J.A., Wadhams, L.J., and Araujo, J. (2002). Encoding of host and non-host plant odours by receptor neurones in the eucalyptus woodborer, *Phoracantha semipunctata* (Coleoptera: Cerambycidae). *Journal of Comparative Physiology A*, **188**, 121–33.
13. Barton Browne, L. (1993). Physiologically induced changes in resource oriented behavior. *Annual Review of Entomology*, **38**, 1–25.
14. Bau, J., Justus, K.A., and Cardé, R.T. (2002). Antennal resolution of pulsed pheromone plumes in three moth species. *Journal of Insect Physiology*, **48**, 433–42.
15. Baur, R., Feeny, P., and Städler, E. (1993). Oviposition stimulants for the black swallowtail butterfly: identification of electrophysiologically active compounds in carrot volatiles. *Journal of Chemical Ecology*, **19**, 919–37.
16. Bell, W.J. (1984). Chemo-orientation in walking insects. In *Chemical ecology of insects* (ed. W.J. Bell and R.T. Cardé), pp. 93–109. Chapman & Hall, London.
17. Bell, W.J. (1991). *Searching behaviour. The behavioural ecology of finding resources*. Chapman & Hall, London.
18. Berg, B.G., Galizia, C.G., Brandt, R., and Mustaparta, H. (2002). Digital atlases of the antennal lobe in two species of tobacco budworm moths, the oriental *Helicoverpa assulta* (male) and the American *Heliothis virescens* (male and female). *Journal of Comparative Neurology*, **446**, 123–34.
19. Bernays, E.A. and Chapman, R.F. (1994). *Host-plant selection by phytophagous insects*. Chapman & Hall, New York.
20. Bichao, H., Borg-Karlson, A.K., Araujo, J., and Mustaparta, H. (2003). Identification of plant odours activating receptor neurones in the weevil *Pissodes notatus* F. (Coleoptera, Curculionidae). *Journal of Comparative Physiology A*, **189**, 203–12.
21. Blaakmeer, A., Geervliet, J.B.F., Van Loon, J.J.A., Posthumus, M.A., Van Beek, T.A., and De Groot, A.E. (1994). Comparative headspace analysis of cabbage plants damaged by two species of *Pieris* caterpillars: consequences for inflight host location by *Cotesia* parasitoids. *Entomologia Experimentalis et Applicata*, **73**, 175–82.
22. Blight, M.M., Pickett, J.A., Wadhams, L.J., and Woodcock, C.M. (1989). Antennal responses of *Ceutorhynchus assimilis* and *Psylliodes chrysocephala* to volatiles from oilseed rape. *Aspects of Applied Biology*, **23**, 329–34.
23. Boeckh, J. and Ernst, K.D. (1983). Olfactory food and mate recognition. In *Neuroethology and behavioral physiology* (ed. F. Huber and H. Markl), pp. 78–94. Springer, Berlin.
24. Briscoe, A.D. and Chittka, L. (2001). The evolution of color vision in insects. *Annual Review of Entomology*, **46**, 471–510.
25. Byers, J.A. (1995). Host-tree chemistry affecting colonization of bark beetles. In *Chemical ecology of insects*, Vol. 2 (ed. R.T. Cardé and W.J. Bell), pp. 154–213. Chapman & Hall, New York.
26. Byers, J.A., Anderbrant, O., and Löfqvist, J. (1989). Effective attraction radius: a method for comparing species attractants and determining densities of flying insects. *Journal of Chemical Ecology*, **15**, 749–65.
27. Byers, J.A., Birgersson, G., Löfqvist, J., Appelgren, M., and Bergström, G. (1990). Isolation of pheromone synergists of bark beetle, *Pityogenes chalcographus*, from complex insect-plant odors by fractionation and subtractive-combination bioassay. *Journal of Chemical Ecology*, **16**, 861–76.
28. Campbell, C.A.M., Pettersson, J., Pickett, J.A., Wadhams, L.J., and Woodcock, C.M. (1993). Spring

- migration of damsonhop aphid *Phorodon humuli* (Homoptera, Aphididae), and summer host plant-derived semiochemicals released on feeding. *Journal of Chemical Ecology*, **19**, 1569–76.
29. Cantelo, W.W. and Jacobson, M. (1979). Corn silk volatiles attract many pest species of moths. *Journal of Environmental Science and Health A*, **14**, 695–707.
 30. Cappuccino, N. and Kareiva, P.M. (1985). Coping with capricious environment: a population study of a rare pierid butterfly. *Ecology*, **66**, 152–61.
 31. Carlsson, M.A. and Hansson, B.S. (2003). Plasticity and coding mechanisms in the insect antennal lobe. In *Insect pheromone biochemistry and molecular biology* (ed. G.J. Blomquist and R.G. Vogt), pp. 699–728. Elsevier, Amsterdam.
 32. Chapman, R.F. (1982). Chemoreception: the significance of sensillum numbers. *Advances in Insect Physiology*, **16**, 247–356.
 33. Chapman, R.F. (1988). Odors and the feeding behavior of insects. *ISI Atlas of Science: Animal and Plant Sciences*, pp. 208–12.
 34. Chapman, R.F., Bernays, E.A., and Simpson, S.J. (1981). Attraction and repulsion of the aphid, *Cavariella aegopodii*, by plant odors. *Journal of Chemical Ecology*, **7**, 881–8.
 35. Chittka, L. and Waser, N.M. (1997). Why red flowers are not invisible to bees. *Israel Journal of Plant Sciences*, **45**, 169–83.
 36. Clyne, P.J., Warr, C.G., and Carlson, J.R. (2000). Candidate taste receptors in *Drosophila*. *Science*, **287**, 1830–4.
 37. Coombe, P.E. (1982). Visual behaviour of the greenhouse whitefly *Trialeurodes vaporariorum*. *Physiological Entomology*, **7**, 243–51.
 38. Coracini, M., Bengtsson, M., Liblikas, I., and Witzgall, P. (2004). Attraction of codling moth males to apple volatiles. *Entomologia Experimentalis et Applicata*, **110**, 1–10.
 39. De Bruyne, M., Foster, K., and Carlson, J.R. (2001). Odor coding in the *Drosophila* antenna. *Neuron*, **30**, 537–52.
 40. De Jong, R. and Städler, E. (1999). The influence of odour on the oviposition behaviour of the cabbage root fly. *Chemoecology*, **9**, 151–4.
 41. De Jong, R. and Visser, J.H. (1988). Integration of olfactory information in the Colorado potato beetle brain. *Brain Research*, **447**, 10–17.
 42. De Moraes, C.M., Mescher, M.C., and Tumlinson, J.H. (2001). Caterpillar-induced nocturnal plant volatiles repel conspecific females. *Nature*, **410**, 577–80.
 43. Den Otter, C.J., Behan, M., and Maes, F.W. (1980). Single cell responses in female *Pieris brassicae* (Lep.: Pieridae) to plant volatiles and conspecific egg odours. *Journal of Insect Physiology*, **26**, 465–72.
 44. Dethier, V.G. (1959). Foodplant distribution and density and larval dispersal as factors affecting insect populations. *Canadian Entomologist*, **91**, 581–96.
 45. Dethier, V.G. (1982). Mechanisms of host plant recognition. *Entomologia Experimentalis et Applicata*, **31**, 49–56.
 46. Dethier, V.G. (1989). Patterns of locomotion of polyphagous arctiid caterpillars in relation to foraging. *Ecological Entomology*, **14**, 375–86.
 47. Dethier, V.G. and Schoonhoven, L.M. (1968). Evaluation of evaporation by cold and humidity receptors in caterpillars. *Journal of Insect Physiology*, **14**, 1049–54.
 48. Dethier, V.G., Barton Browne, L., and Smith, C.N. (1960). The designation of chemicals in terms of the responses they elicit from insects. *Journal of Economic Entomology*, **53**, 134–6.
 49. De Wilde, J. (1976). The olfactory component in host-plant selection in the adult Colorado beetle (*Leptinotarsa decemlineata* Say). *Symposia Biologica Hungarica*, **16**, 291–300.
 50. Dicke, M. and Sabelis, M.W. (1988). Infochemical terminology: based on cost-benefit analysis rather than origin of compounds? *Functional Ecology*, **2**, 131–9.
 51. Dicke, M. and Van Loon, J.J.A. (2000). Multitrophic effects of herbivore-induced plant volatiles in an evolutionary context. *Entomologia Experimentalis et Applicata*, **97**, 237–49.
 52. Dickens, J.C. (1984). Olfaction in the boll weevil, *Anthonomus grandis* Boh. (Coleoptera: Curculionidae): electroantennogram studies. *Journal of Chemical Ecology*, **10**, 1759–85.
 53. Dickens, J.C. (1986). Orientation of boll weevil *Anthonomus grandis* Boh. (Coleoptera: Curculionidae), to pheromone and volatile host compound in the laboratory. *Journal of Chemical Ecology*, **12**, 91–8.
 54. Dickens, J.C. (1990). Specialized receptor neurons for pheromones and host plant odors in the boll weevil, *Anthonomus grandis* Boh. (Coleoptera: Curculionidae). *Chemical Senses*, **15**, 311–31.
 55. Douwes, P. (1968). Host selection and host finding in the egg-laying female *Cidaria albulata* L. (Lep. Geometridae). *Opuscula Entomologica*, **33**, 233–79.
 56. Drew, R.A.I., Prokopy, R.J., and Romig, M.C. (2003). Attraction of fruit flies of the genus *Bactrocera* to colored mimics of host fruit. *Entomologia Experimentalis et Applicata*, **107**, 39–45.
 57. Eigenbrode, S.D., Ding, H., Shiel, P., and Berger, P.H. (2002). Volatiles from potato plants infected with potato leafroll virus attract and arrest the virus

- vector, *Myzus persicae* (Homoptera: Aphididae). *Proceedings of the Royal Society of London, Series B*, **269**, 455–60.
58. Evans, K.A. and Allen-Williams, L.J. (1993). Distant olfactory response of the cabbage seed weevil, *Ceutorhynchus assimilis*, to oilseed rape odour in the field. *Physiological Entomology*, **18**, 251–6.
 59. Fadamiro, H.Y., Wyatt, T.D., and Birch, M.C. (1998). Flying beetles respond as moths predict: optomotor anemotaxis to pheromone plumes at different heights. *Journal of Insect Behavior*, **11**, 549–57.
 60. Fein, B.L., Reissig, W.H., and Roelofs, W.L. (1982). Identification of apple volatiles attractive to the apple maggot, *Rhagoletis pomonella*. *Journal of Chemical Ecology*, **8**, 1473–87.
 61. Finch, S. (1986). Assessing hostplant finding by insects. In *Insect-plant interactions* (ed. J.R. Miller and T.A. Miller), pp. 23–63. Springer, New York.
 62. Finch, S. and Collier, R.H. (2001). Host-plant selection by insects—a theory based on ‘appropriate/inappropriate landings’ by pest insects of cruciferous plants. *Entomologia Experimentalis et Applicata*, **96**, 91–102.
 63. Finch, S. and Skinner, G. (1982). Upwind flight by the cabbage root fly, *Delia radicum*. *Physiological Entomology*, **7**, 387–99.
 64. Fire, A. (1999). RNA-triggered gene silencing. *Trends in Genetics*, **15**, 358–63.
 65. Frey, J.E. and Bush, G.L. (1990). Rhagoletis sibling species and host races differ in host odor recognition. *Entomologia Experimentalis et Applicata*, **57**, 123–31.
 66. Galizia, C.G. and Menzel, R. (2000). Odour perception in honeybees: coding information in glomerular patterns. *Current Opinion in Neurobiology*, **10**, 504–10.
 67. Galizia, C.G. and Menzel, R. (2001). The role of glomeruli in the neural representation of odours: results from optical recording studies. *Journal of Insect Physiology*, **47**, 115–30.
 68. Galizia, C.G., Sachse, S., and Mustaparta, H. (2000). Calcium responses to pheromones and plant odours in the antennal lobe of the male and female moth *Heliothis virescens*. *Journal of Comparative Physiology A*, **186**, 1049–63.
 69. Getz, W.M. and Akers, R.P. (1994). Honeybee olfactory sensilla behave as integrated processing units. *Behavioral and Neural Biology*, **61**, 191–5.
 70. Guerin, P.M. and Städler, E. (1982). Host odour perception in three phytophagous Diptera—a comparative study. In *Proceedings of the 5th international symposium on insect-plant relationships, Wageningen, 1982* (ed. J.H. Visser and A.K. Minks), pp. 95–105. Pudoc, Wageningen.
 71. Guerin, P.M. and Städler, E. (1984). Carrot fly cultivar preferences: some influencing factors. *Ecological Entomology*, **9**, 413–20.
 72. Hallem, E.A., Ho, M.G., and Carlson, J.R. (2004). The molecular basis of odor coding in the *Drosophila* antenna. *Cell*, **117**, 965–79.
 73. Hansson, B.S., Van der Pers, J.N.C., and Löfqvist, J. (1989). Comparison of male and female olfactory cell response to pheromone compounds and plant volatiles in the turnip moth, *Agrotis segetum*. *Physiological Entomology*, **14**, 147–55.
 74. Hansson, B.S., Larsson, M.C., and Leal, W.S. (1999). Green leaf volatile-detecting olfactory receptor neurons display very high sensitivity and specificity in a scarab beetle. *Physiological Entomology*, **24**, 121–6.
 75. Harris, M.O. and Foster, S.P. (1995). Behavior and Integration. In *Chemical ecology of insects*, Vol. 2 (ed. R.T. Cardé and W.J. Bell), pp. 3–46. Chapman & Hall, New York.
 76. Hern, A. and Dorn, S. (2004). A female-specific attractant for the codling moth, *Cydia pomonella*, from apple fruit volatiles. *Naturwissenschaften*, **91**, 77–80.
 77. Hesler, L.S., Lance, D.R., and Sutter, G.R. (1994). Attractancy of volatile non-pheromonal semiochemicals to northern corn rootworm beetles (Coleoptera: Chrysomelidae) in eastern South Dakota. *Journal of the Kansas Entomological Society*, **67**, 186–92.
 78. Hildebrand, J.G. (1996). Olfactory control of behavior in moths: central processing of odor information and the functional significance of olfactory glomeruli. *Journal of Comparative Physiology A*, **178**, 5–19.
 79. Hirota, T. and Kato, Y. (1999). Influence of visual stimuli on host location in the butterfly, *Eurema hecabe*. *Entomologia Experimentalis et Applicata*, **101**, 199–206.
 80. Honda, I., Ishikawa, Y. and Matsumoto, Y. (1987). Electrophysiological studies on the antennal olfactory cells of the onion fly, *Hylemya antiqua* Meigen (Diptera: Anthomyiidae). *Applied Entomology and Zoology*, **22**, 417–23.
 81. Isaacs, R., Willis, M.A., and Byrne, D.N. (1999). Modulation of whitefly take-off and flight orientation by wind speed and visual cues. *Physiological Entomology*, **24**, 311–18.
 82. Jackson, D.M., Severson, R.F., Johnson, A.W., and Herzog, G.A. (1986). Effects of cuticular duvane diterpenes from green tobacco leaves on tobacco budworm (Lepidoptera: Noctuidae). *Journal of Chemical Ecology*, **12**, 1349–59.
 83. Jermy, T., Szentesi, Á., and Horváth, J. (1988). Host plant finding in phytophagous insects: the case of the

- Colorado potato beetle. *Entomologia Experimentalis et Applicata*, **49**, 83–98.
84. Jönsson, M. and Anderson, P. (1999). Electrophysiological response to herbivore-induced host-plant volatiles in the moth *Spodoptera littoralis*. *Physiological Entomology*, **24**, 377–85.
 85. Judd, J.G.R. and Borden, J. (1989). Distant olfactory response of the onion fly, *Delia antiqua*, to host-plant odour in the field. *Physiological Entomology*, **14**, 429–41.
 86. Kalberer, N.M., Turlings, T.C.J., and Rahier, M. (2001). Attraction of a leaf beetle (*Oreina cacaliae*) to damaged host plants. *Journal of Chemical Ecology*, **27**, 647–61.
 87. Keil, T.A. (1999). Morphology and development of the peripheral olfactory organs. In *Insect olfaction* (ed. B.S. Hansson), pp. 5–47. Springer, Berlin.
 88. Kelber, A. (1999). Why 'false' colours are seen by butterflies. *Nature*, **402**, 251.
 89. Kennedy, J.S. (1986). Some current issues in orientation to odour sources. In *Mechanisms in insect olfaction* (ed. T.L. Payne, M.C. Birch, and C.E.J. Kennedy), pp. 11–25. Oxford University Press, Oxford.
 90. Kennedy, J.S., Booth, C.O., and Kershaw, W.J.S. (1959). Host finding by aphids in the field. II. *Aphis fabae* Scop. (gynoparae) and *Brevicoryne brassicae* L., with a reappraisal of the role of host finding behaviour in virus spread. *Annals of Applied Biology*, **47**, 424–44.
 91. Kennedy, J.S., Booth, C.O., and Kershaw, W.J.S. (1961). Host finding by aphids in the field. III. Visual attraction. *Annals of Applied Biology*, **49**, 1–21.
 92. King, J.R., Christensen, T., and Hildebrand, J.G. (2000). Response characteristics of an identified, sexually dimorphic olfactory glomerulus. *Journal of Neuroscience*, **20**, 2391–9.
 93. Klingler, J. (1958). Die Bedeutung der Kohlendioxyd Ausscheidung der Wurzeln für die Orientierung der Larven von *Otiorhynchus sulcatus* F. und anderer bodenbewohnender phytophager Insektenarten. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft*, **31**, 205–69.
 94. Kuenen, L.P.S. and Cardé, R.T. (1994). Strategies for recontacting a lost pheromone plume: casting and upwind flight in the male gypsy moth. *Physiological Entomology*, **19**, 15–29.
 95. Laissue, P.P., Reiter, C., Hiesinger, P.R., Halter, S., Fischbach, K.F., and Stocker, R.F. (1999). Three-dimensional reconstruction of the antennal lobe in *Drosophila melanogaster*. *Journal of Comparative Neurology*, **405**, 543–52.
 96. Landolt, P.J. (1989). Attraction of the cabbage looper to host plants and host plant odor in the laboratory. *Entomologia Experimentalis et Applicata*, **53**, 117–24.
 97. Langer, H., Hamann, B., and Meinecke, C.C. (1979). Tetrachromatic visual system system in the moth *Spodoptera exempta* (Insecta: Noctuidae). *Journal of Comparative Physiology*, **129**, 235–9.
 98. Ma, W.C. and Visser, J.H. (1978). Single unit analysis of odour quality coding by the olfactory antennal receptor system of the Colorado beetle. *Entomologia Experimentalis et Applicata*, **24**, 520–33.
 99. Matsumoto, Y. (1970). Volatile organic sulfur compounds as insect attractants with special reference to host selection. In *Control of insect behavior by natural products* (ed. D.L. Wood, R.M. Silverstein, and M. Nakajima), pp. 133–160. Academic Press, New York.
 100. Mechaber, W.L., Capaldo, C.T., and Hildebrand, J.G. (2002). Behavioral responses of adult female tobacco hornworms, *Manduca sexta*, to hostplant volatiles change with age and mating status. *Journal of Insect Science*, **2**, 1–8.
 101. Meisner, J. and Ascher, K.R.S. (1973). Attraction of *Spodoptera littoralis* larvae to colours. *Nature*, **242**, 332–4.
 102. Metcalf, R.L. and Metcalf, E.R. (1992). *Plant kairomones in insect ecology and control*. Chapman & Hall, New York.
 103. Miller, D.R. and Borden, J.H. (2000). Dose-dependent and species-specific responses of pine bark beetles (Coleoptera: Scolytidae) to monoterpenes in association with pheromones. *Canadian Entomologist*, **132**, 183–95.
 104. Miller, J.R. and Strickler, K.L. (1984). Finding and accepting host plants. In *Chemical ecology of insects* (ed. W.J. Bell and R.T. Cardé), pp. 127–57. Chapman & Hall, London.
 105. Moeckh, H.A. (1981). Host selection behavior of bark beetles (Col: Scolytidae) attacking *Pinus ponderosa*, with special emphasis on the western pine beetle, *Dendroctonus brevicomis*. *Journal of Chemical Ecology*, **7**, 49–83.
 106. Moericke, V. (1969). Hostplant specific colour behaviour by *Hyalopterus pruni* (Aphididae). *Entomologia Experimentalis et Applicata*, **12**, 524–34.
 107. Morris, W.F. and Kareiva, P.M. (1991). How insect herbivores find suitable host plants: the interplay between random and nonrandom movement. In *Insect-plant interactions*, Vol. 3 (ed. E.A. Bernays), pp. 175–208. CRC Press, Boca Raton.

AQ: Please check the repetition of the word 'system' in the ref. 97.

108. Mulkern, G.B. (1969). Behavioral influences on food selection in grasshoppers (Orthoptera: Acrididae). *Entomologia Experimentalis et Applicata*, **12**, 509–23.
109. Murlis, J. (1986). The structure of odour plumes. In *Mechanisms in insect olfaction* (ed. T.L. Payne, M.C. Birch, and C.E.J. Kennedy), pp. 27–38. Oxford University Press, Oxford.
110. Murlis, J., J.S. Elkinton, and R.T. Cardé (1992). Odor plumes and how insects use them. *Annual Review of Entomology*, **37**, 505–32.
111. Murlis, J., Willis, M.A., and Cardé, R.T. (2000). Spatial and temporal structures of pheromone plumes in fields and forests. *Physiological Entomology*, **25**, 211–22.
112. Mustaparta, H. (1984). Olfaction. In *Chemical ecology of insects* (ed. W.J. Bell and R.T. Cardé), pp. 37–70. Chapman & Hall, London.
113. Mustaparta, H. (2002). Encoding of plant odour information in insects: peripheral and central mechanisms. *Entomologia Experimentalis et Applicata*, **104**, 1–13.
114. Nojima, S., Linn, C., and Roelofs, W. (2003). Identification of host fruit volatiles from flowering dogwood (*Cornus florida*) attractive to dogwood-origin *Rhagoletis pomonella* flies. *Journal of Chemical Ecology*, **29**, 2347–57.
115. Nordenhem, H. and Nordlander, G. (1994). Olfactory oriented migration through soil by root-living *Hylobius abietis* (L.) larvae (Col., Curculionidae). *Journal of Applied Entomology*, **117**, 457–62.
116. Nordlund, D.A. and Lewis, W.J. (1976). Terminology of specific releasing stimuli in intraspecific and interspecific interactions. *Journal of Chemical Ecology*, **2**, 211–20.
117. Nottingham, S.F. (1987). Effects of nonhost-plant odors on anemotactic response to host-plant odor in female cabbage root fly, *Delia radicum*, and carrot rust fly, *Psila rosae*. *Journal of Chemical Ecology*, **13**, 1313–18.
118. Nottingham, S.F., Hardie, J., Dawson, G.W., Hick, A.J., Pickett, J.A., Wadhams, L.J., et al. (1991). Behavioral and electrophysiological responses of aphids to host and nonhost plant volatiles. *Journal of Chemical Ecology*, **17**, 1231–42.
119. Ochieng, S.A., Park, K.C., and Baker, T.C. (2002). Host plant volatiles synergize responses of sex pheromone-specific olfactory receptor neurons in male *Helicoverpa zea*. *Journal of Comparative Physiology A*, **188**, 325–33.
120. Paliniswamy, P. and Gillot, C. (1986). Attraction of diamondback moths, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae), by volatile compounds of canola, white mustard, and faba bean. *Canadian Entomologist*, **118**, 1279–85.
121. Papaj, D.R. and Prokopy, R.J. (1989). Ecological and evolutionary aspects of learning in phytophagous insects. *Annual Review of Entomology*, **34**, 315–50.
122. Pettersson, J. (1970). Studies on *Rhopalosiphum padi* (L.). I. Laboratory studies on olfactometric responses to the winter host *Prunus padus* L. *Lantbrukshoegskolan Annaler*, **36**, 381–99.
123. Pettersson, J. (1973). Olfactory reactions of *Brevicoryne brassicae* (L.) (Hom.: Aph.). *Swedish Journal of Agricultural Research*, **3**, 95–103.
124. Pivnick, K.A., Lamb, R.J., and Reed, D. (1992). Responses of flea beetles, *Phyllotreta* spp., to mustard oils and nitriles in field trapping experiments. *Journal of Chemical Ecology*, **18**, 863–73.
125. Pospisil, J. (1972). Olfactory orientation of certain phytophagous insects in Cuba. *Acta Entomologica Bohemoslovaca*, **69**, 7–17.
126. Prokopy, R.J. (1968). Visual responses of apple maggot flies, *Rhagoletis pomonella* (Diptera: Tephritidae): orchard studies. *Entomologia Experimentalis et Applicata*, **11**, 403–22.
127. Prokopy, R.J. (1986). Visual and olfactory stimulus interaction in resource finding by insects. In *Mechanisms in insect olfaction* (ed. T.L. Payne, M.C. Birch, and C.E.J. Kennedy), pp. 81–9. Oxford University Press, Oxford.
128. Prokopy, R.J. and Owens, E.D. (1983). Visual detection of plants by herbivorous insects. *Annual Review of Entomology*, **28**, 337–64.
129. Prokopy, R.J., Collier, R., and Finch, S. (1983a). Leaf color used by cabbage root flies to distinguish among host plants. *Science*, **221**, 190–2.
130. Prokopy, R.J., Collier, R., and Finch, S. (1983b). Visual detection of host plants by cabbage root flies. *Entomologia Experimentalis et Applicata*, **34**, 85–9.
131. Reddy, G.V.P. and Guerrero, A. (2004). Interactions of insect pheromones and plant semiochemicals. *Trends in Plant Science*, **9**, 253–61.
132. Roden, D.B., Miller, J.R., and Simmons, G.A. (1992). Visual stimuli influencing orientation by larval gypsy moth *Lymantria dispar* (L.). *Canadian Entomologist*, **124**, 287–304.
133. Roessingh, P. and Städler, E. (1990). Foliar form, colour and surface characteristics influence oviposition behaviour in the cabbage root fly *Delia radicum*. *Entomologia Experimentalis et Applicata*, **57**, 93–100.
134. Rojas, J.C. (1999). Electrophysiological and behavioral responses of the cabbage moth to plant volatiles. *Journal of Chemical Ecology*, **25**, 1867–83.

135. Rojas, J.C. and Wyatt, T.D. (1999). Role of visual cues and interaction with host odour during the host-finding behaviour of the cabbage moth. *Entomologia Experimentalis et Applicata*, **91**, 59–65.
136. Rojas, J.C., Wyatt, T.D., and Birch, M.C. (2000). Flight and oviposition behavior toward different host plant species by the cabbage moth, *Mamestra brassicae* (L.) (Lepidoptera: Noctuidae). *Journal of Insect Behavior*, **13**, 247–54.
137. Røsteliën, T., Borg-Karlson, A.K., and Mustaparta, H. (2000). Selective receptor neurone responses to *E*- β -ocimene, β -myrcene, *E,E*- α -farnesene and homo-farnesene in the moth *Heliothis virescens*, identified by gas chromatography linked to electrophysiology. *Journal of Comparative Physiology A*, **186**, 833–47.
138. Röttger, U. (1979). Untersuchungen zur Wirtswahl der Rübenfliege *Pegomya betae* Curt. (Diptera, Anthomyiidae). I. Olfaktorische Orientierung zur Wirtspflanze. *Zeitschrift für Angewandte Entomologie*, **87**, 337–48.
139. Rull, J. and Prokopy, R.J. (2000). Attraction of apple maggot flies, *Rhagoletis pomonella* (Diptera: Tephritidae) of different physiological states to odour-baited traps in the presence and absence of food. *Bulletin of Entomological Research*, **90**, 77–88.
140. Sadek, M.M., Hansson, B.S., Rospars, J.-P., and Anton, S. (2002). Glomerular representation of plant volatiles and sex pheromone components in the antennal lobe of the female *Spodoptera littoralis*. *Journal of Experimental Biology*, **205**, 1363–76.
141. Salama, H.S., Rizk, A.F., and Sharaby, A. (1984). Chemical stimuli in flowers and leaves of cotton that affect behaviour in the cotton moth, *Spodoptera littoralis* (Lepidoptera: Noctuidae). *Entomologia Generalis*, **10**, 27–34.
142. Saxena, K.N. and Khattar, P. (1977). Orientation of *Papilio demoleus* larvae in relation to size, distance, and combination pattern of visual stimuli. *Journal of Insect Physiology*, **23**, 1421–8.
143. Scherer, C. and Kolb, G. (1987). Behavioral experiments on the visual processing of color stimuli in *Pieris brassicae* L. (Lepidoptera). *Journal of Comparative Physiology A*, **160**, 645–56.
144. Schneider, D. (1992). 100 years with pheromone research: an assay on Lepidoptera. *Naturwissenschaften*, **79**, 241–50.
145. Schöne, H. (1984). *Spatial orientation: the spatial control of behavior in animals and man*. Princeton University Press, Princeton, NJ.
146. Schoonhoven, L.M. (1987). What makes a caterpillar eat? The sensory code underlying feeding behavior. In *Perspectives in chemoreception and behavior* (ed. R.F. Chapman, E.A. Bernays, and J.G. Stoffolano), pp. 69–97. Springer, New York.
147. Shields, V.D.C. and Hildebrand, J.G. (1999). Fine structure of antennal sensilla of the female sphinx moth, *Manduca sexta* (Lepidoptera: Sphingidae). II. Auriculate, coeloconic, and styliform complex sensilla. *Canadian Journal of Zoology*, **77**, 302–13.
148. Shields, V.D.C. and Hildebrand, J.G. (2001). Responses of a population of antennal olfactory receptor cells in the female moth *Manduca sexta* to plant-associated volatile organic compounds. *Journal of Comparative Physiology A*, **186**, 1135–51.
149. Singer, M.C. (2000). Reducing ambiguity in describing plant-insect interactions: 'preference', 'acceptability' and 'electivity'. *Ecology Letters*, **3**, 159–62.
150. Singer, M.C., Stefanescu, C., and Pen, I. (2002). When random sampling does not work: standard design falsely indicates maladaptive host preferences in a butterfly. *Ecology Letters*, **5**, 1–6.
151. Skiri, H.T., Galizia, C.G., and Mustaparta, H. (2004). Representation of primary plant odorants in the antennal lobe of the moth *Heliothis virescens* using calcium imaging. *Chemical Senses*, **29**, 253–67.
152. Smith, B.H. and Getz, W.M. (1994). Nonpheromonal olfactory processing in insects. *Annual Review of Entomology*, **39**, 351–75.
153. Srinivasan, M.V., Poteser, M., and Kral, K. (1999). Motion detection in insect orientation and navigation. *Vision Research*, **39**, 2749–66.
154. Städler, E. (1992). Behavioral responses of insects to plant secondary compounds. In *Herbivores: their interactions with secondary plant metabolites*, Vol. II (2nd edn) (ed. G.A. Rosenthal and M.R. Berenbaum), pp. 45–87. Academic Press, New York.
155. Städler, E. (2002). Plant chemical cues important for egg deposition by herbivorous insects. In *Chemical ecology of insect eggs and egg deposition* (ed. M. Hilker and T. Meiners), pp. 171–204. Blackwell, Berlin.
156. Städler, E. and Hanson, F.E. (1975). Olfactory capabilities of the 'gustatory' chemoreceptors of the tobacco hornworm larvae. *Journal of Comparative Physiology*, **104**, 97–102.
157. Steidle, J.L.M. and Van Loon, J.J.A. (2003). Dietary specialization and infochemical use in carnivorous arthropods: testing a concept. *Entomologia Experimentalis et Applicata*, **108**, 133–48.
158. Steinbrecht, R.A. (1997). Pore structures in insect olfactory sensilla: a review of data and concepts. *International Journal of Insect Morphology and Embryology*, **26**, 229–45.
159. Strandén, M., Liblikas, I., Koenig, W.A., Almaas, T.J., Borg-Karlson, A.K., and Mustaparta, H. (2003).

- (–)–Germacrene D receptor neurones in three species of heliothine moths: structure–activity relationships. *Journal of Comparative Physiology A*, **189**, 563–77.
160. Takabayashi, J., Dicke, M., and Posthumus, M.A. (1994). Volatile herbivore-induced terpenoids in plant–mite interactions: variation caused by biotic and abiotic factors. *Journal of Chemical Ecology*, **20**, 1329–54.
 161. Thibout, E., Auger, J., and Lecomte, C. (1982). Host plant chemicals responsible for attraction and oviposition in *Acrolepiopsis assectella*. In *Proceedings of the 5th international symposium on insect–plant relationships*, Wageningen, 1982 (ed. J.H. Visser and A.K. Minks), pp. 107–15. Pudoc, Wageningen.
 162. Thiéry, D. and Visser, J.H. (1986). Masking of host plant odour in the olfactory orientation of the Colorado potato beetle. *Entomologia Experimentalis et Applicata*, **41**, 165–172.
 163. Thiéry, D. and Visser, J.H. (1987). Misleading the Colorado potato beetle with an odor blend. *Journal of Chemical Ecology*, **13**, 1139–46.
 164. Tichenor, L.H. and Seigler, D.S. (1980). Electroantennogram and oviposition responses of *Manduca sexta* to volatile components of tobacco and tomato. *Journal of Insect Physiology*, **26**, 309–14.
 165. Tingle, F.C., Heath, R.R., and Mitchell, E.R. (1989). Flight response of *Heliothis subflexa* (Gn.) females (Lepidoptera: Noctuidae) to an attractant from groundcherry, *Physalis angulata* L. *Journal of Chemical Ecology*, **15**, 221–31.
 166. Tingle, F.C. and Mitchell, E.R. (1992). Attraction of *Heliothis virescens* (F.) (Lepidoptera: Noctuidae) to volatiles from extracts of cotton flowers. *Journal of Chemical Ecology*, **18**, 907–14.
 167. Todd, J.L. and Baker, T.C. (1999). Function of peripheral olfactory organs. In *Insect olfaction* (ed. B.S. Hansson), pp. 67–97. Springer, Berlin.
 168. Tommerås, B.A. and Mustaparta, H. (1987). Chemoreception of host volatiles in the bark beetle *Ips typographus*. *Journal of Comparative Physiology A*, **161**, 705–10.
 169. Traynier, R.M.M. (1986). Visual learning in assays of sinigrin solution as an oviposition releaser for the cabbage butterfly, *Pieris rapae*. *Entomologia Experimentalis et Applicata*, **40**, 25–33.
 170. Valterova, I., Bolgar, T.S., Kalinova, B., Kovalev, B.G., and Vrkoc, J. (1990). Host plant components from maize tassel and electroantennogram responses of *Ostrinia nubilalis* to the identified compounds and their analogues. *Acta Entomologica Bohemoslovaca*, **87**, 435–44.
 171. Van der Ent, L.J. and Visser, J.H. (1991). The visual world of the Colorado potato beetle. *Proceedings of the Section Experimental and Applied Entomology of the Netherlands Entomological Society*, **2**, 80–5.
 172. Van der Pers, J.N.C. (1981). Comparison of electroantennogram response spectra to plant volatiles in seven species of *Yponomeuta* and in the tortricid *Adoxophyes orana*. *Entomologia Experimentalis et Applicata*, **30**, 181–92.
 173. Van der Pers, J.N.C., Thomas, G., and Den Otter, C.J. (1980). Interactions between plant odors and pheromone reception in small ermine moths (Lepidoptera: Yponomeutidae). *Chemical Senses*, **5**, 367–71.
 174. Van Loon, J.J.A., Everaarts, T.C., and Smallegange, R.C. (1992). Associative learning in host-finding by female *Pieris brassicae* butterflies: relearning preferences. In *Proceedings of the 8th International Symposium on Insect–Plant Relationships* (ed. S.B.J. Menken, J.H. Visser, and P. Harrewijn), pp. 162–4. Kluwer Academic Publishers, Dordrecht.
 175. Vickers, N.J., Christensen, T.A., Baker, T.C., and Hildebrand, J.G. (2001). Odour-plume dynamics influence the brain’s olfactory code. *Nature*, **410**, 466–70.
 176. Visser, J.H. (1976). Electroantennogram responses of the Colorado beetle, *Leptinotarsa decemlineata*, to plant volatiles. *Entomologia Experimentalis et Applicata*, **25**, 86–97.
 177. Visser, J.H. (1986). Host odor perception in phytophagous insects. *Annual Review of Entomology*, **31**, 121–44.
 178. Visser, J.H. (1987). Cited in Ref. 146
 179. Visser, J.H. (1988). Host-plant finding by insects: orientation, sensory input and search patterns. *Journal of Insect Physiology*, **34**, 259–68.
 180. Visser, J.H. and De Jong, R. (1988). Olfactory coding in the perception of semiochemicals. *Journal of Chemical Ecology*, **14**, 2005–18.
 181. Vité, J.P. and Gara, R.I. (1962). Volatile attractants from ponderosa pine attacked by bark beetles. (Coleoptera: Scolytidae). *Contributions of the Boyce Thompson Institute*, **21**, 251–73.
 182. Vogt, R.G. (2003). Biochemical diversity of odor detection: OBPs, ODEs and SMNPs. In *Insect pheromone biochemistry and molecular biology* (ed. G.J. Blomquist and R.G. Vogt), pp. 391–445. Elsevier, Amsterdam.
 183. Vosshall, L.B. (2003). Diversity and expression of odorant receptors in *Drosophila*. In *Insect pheromone biochemistry and molecular biology* (ed. G.J. Blomquist and R.G. Vogt), pp. 567–91. Elsevier, Amsterdam.
 184. White, C. and Eigenbrode, S.D. (2000). Effects of surface wax variation in *Pisum sativum* on herbivorous

- and entomophagous insects in the field. *Environmental Entomology*, **29**, 773–80.
185. Wibe, A. (2004). How the choice of method influence on the results in electrophysiological studies of insect olfaction. *Journal of Insect Physiology*, **50**, 497–503.
186. Wibe, A., Borg-Karlson, A.K., Norin, T., and Mustaparta, H. (1997). Identification of plant volatiles activating single receptor neurons in the pine weevil (*Hyllobius abietis*). *Journal of Comparative Physiology A*, **180**, 585–95.
187. Willis, M.A. and Arbas, E.A. (1991). Odor-modulated upwind flight of the sphinx moth, *Manduca sexta* L. *Journal of Comparative Physiology A*, **169**, 427–40.
188. Zacharuk, R.Y. and Shields, V.D. (1991). Sensilla of immature insects. *Annual Review of Entomology*, **36**, 331–54.
189. Zohren, E. (1968). Laboruntersuchungen zu Massenanzucht, Lebensweise, Eiablage und Eiablageverhalten der Kohlflye, *Chortophila brassicae* (Bouché) (Diptera: Anthomyiidae). *Zeitschrift für Angewandte Entomologie*, **62**, 139–88.
190. Zwiebel, L.J. (2003). The biochemistry of odour detection and its future prospects. In *Insect pheromone biochemistry and molecular biology* (ed. G.J. Blomquist and R.G. Vogt), pp. 371–90. Elsevier, Amsterdam.