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HOST ODOR PERCEPTION IN PHYTOPHAGOUS INSECTS

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INTRODUCTION

Phytophagous insects show specialized feeding habits. In general, each species feeds on a restricted range of taxonomically related plant species and in addition limits its feeding to particular plant parts. Most studies on insect-plant relationships concern pest species in agricultural systems, which do not show the stability of the insect's original ecosystem. In monocultures host plants of high quality are present over large areas. Despite the biased nature of these interactions, some generations of insects are forced to disperse and must find new host plants on which feeding results in growth and reproduction (182). Host selection in phytophagous insects consists of a sequence of behavioral responses to an array of stimuli associated with host and nonhost plants. The insects are equipped with sensory receptors enabling them to perceive these stimuli. Plant stimuli involved include in varying proportions visual, mechanical, gustatory, and olfactory characteristics (158). Plant odors have been considered of minor importance in host selection for many insect species, especially those that perform as *r*-strategists (93). This view needs to be reconsidered because such insects as aphids (21, 121, 122), whiteflies (173), and rice brown planthoppers (117), possess the full equipment of olfactory receptors and are attracted by host plant odors.

In the present review selection was made mainly from the literature of the last 20 years. Floral relationships and social insects were excluded. Readers are invited to consult related reviews (49, 145, 158) as well as Dethier (27) for older literature.

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HOST PLANT ODORS

A large number of volatile plant compounds leave the plant surface and on arrival in the new surroundings, air or soil, are transported away from their source of production. Olfactory receptor systems have evolved in phytophagous insects enabling them to perceive some of these plant volatiles, which then compile an odor that acts as a chemical message. The elements of host-odor perception are shown in Figure 1. The role of plant odors in host selection can be traced in the orientation of phytophagous insects toward particular plants, and in the ultimate recognition of host plants for feeding and oviposition.

Host plants can act, in addition, as rendezvous sites, where the sexes meet and copulate. This is obvious when adults and larvae share the same food plants. When adults explore different food sources, odors of oviposition sites are attractive for females as well as males. *Acrolepiopsis assectella* males are attracted to leek (96). Traps emitting allylisothiocyanate also catch male cabbage root flies *Delia brassicae* (50). *Ostrinia nubilalis* males are trapped with phenylacetaldehyde, a corn silk odor constituent (20). Male *Rhagoletis pomonella* flies are attracted by the odor of apples (47). Males possess plant-odor receptors as shown by antennal receptor responses in carrot flies *Psila rosae* (59), *Yponomeuta* species (174), *Manduca sexta* (148), and *Antheraea pernyi* (143). In polygamous bark beetle species, males primarily select the host

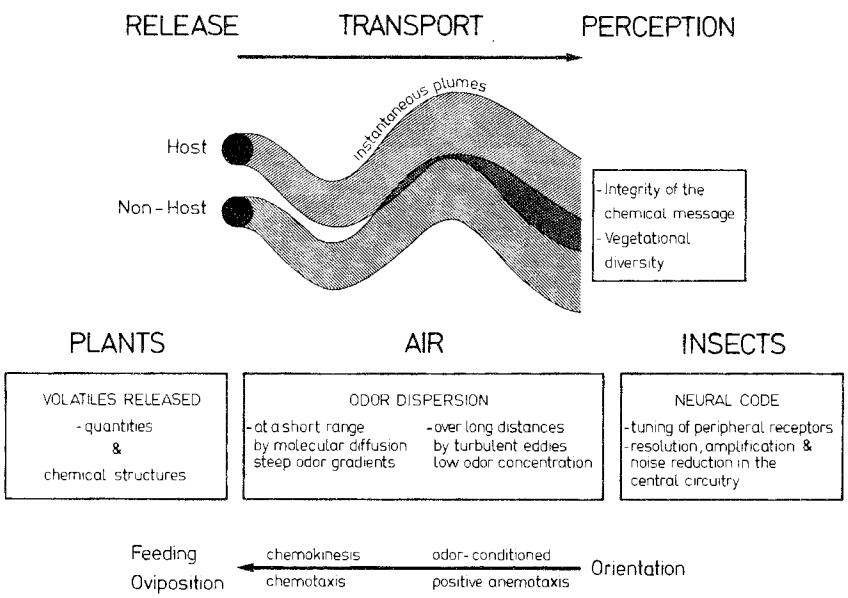

Figure 1 Elements of host odor perception in phytophagous insects.

tree and females follow, lured by the interplay of pheromones and host odors (194). Male oriental fruit flies *Dacus dorsalis* are attracted by methyleugenol, and male melon flies *Dacus cucurbitae* by 4-(*p*-hydroxyphenyl)-2-butanone (106). Females are not trapped by these lures, but might be attracted to the plant sites by male sex pheromones (92, 106).

General and Specific Odor Components

Two alternative hypotheses can be considered in regard to the composition of plant odor blends: (*a*) Plant odors are highly specific and composed of compounds not found in unrelated plant species, or (*b*) plant odor specificity is achieved by the particular ratio between constituent compounds, which are generally distributed among plant species. The validity of both hypotheses can be checked by consulting Table 1. General odor components are formed via biosynthetic pathways generally present in plants. Examples are the production of leaf alcohols, aldehydes, and derivatives from unsaturated fatty acids (187), fermentation products like ethanol and ethyl acetate, and the biosyntheses of terpenes by the polymerization of isopentenyl pyrophosphate (97). Specific odor components arise from the breakdown of secondary plant substances, like the formation of isothiocyanates from the nonvolatile glucosinolates in Cruciferae (23, 48, 49, 97), the formation of sulfides from S-propenylcysteine sulfoxide in onions (75, 97), and the breakdown of prunasin to benzaldehyde in *Prunus padus* (97, 121).

Various insect species are caught in traps emitting plant components, are attracted by odors in laboratory assays, and deposit eggs in the vicinity of an odor source (Table 1). Both general and specific odor components are involved, and the latter have long been recognized. Allylisothiocyanate attracts a number of crucifer-feeding insect species [e.g. *Delia brassicae* as well as pollen beetles *Meligethes aeneus* (53) and flea beetles *Phyllotreta cruciferae* (46)] and stimulates oviposition in diamond-back moths *Plutella maculipennis* (61). General odor components include several groups of chemicals. Fermentation products attract *Drosophila* species (70, 118) and members of the Scolytidae, Cerambycidae, and Cleridae (109). Terpenes and derivatives that are present at high levels in conifer resins attract a number of forest pest insects, as well as insects associated with angiosperms. These compounds are evidently not restricted to conifers. A third group of general odor components is of special interest to a variety of phytophagous insects: the leaf alcohols, aldehydes, and derivatives (182, 183, 187). These so-called green odor components affect the behavior of adult Colorado potato beetles *Leptinotarsa decemlineata, Delia brassicae, Psila rosae, Rhagoletis pomonella, Acrolepiopsis assectella* (Table 1), black fig flies *Silba adipata* (85), vegetable weevils *Listroderes costirostris obliquus* (101), and alfalfa seed chalcids *Bruchophagus roddi* (83).

Although host plants are principally selected by ovipositing females, larvae

do not lack abilities to detect plant odors. Compounds attractive to adult *Drosophila melanogaster* also attract the larvae (118, 127). *Bombyx mori* larvae are attracted by volatiles extracted from mulberry leaves (62, 190). *Papilio demoleus* larvae are drawn to the main constituents of *Citrus* leaf odor (138). Cotton leafworms *Spodoptera littoralis* respond to components isolated from a steam distillate of cotton leaves (90). Larvae of *Plutella maculipennis* and the mustard beetle *Phaedon cochleariae* react to allylisothiocyanate (60, 168). *Psila rosae* larvae show directed responses towards carrot root components (80, 132). A wide range of organic sulfur compounds attracts newly hatched onion maggots *Delia antiqua* (103, 155), whereas adults of this species seem more selective in responding to a limited array of these chemicals (Table 1).

Our knowledge about the chemistry of plant odors is very incomplete. This is illustrated by what we know about cabbage leaf odor. Trap catches of *Delia*

Table 1 Plant odor components that elicit behavioral responses in adult phytophagous insects

Species	Assay[a]	Compounds	Class[b]	Reference
Amrasca devastans	A	Camphene, α-Pinene	G	139
Cavariella aegopodii	T	Carvone	G	21
Rhopalosiphum padi	A	Benzaldehyde	S	121
Leptinotarsa decemlineata	A	*trans*-2-Hexenal, *cis*-3-Hexenyl acetate, *cis*-3-Hexen-1-ol, *trans*-2-Hexen-1-ol	G	182, 183
Popillia japonica	T	Phenethyl propanoate, Eugenol, Geraniol	G	95
Carpophilus hemipterus	T	Acetaldehyde, Ethanol, Ethyl acetate	G	154
Anthonomus grandis	A	α-Pinene, Limonene, β-Caryophyllene, Caryophyllene oxide, β-Bisabolol	G	107
Hylobius abietis	A	α-Pinene, 3-Carene, α-Terpineol	G	114, 149
Ips grandicollis	A	Geraniol, Limonene, Methyl chavicol, Myrcene	G	192
Dendroctonus pseudotsugae	T	α-Pinene, Limonene, Camphene	G	130
Trypodendron lineatum	A	Ethanol	G	108
Delia antiqua	AO	Propanethiol, Dipropyl disulfide,	S	76, 102, 123
	O	Dipropyl trisulfide, Methyl propyl disulfide, Methyl propyl trisulfide, Propenyl propyl disulfide	S	76, 102, 123
	T	2-Phenylethanol, Pentanoic acid	G	77
Delia brassicae	AOT	Allylisothiocyanate	S	50, 66, 172, 189
	A	Hexyl acetate	G	189

Table 1 *(continued)*

Species	Assay[a]	Compounds	Class[b]	Reference
Psila rosae	OT	*trans*-Methylisoeugenol, *trans*-Asarone	S	58, 156, 160
	T	Hexanal, *trans*-2-Hexenal	G	58
Drosophila melanogaster	A	Ethanol, 1-Propanol, Ethyl acetate, Ethyl propanoate, Acetic acid, Propanoic acid, Lactic acid, Butanal, Acetaldehyde, 2-Butanone, 2-Pentanone, 3-Pentanone	G	54, 55, 69, 70, 91, 127
	O	Lactic acid	G	78
Dacus dorsalis	A	Methyleugenol	G	105, 106
Dacus cucurbitae	A	4-(*p*-Hydroxyphenyl)-2-butanone	G	106
Rhagoletis pomonella	A	Hexyl acetate, Hexyl propanoate, Hexyl butanoate, *trans*-2-Hexenyl acetate, Butyl 2-methylbutanoate, Propyl hexanoate, Butyl hexanoate	G	47
Acrolepiopsis assectella	A	Propylthiosulfinate, Methylthiosulfinate	S	170
	A	*cis*-3-Hexen-1-ol	G	170
Laspeyresia pomonella	O	α-Farnesene	G	191
Ostrinia nubilalis	T	Phenylacetaldehyde	G	20
Choristoneura fumiferana	O	*d*-α-Pinene, *l*-β-Pinene	G	157

[a]Compounds are attractive (A), stimulate oviposition (O), or increase trap catches (T).
[b]Chemicals are classified according to their distribution in plant species, as general (G) or specific (S) odor components.

brassicae are increased by allylisothiocyanate, but at release rates much higher than those from healthy cruciferous plants (49). Allylisothiocyanate is the main component of mustard odor, but not of other crucifers. The predominant vapor component of disrupted leaf tissues of crucifers is *cis*-3-hexenyl acetate, but other leaf odor components are present as well (99, 188, 189). For these reasons, allylisothiocyanate is considered as only part of the system involved in attracting *Delia brassicae*. A group of chemically related compounds have been suggested as being involved (23, 48).

Synergistic Effects

Plant odors are complex blends. In the atmosphere around corn leaves more than 90 components have been detected (19). Synergistic effects among the components of an odor blend are likely to contribute to the attraction of insects to plants. Phenethyl propanoate, eugenol, and geraniol show synergism in the trap catches of *Popillia japonica* (95). In trapping *Delia antiqua* and *Hylemya platura* flies, mixtures of 2-phenylethanol and pentanoic acid act syn-

ergistically (77). *Rhagoletis pomonella* flies are slightly attracted by the fatty acid esters isolated from apple odor, but not by the acetate components. The mix of both fractions is as effective as the crude extract (47). Synergism between specific and general odor components has been suggested to explain the higher attraction of *Psila rosae* to traps containing *trans*-asarone and hexanal (58). Several compounds have been identified in the potato leaf odor (182, 187) but none of these components, when applied singly, is attractive for *Leptinotarsa decemlineata* beetles. In fact, if the level of one component in the natural potato plant odor is increased, the beetle's olfactory orientation is prevented (183). The complete odor blend is still not known, but this example illustrates the importance of the concentration ratios among the components present in plant odor blends.

Plant odors can synergize with pheromones as well, as shown in bark beetles (194). In boll weevils *Anthonomus grandis*, the responses to male pheromone are increased by the addition of a mixture of cotton bud volatiles (68).

Phytophagous insects recognize their hosts by a variety of plant characteristics, plant stimuli of different modalities (158). Synergism among modalities is illustrated in the oviposition behavior of *Delia antiqua*. The female needs visual stimuli to land, a stem on which to walk down to the soil, and onion odor to release egg laying (64).

Host Selection

In host-plant selection insects make a number of decisions. An insect continuously evaluates the information from its surroundings, compares this impression with its own internal standards, and decides to continue or change its motor patterns. The adjustment of behavior is triggered by changes in the external information or by transformations in the insect's internal standards, which may be caused by food deprivation, for example. Host-plant selection is divided into several steps—orientation, landing, probing, feeding, and oviposition—that imply sudden changes of external information (145, 182). Most of the available data, (e.g. trap catches, number of eggs, and number of individuals at certain positions in test chambers) are related to the outcomes of a sequence of behavioral responses. Direct observations of insect behavior are scarce.

Host-plant odors induce landing responses followed by oviposition trials in *Psila rosae* and *Delia antiqua* (58, 102). Odor perception releases biting responses in *Phaedon cochleariae* and *Leptinotarsa decemlineata* larvae (22, 33, 168) and feeding responses in *Listroderes costirostris obliquus* adults (101). Cotton odor increases food ingestion of *Amrasca devastans* leafhoppers (139). On artificial diets *Xyleborus ferrugineus* females tunnel further in the presence of ethanol (116). Odor components act as feeding deterrents for *Locusta migratoria* (6). A number of alfalfa odor components attract

Bruchophagus roddi, while other volatile chemicals probably act solely as short-range cues (83). The perceived odor composition is not the same for any given step in host-plant selection. Odor concentrations differ extremely, from minute when the insect is far downwind of the source, to dense when plant tissues are macerated by the insect's mouthparts on the first bite. The number of perceived odor constituents increases as the insect proceeds in host selection; the plant odor becomes more profiled than at the start.

OLFACTORY RECEPTORS

Structures and Numbers

Most olfactory receptors are located on the antennae. Relatively few of these sensilla are found on other head appendages, such as the maxillary palps of lepidopterous larvae (146, 147) and *Locusta migratoria* (7). Olfactory receptors are functionally adapted to respond to airborne volatiles. In root-boring insects these receptors also encounter plant emanations in soil and water. Such sensilla are present in the cephalic sensory organs of *Delia antiqua* (196) and *Psila rosae* larvae (131). In the latter species, the smaller ampullaceous sensillum responds to carrot root components, 2,4-dimethyl styrene and terpinolene (P. M. Guerin, J. H. Visser, unpublished data). Gustatory receptors exhibit olfactory abilities in two cases, the labellar gustatory hairs of the blowfly *Phormia regina* (29) and the lateral sensilla styloconica of *Manduca sexta* larvae (159, 161).

Olfactory sensilla walls possess many pores (198). After adsorption on the cuticular surface, the odor molecules diffuse through the pores and underlying pore tubules to the dendrites of sensory cells. Acceptors for the stimulus molecules are thought to be present in the dendritic membranes. When odor molecules bind with the acceptors, the membrane conductance is changed, generating a decrease in the resting potential. Nerve impulses are subsequently generated and conducted to the central nervous system (10, 82). The time interval from stimulus onset to the generation of nerve impulses ranges up to about 500 ms at very low odor concentrations (81, 82). The antennal receptor cells send their axons to the antennal lobe where the axons terminate in glomeruli (10, 11). The information that is conducted to the brain can be studied by single sensillum recordings of nerve impulses and, in an indirect way, by electroantennograms, which are thought to reflect the summation of receptor potentials in the antenna (12, 97a, 180).

The number of receptor cells involved in plant-odor perception varies widely. Lepidopterous larvae possess approximately 78 olfactory receptors on the maxillary palpi and antennae (32, 147). The antennal nerve of *Drosophila melanogaster* adults contains about 1800 axons (178). The funicle of *Delia antiqua* is estimated to possess 3000 olfactory neurons (74). The number of

antennal axons in adult *Locusta migratoria* is about 50,000 (9, 45). In *Manduca sexta* adults, the flagellum contains approximately 177,000 food odor–sensitive receptors (135). Even within an insect species the number of olfactory neurons varies for different phases in the life cycle. Alate aphids possess more placoid sensilla than apterous forms (18). In *Sitobion avenae* this causes alate forms to have higher sensitivities to leaf odor components (197). Solitary *Locusta migratoria* have more basiconic and coeloconic sensilla than gregarious individuals (56). Social facilitation might compensate for the decrease in olfactory sensitivity.

Receptor Selectivity

The principal function of sensory systems consists of their filter capacity, which permits the discrimination of a limited array of stimuli from the surroundings. Therefore, it is expected that not all plant volatiles are detected by a particular insect, but only those components that convey essential information about plants to which the insect species was adapted in evolution (180, 182). Table 2 shows receptor specificities. The data were extracted from published records and restricted to compounds in plant odors that are stimulating at low concentrations. All olfactory receptor systems respond to general odor components, like the leaf odor components or terpenes and their derivatives. In *Delia antiqua, Delia brassicae,* and *Psila rosae,* olfactory receptors are tuned to specific odor components as well.

Odor Quality Coding

The insect's discrimination of plant odors implies that the olfactory receptors code for odor composition or quality. Individual receptor cells are called specialists or generalists (12). Specialist receptor cells are narrowly tuned to the reception of one or only a few compounds; these are the pheromone sensitive receptors. Generalist receptor cells show broad response profiles and will detect a variety of food-odor components. This classification is not always valid, however. *Hylobius abietis* weevils (113), *Dendroctonus pseudotsugae* (39), and *Dendroctonus frontalis* beetles (37, 38, 120) have receptor cells that are stimulated by pheromones as well as host-tree odors. These do not occur in *Ips pini* (115).

Food-odor receptors have been studied extensively, and their response profiles have been interpreted in numerous ways. In the sensilla basiconica of *Antheraea pernyi,* each olfactory receptor cell shows a unique response profile that overlaps considerably with the response profiles of other receptors (143). On the basis of similarities among the reaction spectra, olfactory neurons have been classified into reaction groups (8, 10, 26, 81, 97a, 113, 151, 171, 176). In the various insect species studied the response profiles of reaction groups display different degrees of separation. The two extremes are (*a*) groups that

Table 2 Selectivity of antennal receptors for plant odor components in adult insects, as evaluated by electrophysiological studies

Species	Compounds	Reference[a]
Carausius morosus	1-Hexanol, Linalool, Citronellol	**171**
Locusta migratoria	*trans*-2-Hexenal, 1-Hexanol, 1-Butylamine	**8, 9, 81,** *182*
Nasonovia ribis-nigri	*trans*-2-Hexenal, Limonene, Linalool	**17**
Sitobion avenae	*trans*-2-Hexenal, Hexanal, Benzaldehyde	*197*
Sirex noctilio	Pinocamphone, Isopinocamphone, Camphor, *trans*-Pinocarveol	*152, 153*
Leptinotarsa decemlineata	*trans*-2-Hexen-1-ol, *cis*-3-Hexen-1-ol, Methyl salicylate	**97a,** *180,* **182**
Rhynchaenus quercus	*trans*-2-Hexen-1-ol, *cis*-3-Hexenyl acetate, Geraniol, Linalool	*94*
Hylobius abietis	α-Pinene, β-Pinene, Camphene, Terpineol, Anethol	**113,** *114*
Monochamus notatus	α-Pinene, Limonene, Camphene	**42**
Ips pini	Linalool, Camphor, α-Pinene, Myrcene	*2,* **115**
Dendroctonus pseudotsugae	Limonene, α-Pinene, Camphene	*36,* **39**
Delia antiqua	Dipropyl disulfide, Dipropyl sulfide, 1-Hexanol, Octanal	*57*
Delia brassicae	Dimethyl disulfide, Nonanal, *trans*-2-Hexenal	*57*
	Allylisothiocyanate, Hexyl acetate, 3-Hexen-1-ol	*189*
Psila rosae	*trans*-Asarone, *trans*-Methylisoeugenol, *trans*-2-Hexenal, Hexanal	*57, 58, 59*
Antheraea pernyi	Terpineol, Isosafrole, Phenylethanol, Geraniol	**143**
Yponomeuta padellus	*trans*-2-Hexen-1-ol, *cis*-3-Hexenyl acetate, Terpinolene	*174*
Adoxophyes orana	1-Hexanol, *trans*-2-Hexen-1-ol, Heptanoic acid, Linalool	*174, 182*
Manduca sexta	*trans*-2-Hexenal, *trans*-2-Hexen-1-ol, 3-Hexen-1-ol	*148*
Pieris brassicae	*trans*-2-Hexenal, *cis*-3-Hexenyl acetate, Phenylethanol, Citral	***3, 26,*** *182*

[a]Boldface = single sensillum recordings; italics = electroantennogram responses.

respond solely to one class of chemicals (81, 176) and (*b*) groups that show considerable overlap in their responses to leaf odor components (97a). Plant odors are differentially detected by the array of olfactory receptor cells belonging to different reaction groups. In one group of cells an odor component evokes higher responses than in other groups. In this way an across-fiber pattern codes for odor quality.

Olfactory receptor cells change their spontaneous activities on stimulation, either increasing or decreasing the frequency of nerve impulses (12, 17, 26, 42, 81, 97a, 113, 143). A decrease is clearly observed at high levels of spontaneous

activity and on application of strong stimuli (81, 97a). In the placoid sensilla of alate viviparae of *Nasonovia ribis-nigri,* antagonistic responses have been observed and interpreted as a refinement of the sensory code (17). Terpenes excited cells in the proximal rhinarium but inhibited cells in the distal rhinarium. Individual neurons, however, could not be identified. Sensilla coeloconica on *Locusta migratoria* antennae contain in variable combinations both *trans*-2-hexenal-sensitive and 1-butylamine-sensitive cells (81). Compounds that stimulate one cell type often inhibit the other receptor. The contribution of the coeloconic sensilla to the brain input, however, is not clearly understood. The sensilla basiconica, which are present in large numbers, are thought to release the principal input for the second-order neurons in the deutocerebrum of *Locusta* (9). The response intensity in a single olfactory receptor depends on stimulus quality and strength. The overall impulse frequency of a single cell cannot code at the same time for quality and concentration. It has been suggested that odor quality coding involves the comparison of impulse frequencies in paired types of receptors (171). In this way, odor quality can be coded over a wide range of concentrations.

The three large sensilla basiconica on the antennae of lepidopterous larvae form a relatively simple olfactory system, as they contain in total 16 neurons (32, 147). In *Bombyx mori* larvae, the cells associated with the sensillum on the antennal headpiece respond to 1-hexanol, 3-hexen-1-ol, and butanal (111). These sensilla have been studied, in addition, in *Manduca sexta* (32, 147), *Hyalophora gloveri* (147), and *Malacosoma americanum* caterpillars (30). In response to stimulation by leaf vapors or chemicals, the associated receptor cells show varying degrees of excitation or inhibition. Furthermore, differences in latency times and interspike intervals have been interpreted as temporal patterns that code for discrimination among odors (32, 147). Temporal patterns, however, are not observed in the antennal receptors of *Pieris brassicae* larvae; on stimulation they respond in a phasic-tonic way (J. H. Visser, H. T. A. M. Schepers, unpublished data). Inactivation of sensilla in *Papilio demoleus* larvae demonstrates that each sensillum contributes in different ways to the reception of individual odor components (138). The perception of a blend probably involves all three basiconic sensilla.

Discussions on odor quality coding will continue because the classification of olfactory receptors in reaction groups is made arbitrarily and depends to a high degree on the treatment of electrophysiological data (151; 97a versus 182).

STRUCTURE-ACTIVITY RELATIONSHIPS

The prerequisite for olfactory reception is the recognition of stimulus molecules thought to bind with acceptor sites on the dendritic membrane, in a fashion similar to that of enzyme-substrate complexes (82). The affinity of a stimulus

molecule to an acceptor is considered to be specifically related to its chemical structure. The specific binding with acceptors implies a definite relationship between the chemical structure of stimulus molecules and their biological activity, which is manifested in the insect's response to odor components. Newly hatched *Laspeyresia pomonella* larvae are attracted to *(trans,trans)*- and *(cis,trans)*-α-farnesene, but the other stereoisomers do not release responses (166). *Trans*-methylisoeugenol is more effective than the *cis*-isomer in eliciting egg laying by *Psila rosae* (156). Synthetic *d*-α- and *l*-β-pinene stimulate oviposition in *Choristoneura fumiferana,* but the optical isomer *l*-α-pinene is not active (157). The low attractiveness to *Dacus* flies of kairomone analogues is overcome by increasing their concentrations to compensate for low acceptor affinities (106).

Structure-activity relationships are well documented in the olfactory responses of insect sensilla (8, 35, 58, 81, 152, 180). Binary mixtures that evoke electroantennograms of additive size have been interpreted to affect two different acceptors (14, 58). The attraction of *Drosophila melanogaster* larvae to test chemicals is affected by a background odor that competes strongly when it has a similar chemical structure and thus affinities for the same acceptors (127). This conclusion is supported by the isolation of several olfactory mutants displaying deficient responses to particular chemicals (127). These mutations affect the peripheral olfactory membrane, as can be deduced from the reductions in electroantennogram responses (177).

The concept of acceptor sites implies that the distributions of acceptor types differentiate the response profiles of individual olfactory neurons belonging to different reaction groups.

CENTRAL PROCESSING

The information running through the antennal nerve is processed and evaluated in the brain at several levels (9–11, 45, 100). The first relay station is found in the antennal lobe. The axons of olfactory receptor cells terminate in glomeruli, where they contact in a network of fine arborizations, local interneurons and output neurons. Local interneurons innervate many glomeruli at the same time, and their axons remain within the deutocerebrum. The output neurons send their axons via the tractus olfactorio-globularis towards other brain centers, and terminate in the calyces of the mushroom bodies (corpora pedunculata) as well as in the lobus lateralis protocerebralis. In olfactory-deprived *Drosophila melanogaster* flies, the total number of fibers in the mushroom bodies is reduced (169). The deutocerebral output diverges extremely in this brain structure (11), and is combined with visual inputs (44, 72).

Input Convergence

The number of glomeruli in the deutocerebrum varies considerably among insect species: *Locusta migratoria* has about 1000 very small glomeruli (45), *Manduca sexta* 57–61 (144), *Mamestra brassicae* about 70 (128), *Pieris brassicae* about 60 (128), and *Drosophila melanogaster* 19 (163). In *Locusta* and *Manduca* the glomeruli receive input solely from the ipsilateral antenna (9, 45, 100), whereas in *Drosophila* the majority of glomeruli are connected to the contralateral side (163).

In the antennal lobe, the number of output neurons is small compared to the number of input elements. In *Locusta,* 800 axons leave the deutocerebrum, compared to an input of approximately 50,000 antennal fibers (9, 45). In *Manduca,* each glomerulus is innervated by one output neuron, implying that 177,000 food odor–sensitive neurons converge onto about 60 output elements (100, 135). The high convergence ratios found in this first relay station indicate several characteristics of the central processing of olfactory signals. First, the incoming signal is amplified and the signal-to-noise ratio is improved (10, 11, 175). The amplification factor ranges from about 3000 *(Manduca)* to 60 *(Locusta).* In addition, olfactory receptors of different reaction groups converge onto the same second-order neurons. Because of this quality convergence, the response profiles of second-order neurons differ from those of peripheral receptors and the odor image is changed (10, 11, 150).

OLFACTORY ORIENTATION

The potential of plant odors for application in pest control raises questions on the effective distance of lures for attraction of insects. Three factors determine the active range of attractants: (*a*) the initial amount of odor released by the source per unit time, (*b*) the manner of dispersion in the air or soil, and (*c*) the insect's orientation mechanisms. No reliable data are available on the first item because plant-odor concentrations in the atmosphere around plants growing in the field are difficult to assess. The other two factors are closely related.

Odor Dispersion

Odor released into the air is transported by the wind. Odor dispersion in the atmosphere is caused by the turbulent nature of wind, which mixes the odor with surrounding air (16, 43, 71, 195). The degree of turbulence is not a fixed measure but varies with location and meteorological conditions, namely the vertical gradients of temperature and wind speed (71). Close to the source the spread of odor molecules is by molecular diffusion and further away by turbulent eddies (16, 43). As a consequence, the odor concentration gradient close to the source is disrupted further downwind. The filamentary structure of odor clouds was early recognized by Wright (195). More recently, Murlis &

Jones confirmed these findings; odor released from a point source appears at a fixed point downwind as a series of odor bursts (112). Dispersion models that predict the average concentration of odor in space are available (43). The Sutton equation has been adopted to calculate the active space for insects responding to sex pheromones (16, 43, 195). Actual stimulus situations, however, differ from those predicted by these time-averaging models. The odor is transported within a narrow instantaneous plume with dimensions that are affected by local conditions and that vary with the time of day when turbulence changes (43, 71).

Orientation Mechanisms

For a long time, orientation mechanisms of animals have been classified in kineses and taxes (52, 87). Taxes are responses directed towards or away from the stimulus source. Kineses are undirected responses like changes in speed or in rate of turning. Animals show orientation responses to stimuli that are unevenly distributed in space. An animal measures intensity differences directly with a paired set of receptors, or responds to different stimulus intensities as the animal progresses. Chemotaxes and chemokineses have been reported for a number of insect species responding to plant odors, in larvae of *Costelytra zealandica* (164), *Psila rosae* (132), and *Drosophila melanogaster* (1). Because these orientation responses depend on steep odor gradients, they occur only at short distances from the odor source. The effective distance for attraction of insect larvae ranges from 0.5 to 4 cm (22, 103, 190). Adult insects are more sensitive to odors. *Drosophila melanogaster* adults show osmotropotaxis at distances up to 23 cm (51). The smallest concentration ratio effective to elicit osmotropotaxis in this insect is 6:10 (15).

Insects use another modality for olfactory orientation, as they are mechanically stimulated by wind. On the perception of an attractive odor, they move upwind. This odor-conditioned anemotaxis has been demonstrated in *Drosophila melanogaster* (51, 86), *Schistocerca gregaria* (89, 110), *Leptinotarsa decemlineata* (34, 179, 185, 186), *Delia brassicae* (66), and apterous viviparae of *Cryptomyzus korschelti* (J. W. Taanman, J. H. Visser, unpublished data). This orientation mechanism operates as soon as the odor concentration is above the threshold of detection; it is thought to be effective over long distances. Two other orientation mechanisms are integrated with odor-conditioned anemotaxis: (*a*) optomotor control, which regulates flight, and (*b*) counterturning (longitudinal klinotaxis) at the edge of an odor plume (88, 193).

Recently a new classification for chemo-orientation has been suggested (5). An insect can change two variables in its motor patterns, namely speed and direction. The insect's steering of these variables is controlled by an internal program (idiothetic control) and by the perception of stimuli from the outside (allothetic control). This approach offers advantages, explaining the processing of information in simple steps while avoiding semantic discussions (e.g. longitudinal klinotaxis in 88; 186).

Repellents

Plant odors can inhibit particular steps in host-plant selection. Repellents have been reported for *Papilio demoleus* larvae (138), *Psila rosae* larvae (132), *Leptinotarsa decemlineata* beetles (142), and crawlers of the red scale *Aonidiella aurantii* (134). The resistance of southern pea lines for *Chalcodermus aeneus* is correlated with repellency (133). A steam distillate of cabbage leaves deters oviposition of *Trichoplusia ni* (126). The plant odor produced on maceration of leaf tissues by feeding larvae may thus signal the unsuitability of plants for oviposition. Compounds that normally attract insects exert repellency at high concentrations (155, 189).

Repellents have been defined as "chemicals which cause insects to make oriented movements away from its source" (31). This definition is solely valid for oriented responses at a short distance from the source, relying on chemotaxis and chemokinesis. In a few cases negative odor-conditioned anemotaxis has been observed (34, 65, 89); however, in these studies chemotaxes cannot be excluded. The action of repellents is restricted to close range (182).

MODIFICATION OF ODOR PREFERENCE

The odor preference of phytophagous insects can be modified in two ways: (*a*) altering the genetic basis and (*b*) olfactory conditioning. When effective for insect populations, modification of odor preference contributes to the formation of biological races, the very beginning of speciation (28). *Dacus* species are attracted exclusively by methyleugenol or 4-(*p*-hydroxyphenyl)-2-butanone (40, 106). It has been suggested that primitive Dacinae coevolved with plants containing the common precursor of these volatile compounds, *p*-hydroxycinnamic acid, and that two subgroups segregated, each subgroup responding exclusively to one of two compounds (105, 106).

Genetic Variation

In *Drosophila melanogaster,* geographic strains differ in their attraction towards several odor components (54). The alcohol preference of larvae is higher in southern Australian populations than in the northern populations (119). This trend might reflect a progressive link with human activities such as artificial fruit fermentation (118). Lines have been extracted from natural populations that differ in attraction (55). In addition, selections for increased or decreased olfactory responses to ethanol, acetaldehyde, and acetic acid have been successful (69, 91). It is obvious that *D. melanogaster* can rapidly adopt new olfactory characteristics. Related insect species differ in their olfactory

responses. *Drosophila immigrans,* which belongs to another subgenus, is very distinct from *D. melanogaster,* as it avoids ethanol (70, 118).

The modification of odor preference can result from, among other things, transformations in the peripheral olfactory receptors (177). The olfactory receptor systems of *Leptinotarsa decemlineata* populations from Utah and Wageningen possess different sensitivities for leaf odor components (182). On the other hand, electroantennograms in populations of *Ips pini* from Idaho and New York are very similar (2). A resemblance is also present between *Dendroctonus frontalis* and *D. brevicomis* (120). Divergence of olfactory tuning is striking between related insect species *Delia antiqua* and *D. brassicae* (57). In *Yponomeuta* species no conclusions about the taxonomic relationships can be drawn from the species-specific response profiles (174).

Olfactory Conditioning

With early exposure, the odor preference of individual insects can change. When tested in the final instar, *Manduca sexta* larvae show increased preference for the food on which they were reared. This phenomenon is called food plant induction (see 25). Amputation of the sensilla styloconica, the gustatory receptors, impairs both induction of preference and food discrimination. Ablations of the maxillary palpi and antennae, bearing the olfactory receptors, do not cause such pronounced effects (63). Also for *M. sexta,* a diet containing citral induces larval feeding preference, and last-instar larvae exhibit increased orientation responses to this diet (140). The induction of odor preference also occurs when the larvae are reared on tomato or radish (141). Larvae evidently possess some sort of memory for plant-odor quality.

Unambiguous evidence that this larval memory is transferred to the adult stage is lacking. In *Drosophila* species, the larval environment does not have a significant effect on the oviposition preference of adults (78). Exposure of *Drosophila melanogaster* adults to peppermint oil or high concentrations of ethanol reduces their aversion to these chemicals in subsequent tests. Oviposition preference for apple or tomato is enhanced, or aversion is reduced, when insects are exposed to one of these foods as adults but not as larvae (79). Associative learning in oviposition site selection occurs also in *Rhagoletis pomonella* flies (124, 125). Learning facilitates the olfactory orientation of *Leptinotarsa decemlineata*. Compared to "naive" individuals, newly emerged beetles fed potato leaves for 2 hr and subsequently starved for 12 hr exhibit increased upwind responses to potato plant odor (J. H. Visser, D. Thiery, unpublished data).

Odor conditioning has been studied extensively in *Drosophila melanogaster*. Larvae can learn to avoid an odor that is paired with shock during their training (1). Adults can be conditioned in the same way (41) or can learn to discriminate

odors on reward with sugar (13). Adults of this species can learn several elements of odor quality; they can discriminate between concentrations, discriminate odor against a background smell, and recognize similarities in odor compositions (13, 41).

ODOR VARIATION AND INTERFERENCE

The compositions of plant odors are subjected to large variations that thereupon raise variations in insect responses. Odor compositions reflect plant conditions and change with plant age (153, 165, 179, 181, 188), plant physiological state (73, 192), crop spacing (99), and season (67, 98; see 187). Sometimes odor components are formed by microorganisms (75), and their inconsistent presence forms another source of variation.

Herbivore loads per plant can be lower in mixed cropping systems (24, 84, 162). Flea beetles *Phyllotreta cruciferae* are more abundant on collards grown in monocultures than on stands of collards interplanted with tomatoes and tobacco (167). It has been suggested that plant diversity reduces the attractiveness of the mixed crop because of interference with the insect's orientation (24, 84, 162). This thought is supported by the present review because (*a*) the general components of plant odors overlap; (*b*) insect olfactory receptors are not solely tuned to specific compounds; and (*c*) plant odors are mixed as they are dispersed by wind (see Figure 1). The chemical message might lose its integrity on mixing and not attract the insect's attention. Evidence on this subject is controversial. *Pegomya betae* flies have been reported to respond to beet leaf odor over a distance of 50 m, even though tomatoes, cabbage, and onions were planted in between (129). The odor-conditioned anemotaxis of *Leptinotarsa decemlineata* towards potato plant odor is distorted by artificially changing the ratios of individual odor components (183). Recent evidence shows that olfactory orientation of this insect is also distorted by mixing potato plant odor with odors of nonhost plants such as the wild tomato *Lycopersicon hirsutum* f. *glabratum* and cabbage *Brassica oleracea* var. *gemmifera* (D. Thiery, J. H. Visser, unpublished data). Nonhost plant odor inhibits oviposition by the leafhopper *Amrasca devastans* (136, 137).

Although general evidence on olfactory inhibition by mixed cropping of plants is lacking, this phenomenon urgently needs experimental observation in order for us to understand effects of plant diversity and evaluate useful plant combinations.

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