

Chemical ecology of oviposition in phytophagous insects

J. A. A. Renwick

Boyce Thompson Institute, Ithaca (New York 14853, USA)

Summary. Selection of a suitable site for oviposition by phytophagous insects is critical for successful development of the offspring. The behavioral events leading to oviposition are mediated to a large extent by chemical cues associated with potential host plants. Orientation and landing are primarily guided by volatile constituents of a plant, whereas assessment of a leaf surface depends on contact stimuli. Chemical mechanisms that ensure adequate spacing of progeny on limited resources include the production of oviposition-detering pheromones as well as recognition of plant constituents released as a result of previous damage.

Perception of chemical cues that affect oviposition involves receptors on antennae, tarsi, mouthparts or the ovipositor. Complex behavior such as tarsal 'drumming' or stem runs may serve to provide increased receptor contact with chemical stimuli. Abiotic and biotic environmental factors often influence the production or release of behavior-modifying chemicals by a plant, and therefore affect oviposition preferences. Plant chemistry may be involved in associative learning, but may also lead to 'mistakes'. Thus a clear correlation between oviposition preference and offspring success does not always exist.

Key words. Oviposition; orientation; host plant; attractants; stimulants; deterrents.

One of the most crucial events in the life cycle of phytophagous insects is the selection of a suitable site for oviposition. Newly hatched larvae of many insects are relatively immobile, and depend on the judicious behavior of their mother to find the best source of food for their successful growth and development. The driving forces affecting host finding and acceptance or rejection are governed largely by nutritional quality, competition, and coincidence of favorable conditions that ensure success of offspring.

Chemical stimuli play a major role in mediating the behavioral steps leading to oviposition (fig. 1). Orientation to a plant and landing may depend on the presence of attractants and arrestants or the absence of repellents emanating from the plant^{10, 39}. After alighting, assessment of the plant surface generally involves contact chemoreception of less volatile stimulants and deterrents⁶⁴. An interplay between positive and negative stimuli is likely to affect the final 'decision' whether to accept or reject a particular plant, and a requirement for specific physical characteristics often adds to the complexity of the interactions^{10, 39, 53, 58}. Other factors such as the physiological state or motivation of the gravid insect, environmental conditions, previous experience or the

presence of conspecifics or other organisms can tip the balance either in favor or against acceptance of a particular site³⁹.

Early observations on the host range of certain insects and the chemistry of their host plants provided correlations that have long been used as a basis for explaining phytochemical specificity. But recent advances in analytical methods, more precise bioassays and the application of electrophysiological techniques have provided new insight into the chemical mechanisms involved in the assessment of plants and their environments. Relatively inconspicuous constituents are proving to be just as important as the 'typical' chemicals of a plant⁴⁴, and the role of negative signals in the process of rejection is increasingly evident³⁰. Specialized systems where chemical stimuli serve to ensure spacing of eggs have been discovered⁵⁰, and chemical explanations for oviposition 'mistakes' are now possible⁴.

Sensory factors and behaviors resulting in oviposition vary widely between species, and especially between specialist and generalist insects. But despite differences in strategies, certain generalizations can be made. Chemical mediation of orientation and landing involves plant volatiles, whereas non-volatile contact stimuli are largely responsible for triggering oviposition. The total process of host selection is most likely to depend on the combined input from different chemical as well as physical stimuli, and the chemical signals are influenced by abiotic and biotic environmental factors⁵³.

The role of plant volatiles

Volatile compounds emanating from plants are thought to play a major role in the orientation of insects to their hosts and in avoidance of unsuitable plants. Yet only a few examples of specific chemicals involved in attracting gravid females to oviposition sites are known. The effect

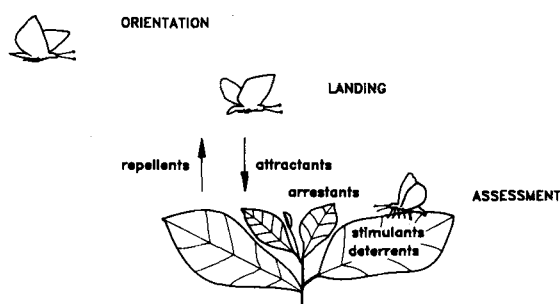


Figure 1. Behavioral events and chemical cues leading to oviposition.

of onion volatiles on host finding and oviposition by the onion fly, *Delia antiqua* (Anthomyiidae), has been widely investigated. Disulfides such as n-propyl mercaptan and dipropyl disulfide are known to be active⁴⁹. A propylthio component appears necessary to elicit an ovipositional response²⁸. However, these compounds appear to stimulate oviposition only at close range, and do not explain the longer range orientation of onion flies to their host plants. Recent studies by Harris and Miller revealed the critical role of visual stimuli of color, shape and size in the process of host finding²⁰.

The well-known chemistry of Cruciferae has provided a basis for many studies on the oviposition and feeding behavior of insects specializing on these plants. The mustard oils, hydrolysis products of glucosinolates, stimulate upwind flight of the cabbage root fly, *Delia radicum*, and thus play a significant role in host finding^{14,46}. Flea beetles (Chrysomelidae) are attracted by allylisothiocyanate, a hydrolysis product of sinigrin¹¹. Short-range attraction of the diamondback moth, *Plutella xylostella* (Yponomeutidae), to volatile extracts of mustard has been demonstrated¹⁹ and allylisothiocyanate appears to increase egg production²².

Essential oils are believed to be involved in attraction of many insects to their host plants. The spruce budworm, *Choristoneura fumiferana* (Tortricidae), oviposits in response to α -pinene and β -pinene present in conifer twigs⁶⁶, and the pine beauty moth, *Panolis flammea* (Noctuidae), can distinguish between different ratios of α - and β -pinene in selecting its oviposition site³⁵. The codling moth, *Laspeyresia pomonella* (Olethreutidae), is stimulated to oviposit by α -farnesene present at the surface of a mature host fruit⁶⁹.

Some insects such as the carrot fly, *Psila rosae* (Psilidae), are guided to their host plants by complex combinations of compounds having varying degrees of volatility. *P. rosae* is attracted to combinations of *trans*-methylisoeugenol and *trans*-asarone with the leaf aldehydes, (E)-2-hexenal, hexanal and heptanal¹⁸. The involvement of the relatively non-volatile *trans*-asarone is likely to be critical in the final step of oviposition after alighting on the plant.

Host plant volatiles may induce landing by gravid insects. An oviposition preference of the brassica pod midge, *Dasineura brassicae* (Cecidomyiidae), for *Brassica napus* over *B. juncea* has been attributed to a higher rate of landing due to olfactory as well as visual cues¹. Similarly, volatiles from citrus hosts of the butterfly, *Papilio demoleus* (Papilionidae), are believed to increase oviposition simply through increased chances of visiting these plants⁶². The black swallowtail butterfly, *Papilio polyxenes*, also lays more eggs in response to umbellifer host volatiles, primarily through an increased frequency in landing¹³. A combination of visual and olfactory cues is responsible for host recognition and oviposition by the cherry fruit fly, *Rhagoletis cerasi* (Tephritidae)³⁶. The rate of oviposition by this insect increases in the presence

of host volatiles, but may be suppressed by odors from non-host fruits.

If an insect depends on volatile cues to guide it to a host plant for oviposition, non-host odors could interfere with orientation. Intercropping experiments in the greenhouse and in the field generally support this idea, and individual chemical constituents have been used to inhibit oviposition in the laboratory⁶¹. However, attempts to disrupt oviposition by the cabbage butterfly, *Pieris rapae* (Pieridae), by interplanting collards with a mixture of herbs resulted in an increase in the number of eggs laid on the collard plants³⁴. However, there is no evidence to suggest that volatiles are involved in the orientation of *P. rapae* to its hosts⁵⁶.

Contact assessment of a plant

After alighting on a plant, a gravid insect depends on a combination of physical and chemical stimuli at the surface to assess the acceptability of that plant for oviposition. Plant glandular structures such as trichomes may serve as physical barriers, but they may also secrete behaviorally active chemicals¹⁷. Other chemicals influencing the evaluation process may be incorporated in leaf waxes or be deposited on the surface through leaching or other secretory processes⁶⁵. Chemical sampling of a leaf surface by the insect may involve 'drumming' with the foretarsi, palpation, or walking to ensure adequate contact of sensory organs with stimulants and nutrients (fig. 2).

Recognition of host plants by many specialists is thought to depend on specific classes of compounds that are characteristic of the plant families utilized. Monarch butterflies (*Danaus plexippus*; Danaidae) prefer to oviposit on a milkweed species (*Asclepias*) that contains higher con-

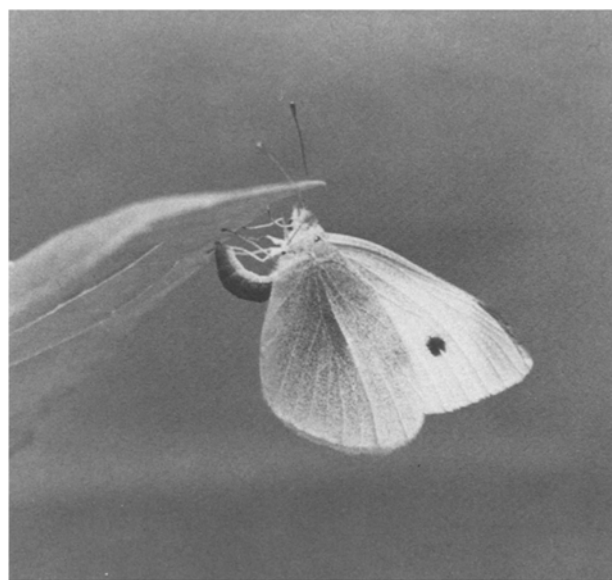


Figure 2. Oviposition following contact assessment by tarsal 'drumming' by the cabbage butterfly, *Pieris rapae*.

centrations of cardenolides³⁷, although stimulation of oviposition by these glycosides has not yet been demonstrated. A similar correlation between host preferences of crucifer-feeding insects and the presence of glucosinolates has been noted, but in some cases, 'key' glucosinolates are thought to be required^{43, 59}. Clear proof that the most conspicuous compounds in a plant can stimulate oviposition has been provided in a few cases. *Delia brassicae* flies require contact with sinigrin or other glucosinolates, but other classes of compounds also appear to be involved at the leaf surface⁴². The buckeye butterfly, *Junonia coenia* (Nymphalidae), oviposits in response to iridoid glycosides that are typical of its host plants in the family Plantaginaceae⁴⁸. Still other insects appear to depend on the presence of mixtures of relatively non-specific compounds that act synergistically.

Many examples of specialist insects ovipositing in response to extracts of their host plants have been reported. Leek moths², tomato pinworm moths⁶, sorghum shootflies⁶⁸, cabbage butterflies⁵⁶, and *Heliothis subflexa* (Noctuidae)⁴⁰ are stimulated by extracts of their respective host plants.

Host selection by moths has received less attention than for other insects until recently, and some real progress has been made in identifying the sensory modalities involved⁵². Cuticular components of green leaves of tobacco stimulate oviposition by tobacco budworm moths, and the active compounds have been identified as divane diterpenes²⁹. Other generalist moths are thought to base their discrimination more on the absence of deterrents than on the presence of specific stimulants⁵³.

Many leaf surface chemicals that stimulate oviposition by swallowtail butterflies have been identified. In all cases, combinations of chemicals appear to be necessary to elicit maximum response. A blend of compounds is responsible for host recognition by the citrus-feeding *Papilio xuthus*⁴⁵. For a related species, *Papilio protenor*, flavone glycosides appear to act synergistically with other constituents of the epicarp of sour orange in stimulating oviposition²⁴, and the black swallowtail butterfly, *Papilio polyxenes*, depends primarily on a combination of trans-chlorogenic acid and luteolin 7-0-(6''-0-malonyl)- β -D-glucopyranoside for recognition of umbellifers for oviposition¹². The results of these studies on swallowtails suggest that blends of plant constituents responsible for host recognition may include generally occurring phytochemicals as well as more specific host compounds.

Since host recognition by specialist insects depends so much on the presence of characteristic chemicals at the leaf surface, a nonhost plant that produces one or more of these chemicals may mislead a gravid insect. Such oviposition 'mistakes' have been reported for several lepidopterans. The crucifer specialist, *Pieris occidentalis*, lays eggs on *Thlaspi arvense*, which is lethal to the larvae⁷. *P. occidentalis* oviposits only on plants that contain glucosinolates, and some of these are present in *T. arvense*.

Although the actual stimulants for oviposition are not yet known, *T. arvense* has chemical features typical of suitable host crucifers. In most cases, such 'mistakes' occur on plants that have been introduced into the insect's habitat⁷. However, at least one example of a native insect ovipositing on an unsuitable native plant has been reported. *Papilio glaucus* eggs were found on an umbellifer which could not support the larvae, but which contained coumarin compounds related to those present in host plants of this swallowtail⁴.

Contact recognition of a host plant for oviposition often involves a complex sequence of behaviors, especially in Diptera. Observations on the turnip root fly, *Delia floralis* (Anthomyiidae), have shown that landing by gravid females is followed by extension of the proboscis and examination of the leaf surface, walking over leaves, running down stems, and walking on the ground at the base of the stem before oviposition occurs²¹. Similar behavior has been described for other specialist flies on onion and cabbage. Chemical extracts of cabbage have been used on artificial leaves to show that the cabbage root fly uses chemical cues during its characteristic exploration of leaf and stem surfaces before laying an egg⁶³.

The role of chemical deterrents at the leaf surface in discrimination by ovipositing insects has recently been emphasized. Extracts of non-host plants are effective in preventing or reducing oviposition on treated host plants in many cases⁵⁴. However, few of the specific chemicals involved have been identified. Studies on 3 species of *Vernonia* (Asteraceae) have suggested that the fall armyworm is deterred by the presence of glaucolide-A in two of the species⁵. Bioassays of extracts from several plants for deterrent activity against cabbage butterflies indicate that non-polar constituents of hosts as well as non-hosts may inhibit oviposition, but polar extracts on non-hosts contain specific deterrents that are not detectable in acceptable plants⁵⁷. The refusal of cabbage butterflies to oviposit on specific crucifers has been explained in the case of Siberian wallflower by the presence of a strophanthidin glycoside⁶⁰. Similar studies on the small white cabbage butterfly have demonstrated the effectiveness of deterrent compounds in the presence of a strong oviposition stimulant⁵⁵. These results suggest that a balance of positive and negative stimuli at the leaf surface could determine whether a plant is acceptable or not.

Spacing mechanisms

Since phytophagous insects depend on an adequate supply of food for their survival and development, species with immobile larvae must have mechanisms to ensure that overcrowding on a limited resource does not occur. In such cases, this is the responsibility of the ovipositing adult, and appropriate mechanisms have evolved to discourage oviposition on food sources that are occupied or where a critical density has been reached. Chemical cues play an important role in signalling the presence of con-

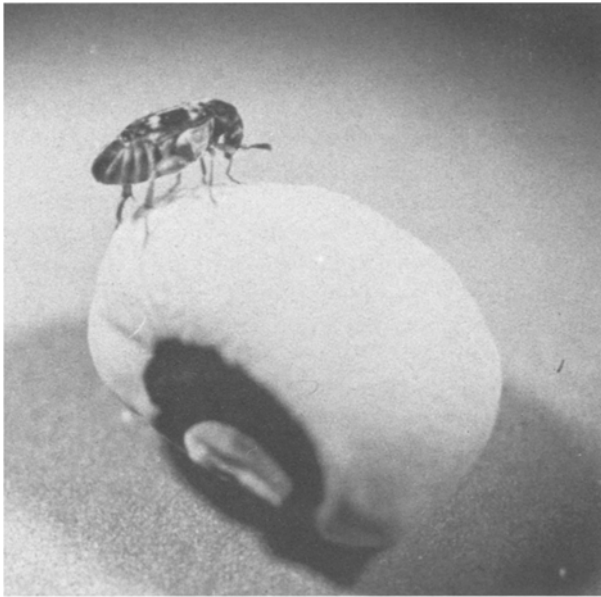


Figure 3. Contact examination of a cowpea surface before oviposition by *Callosobruchus maculatus*.

specific eggs or larvae. Pioneering work on the apple maggot fly, *Rhagoletis pomonella* (Tephritidae), provided the evidence that ovipositing females deposit a pheromone on the surface of the fruit to deter further oviposition on that fruit⁵¹. Subsequent studies have confirmed the existence of oviposition-deterrent, fruit-marking pheromones for several other *Rhagoletis* fruit flies, and similar pheromones for many foliage-feeding insects have been discovered⁵⁰. Seed beetles (Bruchidae) represent another group of insects where total development occurs in one location with limited space, and chemical signals are critical for prevention of overcrowding. Cowpea weevils, *Callosobruchus maculatus*, (fig. 3) utilize a complex combination of physical and chemical cues to detect the presence of conspecific eggs, and have a remarkable ability to assess the number of eggs present³⁸. Other oviposition deterrents of plant origin have been shown to function in the same way. Frass from several insects and plant tissues macerated by larval feeding may contain compounds that deter further oviposition. Juice exuding from olives punctured by ovipositing olive fruit flies, *Dacus oleae* (Tryptidae), provides the signal for distribution of eggs by this species⁸.

The chemistry of oviposition deterrents involved in spacing mechanisms has proved to be extremely difficult to elucidate. However, a Swiss group has recently identified the marking pheromone of the European cherry fruit fly, *Rhagoletis cerasi*, with the aid of an electrophysiological assay²⁶. Some of the active chemicals in olive juice that deter further oviposition by the olive fruit fly have been identified and are included in both oil fractions and water-soluble fractions. Acetophenone and benzaldehyde appear to be involved along with specific diphenols¹⁵.

Environmental effects

Environmental factors may influence host acceptability for oviposition in many different ways. Weather-related changes in the chemistry of the host include removal of oviposition-deterrent pheromone from the surface of fruits by rainfall³. Plants grown in shade or sunlight may be more or less preferred⁶⁷, and this may be a direct result of chlorophyll content, which could make a plant more or less visually attractive⁴⁷.

The physiological condition of the plant plays a major role in the choice of oviposition site by many phytophagous insects. Cabbage butterflies appear to prefer plants that have higher nitrogen and phosphorus contents and higher transpiration rates and a greener color⁴¹. Younger leaves may be preferred by some insects, on the basis of chemistry³², and water content can also affect ovipositional choice⁷⁰. Other environmental factors such as air quality and acidic precipitation are known to have a profound effect on the success of insects on marginal host plants²⁵, and ovipositional behavior is undoubtedly affected by the changes induced by these factors.

Chemical contribution of associated organisms

The utilization of available host plants for oviposition by an insect is often influenced by the presence of the same or other organisms on the plant. The deterrent effect of conspecific larval feeding has already been mentioned, but in some cases, oviposition may be enhanced by larval infestations³³. Chemical emanations from infested maize plants presumably signal the suitability of these plants for oviposition by *Chilo partellus* (Pyralidae) moths. Larval frass of the navel orangeworm, *Amyelois transitella* (Pyralidae), also appears to stimulate oviposition by the adults of this insect on green almond fruits⁹. More often the presence of feeding larvae tends to deter further oviposition, and unrelated insects may also be affected. For example, a chemical released from frass of the garden pebble moth, *Evergestis forficalis* (Pyralidae), has recently been found to deter oviposition by the cabbage root fly, *Delia radicum*. Polar extracts of the frass were effective regardless of the cruciferous plant species on which the caterpillars had been feeding³¹.

Interactions between plants and pathogenic organisms sometimes result in the release of chemicals that affect oviposition by insects. The attraction of onion flies to their oviposition sites is enhanced by the action of bacteria associated with the onion roots. Microbial synergists of the alkyl sulfides in onion have been identified as ethyl acetate and tetramethyl pyrazine²⁷. *Ectomyelois ceratoniae*, a moth that lays its eggs on carob, prefers fruits infested with a fungus, and short-chain alcohols released by the fungus are thought to be responsible for stimulating oviposition¹⁶. Similar attraction and stimulation of oviposition by the yellow peach moth, *Conogethes punc-*

tiferalis (Pyrilidae), has been attributed to volatile constituents of phytopathogenic fungi on the host fruit²³.

Conclusions

Host finding and acceptance for oviposition by phytophagous insects is clearly mediated to a large extent by chemicals associated with encountered plants. However, variations in these chemical cues, caused by one or more abiotic or biotic factors, can profoundly affect the responses of an insect, either positively or negatively. Individual variation in the response of insects to a chemical stimulus may also occur. Such variation may be a result of different thresholds for perception of chemical signals, and learning may be involved in recognition of preferred or unsuitable sites.

The evolution of plant-insect relationships and shifts in host ranges have undoubtedly been influenced by ovipositional responses to plant chemicals. Observed 'mistakes' by females laying eggs on plants that do not support larval development have been traced to chemical similarity of the plants to actual hosts. Although the correlation between oviposition preference and offspring performance is not perfect, the majority of insects can depend on plant chemistry to select the most suitable site for development and survival of their progeny.

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