Lectures of

Insect Physiology 1

(Post – Graduate)

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Lecture: 1

Temperature and Insect Development

Development; The population and fertility of Insects are affected by the habitat temperature in which they live, this gives meaning to the possibility of exploiting the forecasting of pest waves and population dynamics that serve to control programs.

Development of the insect and its relationship with environmental temperature means complex chemical reactions within the physiological insect system which is affected by temperature and might explain how to fit insects with different thermal environments.

Optimal Temperature Rang For Development

The thermal range insect life which capable of wider

range where the insect can maintain the continuity of its evolution and is called the preferred range for evolution and death rates are used to denote in laboratory experiments.

1- Constant Temperature:

Low temperature or high critical temperature caused a sharp increase in death rates, which vary according to the insect species and insect stage, when gypsy moth eggs were exposed to cold temperatures for the habitat, 50 percent of them were exposed to destruction, while the thermal rang for fruit fly eggs survival is between 15 and 35° c, while the appropriate rang for the development of eggs is between 16 and 28 ° c.

Fluctuating Temperature:

Temperature changes play an important role in influencing the evolution of insects, African field crickets when fixed temperature (20 ° c), the percentage of hatching promotes

18%, while if exposed to varying temperatures to this degree hatching rate is between 49 and 65 %.

Therefore, changing the thermal system with a low temperature an average of all day long about the constant temperature is valid for some insects to perform successful development contrary to the constant thermal systems.

But when the thermal range breadth in the direction of high temperature in changing systems, not achieve the same pervious benefit resulting in death of most of the insects.

Death rates depend on the duration of exposure to high-critical temperatures; this may be due to a disturbance in the chemical reactions of the metabolic process, where the food supply and oxygen support is not enough to counter the increased metabolism as a result of high temperature.

Developmental Variables as Affected by Temperature

1- Duration of Development:

Constant Temperature:

It is well known that; the length of period stage during the metamorphosis phases decreases as the temperature increases and increases whenever the temperature decreases than the optimum temperature for development.

When the insect is exposed to a low temperature during its development and with the high temperature in the surrounding environment, the development period decreases until it reaches the optimal temperature of the development and then the growth curve is equal to zero, development rate curve is formed between 20-25 ° c and a maximum of between 25-30 ° c.

It is well known that; the male insects are faster in their development than females within one species. The relationship between the temperature and duration of development can be identified by equations, Janisch 1925.

First equation:

Td= time / 2 [a[T-T opt.] + a [T opt. - T]

Td: development time; Time: the least duration of evolution is empirically proven at the optimal temperature; a: private static type; T: the temperature of the experiment; T opt: optical temperature.

This equation assumes that the thermal activation is shown by two processes, one of which is found in the lower temperatures of the optical temperature (positive effect) and the other higher than the optical temperature (negative effect) as a result of slow growth return on the metabolic disorder.

The relation between the rate of the development and temperature led to the law of thermal constant, which means striking the period of development in the heat effect and this means that there is a thermal point at the beginning of the effect, which then becomes a development time equal to zero for any development,

this should be seen as being by default, because it can't get; Since evolution can be obtained by exposure to temperatures below the effect temperature; in the sense that

there are insects can develop independent of

thermal effects in a wide thermal range such as black carpet beetle insect.

Tc= td [T-T 0]

Tc: Thermal constant; td: development period; T: Experimental temperature; To: Start point effect; T-T 0: Temperature affecting upper starting point effect.

Fluctuating Temperature:

It was noted that the development period becomes less when insects are exposed to a variable thermal system throughout the day by the conditions in which the insect is exposed under field conditions; the insects can under thermal system variable (periodic thermal conditions) when exposed to temperatures below the temperature of non-development; some can develop; probably the thermal needs

of some determinants of the rate of development can covered by. Thermal variation in the lower range of the turning point of the development curve causes speeding of the development rate on the contrary when the thermal change is close to the optimum temperature can slow the rate of development, or be non-existent when compared with constant heat effect with a change over the mid-temperature of the thermal range.

2- Adult longevity:

Constant Temperature:

Under constant temperature conditions, the period of the adult phase is longer on low temperature reverse high temperature; and often the lifespan of the female is shorter than the male at high temperatures, the gravid females of Anticassia have the shortest life of non-gravid at the same temperature

Fluctuating Temperature:

Insects under changing temperature conditions either live longer or shorter depending on insect type; the life of the pink bollworm, Pectinophora gossypiella, is shorter at the fluctuating temperature while the mosquito; Aedes has a longer life span under the same conditions.

3- Size and Weight of the adults:

The size and weight of insects reflect the degree of development and completeness, for example, the ovarian weight of female insects shows how maturity depending on temperature affects females during development and sensibility of ovarian growth with the right temperature for this growth; while the effect of temperature on head capsule and are biometric studies be steadier in change, but body weight is linked to body size when body weight large body size too big (ovaries and body size).

Constant Temperature:

Include numerous relationships by insect type as some insects appear stable in size on a wide range of temperatures, such as the pink bollworm and cabbage white butterfly (pupae and adults), while some insects such as Drosophila and Lixophaga, parasites weigh less in high temperature exposed about 14 ° c; unlike in the European corn borer is getting full insect weight increase temperature.

Fluctuating Temperature:

Changing temperature throughout the day causes adult Appear smaller or larger in size depending on the type of insect, showing large adults with European corn borer and small adults with Egyptian cotton leaf-worm.

4- Fecundity:

Temperature affects the insects produce eggs whether Female sexual maturity before or after metamorphosis, temperature affects ovarian branches before metamorphosis and exit full adult and this goes back to affect body size

Constant Temperature:

Forming the eggs in water insect *Chaoborus* before metamorphosis and laying eggs once off and mating, the female lays eggs in a mass of up to 350 eggs at an egg temperature of 17 ° c; if the experimental temperature rose to 26 ° c decreased the number of eggs to 231 eggs. This means that the appropriate temperature for the growth and development of larvae is suitable for laying eggs. There are insects like pink bollworms where Laying eggs after metamorphosis a thermal optical range for laying eggs; insect of *Platypilia carduidactyla* , lay their eggs in the thermal range from 10 to 28 ° c and the maximum number is placed on the degree of 19 ° c and black field cricket is placed in the range of 20 to 38 ° c and the maximum number a 34 ° c.

Fluctuating Temperature:

Insects that mature their ovaries before forming and are exposed to varying temperatures throughout the day are long warming choices for egg production is the same as for development with his tendency to widen compared to constant temperature; Aphis Therioaphis produces eggs between 8 and 32 °c, while the insect does not lay eggs except in a temperature range between 15 and 30 ° C.

When using heat periods close to those of the insect Habitat Leads produce an enormous number of eggs when compared to constant temperature as in the pink bollworm insect; on the contrary in the black field cricket and Mediterranean flour moth;

Moreover, the size of eggs produced is smaller.

Egg production is also affected by temperature changes associated with changes in the lighting period. For example, the pink bollworm moth puts 272 eggs at a fluctuating temperature of 26 ° C with a prolonged exposure period of light; but when the dark period is up when the same fluctuating temperature is 26 ° c put 171 egg; while putting the number 132 eggs at constant temperature 26° c.

Current Concepts of Temperature Action

Thermal summing theory:

A theory commonly used in pest control to use as the basis formany labor atory experiments to determine the thermal constant for many insect species, through the thermal constant for any stage measurement can predict that within the preferred thermal range ,total temperature to each development period would be the same whether temperature fluctuated around the minimum or the maximum thermal range, meaning that development period is itself under conditions of regular temperature change daily or irregular temperature change and under constant temperature condition; thus the total temperature (total temperature days and total temperature hours) by can predict when increasing the population and outbreak, so if the temperature rise start influencing point meaning begin to influence the average temperature is calculated time to air the region expected risk of pest and added to the total accumulated temperature, , so by applying it experimentally and by calculating

thermal constant and total thermal to an insect, can identify and predict an explosion (outbreak) under the conditions of the field when measured the same temperature; A laboratory computation with field conditions may not be satisfactory, although there is a linear relationship in the correlation curve between the rate of evolution and temperature.

Ts(t)= tsto. T(x) dx

Ts(t) Thermal summing; T0 Threshold ; T x Temporary temp.

In the event of a conflict between the results of temperature change with its equivalent of thermal condition due to lack of a linear relationship between the rate of development and temperature are replacing Thermal summing theory by Development rate summing theory.

Development rate summing theory:

The curves of the relationship between the temperature at the rate of development of the parameters of the rate of metabolism or the rate of chemical reactions, thus , development is a complex set of chemical reactions that controls specific enzyme process rate for rate, the regular sequence of chemical processes to give special compound while developmental interactions to accumulation of development as a final product and the accumulation speed depend on temperature, rate of development, according to this theory is the measurement of chemical reactions behave course addition, this means that under the fluctuating temperature conditions is the same rate of development under constant temperature conditions; it is the result of the collection rate ratios, thus a predictable development rate simply by adding the development rate ratios obtained from relationship to temperature.Depending on the extent of the change, the temperature adjusted ratios must collect either a day or hour or minute this through constant temperature results.

P (t) = tso. P(x) dx; P(x) = rate percentage.

Lecture: 2

Current Concepts of Temperature Action.
Development rate summing theory

Development rate summing theory depends on the relationship between the light and temperature; therefore, the expectation for a generation of insect adult departure conflicts with a prediction by collecting rate ratios, this rule is not able to explain how development rate causes or how to control its rhythm adult exit occurs at a specific time from the day in an insect type.
There is a range of adaptations to fluctuating temperatures
1-Periodical activity throughout the day, when the rest requires metabolism on low temperature relatively less energy (break) after covering its food altogether during high-temperature activity; and it would cost under fluctuating temperatures conditions respiratory metabolism less under conditions of constant temperature, saving energy reflected on the growth and egg pod production.
2-Thermal compensation occurs in metabolic rate leads to a rise in metabolic rate reflects on increasing growth and lack of development period and increased fertility.
3-There's an assumption to explain along the preferred term for development and fertility in low-temperature trend in fluctuating temperatures system; it is a disincentive to development be destroyed and damaged by short-term increase of critical degree to start influencing.
4-The fluctuating temperatures may cause temperature periods that activate the secretion nervous system, accompanied by a accompanied by modification in hormone concentration which in turn influences the stimulation and egg production; this is supported by the increasing concentration of juvenile hormone which has a role in ovarian activation and increase egg production when exposed to fluctuating temperature.
5- Fluctuating temperature may affect the daily organization of metabolic reactions or hormonal control in development; noting that the water insect Chaoborus affected her body weight per day at different times of day temperatures and diapause. Thus the correlation

between the thermal period and photoperiod is a factor in the development time body weight and incidence rate of diapauses.

6-The thermal period may run like a photoperiod, continuous lighting conditions opened or continuous darkness may play fluctuating temperature cycles of rotation such as a succession of night and day; a parasite of Nasonia causes thermal period equal photoperiod responses regarding the percentage of hibernation under conditions of continuous darkness; while under continuous light conditions as in insect Chaobours on thermal cycles around 20 ° c in warm period for 8, 12 and16 hours a day was the time development and body weight is equal to what happens under constant temperature 20 ° c and light 8, 12 and 16 hours; this indicates that the thermal period may play the same role of photoperiod.

Towards- an Improved Concept of Temperature Action

Development in insects has a twofold, growth (quantitative) and differentiation (qualitative face); quantitative change of insect stages is related to time; the duration of each stage is an expression of developmental time, measure mass change accompanying this process by measuring the size at different times and through which the growth curve can get. The rate of development relies on the growth rate and hormonal system that determines the critical size of the differentiation.

Egg production which distinguishes between quantitative and qualitative face, egg mass growth in size quickly adjusted while the number of eggs and egg size in the mass which is the differentiation process output split available of mass growth to the number of eggs and specific size.

The processes of growth and differentiation are temperature zones; where the temperature plays a role in growth processes and differentiation.

Some Fundamentals of Growth, Metamorphosis and Reproduction

Growth in insects is similar to other cold blood, with some deviation from the ideal growth curve might be due to: loss of weight or quantity of water ingestion during moult or timing of metamorphosis; where the insect (Metabola and Hemimetabola) growth terminated by metamorphosis.

The rate of growth achieved in a sufficient source of food, energy and oxygen in the presence of moult hormone (Ecdysone) responsible for moulting after achieving adequate levels of growth and metamorphosis also; it's a catalyst for growth and formation and is a catalyst for growth, and affect critical environmental conditions (light and temperature) to grow to the point where it might lead to growth slows or stops as in the case of diapause.

Environmental temperature has two effects on growth rate one directly through its effect on metabolic reactions, and another indirectly through its influence on glandular organ (catalyst).

Glandular organ in insects has an important role in the process of differentiation, glandular organ consists in insects:

- Neuronal cells of the brain
- Corpora Cardiaca
- Corpora allata
- Prothoracic gland

Endocrine gland secretory neurons consist of hormone secreted directly into the hemolymph.

Some Fundamentals of Growth, Metamorphosis and Reproduction

Rate of temperature development rate is influenced by two possibilities:

1. A critical size is achieved through growth processes.
2. A specific time-critical independent of growth.

The first possibility is consistent with the experimental results, where to reach a critical size, is need necessities of metamorphosis occurs; when the critical mass is, the rate of development will depend on the different processes: first, determine the critical size is achieved through a second operation and growth process,

This means that the metamorphosis depends on achieving critical size before becoming metamorphosis-enabled, and it must be known that critical mass can be reached in the larvae that fed on different food values or in the hungry larvae, where there is a timeline for development and this is reflected in the size.

Glandular system plays an important role in achieving the critical size; this has been demonstrated by typical experimental work, including the removal of the corpora allata gland or its implantation as an addition, or the increase in the concentration of the moulting hormone or the juvenile hormone or similarity; this leads to the exit of the insect growth curve early or late for its normal development (dwarves members when accelerating growth or giants members with slowly growing), thus the critical size of the metamorphosis can be determined as low or high through hormonal concentration, so size detective don't swift or slow growth rate, but due to the hormonal system mutated and its impact on critical size determination.

Certainly, the hormonal effect activates after providing the necessary nutrients to achieve the specified growth of the metamorphosis, and the hormonal system starts here, in case of starving the insect and the arrival of the stage to the period critical for metamorphosis produces small-size members or sterile, so hormonal activity is influenced by starvation.

Ovulation and egg production are affected by the same special effects on growth rate and the hormonal system has a role in controlling the growth, size of egg number and maturity within ovarian branches, when injected Insect ecdysteriodes or JHIII hormones have a role in increasing the weight of eggs and activate egg laying in some insects such as black field cockroach.

Temperature Action on Development and Reproduction

Similar changes to the size of the individual and the size of the eggs are the result of environmental influences such as temperature photoperiod and thermal period and link with the glandular organ of nervous system events, as illustrated by the following examples:

1- The specified weight of the adult insect of Chaoborus is achieved on light periods different with a constant temperature of 20 ° c or thermal periods through about 20 ° c for periods of 8, 12 and 16 hours a day and the conditions that lead to shortening the development period; size is less, this is certainly due to the critical size modification by the glandular organ of the nervous system.

2- Black field cockroach laid fewer eggs under conditions of fluctuating temperature compared with constant temperature, if the number of eggs increases due to the eggs of the same egg mass formed as a result of the influence factors of metamorphosis.

Therefore, nervous glandular sensitivity towards temperature changes, affecting moulting hormone and juvenile hormone concentration; in comparison, the effect of temperature on growth rate is not only more uniform in all insects but in all cold blood, although there are differences in absolute growth rate, the relationship between temperature and rate of growth approximately follows t the theory of addition.

It is clear from the above that the temperature affects the rate of growth; metamorphosis and production of eggs, while the photoperiod affects both the metamorphosis and production of eggs, but it doesn't affect the growth rate, and these effects are mediated by glandular systems.

Evidence for the concept of Dual Temperature Action:

- **Sub-Threshold Development:**

Development can occur and be achieved under sub-threshold level of development, where the slow growth rate associated with certain conditions prevents the insect from achieving its critical size of metamorphosis in a certain period, but when exposed to high temperatures and suitable has been increasing growth followed by access to the critical mass of the metamorphosis.

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- **Varying Temperature Coefficients of the Development Rate:**
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Development in an insect, Pieris rapae, with temperature-dependent achieved almost constant body weight and that means weight independence temperature effect, while the size of insect body of Chaoboura growing in a linear relationship with increasing temperature between 17-26° c, insects can speed up or slow down their development not only by thermal compensation growth rate but by critical size modulation. Perhaps return the harmony of development time with low temperatures in the polar regions to the critical size modulation that is lower in these areas, Slowly growing insects develop relatively rapidly when the critical size required for metamorphosis is small.

Time of Development under Fluctuating Temperature:

Evidenced by the ability to control the duration of development by changing the critical size and growth rate that the rate of development is not a real rate on physical chemical sense such as growth rate, and it can be relied on as evidence of the rate of development as in the cabbage worm leaf cabbage, where the growth rate is rate is equal to the rate of development under the influence of fluctuating temperature, but this theory is not common; cotton leaf worm gives adult small size when the development period is less under the conditions of the fluctuating temperature compared to the constant temperature.

If fluctuating temperature has led to increased critical size, the influence of the duration of development differs:

1- May not offset the effect on the total growth rate increase critical size, of thermal variation, this critical size needs more time (development time) compared to constant temperature conditions.

2- This may offset the effect on the total growth rate increase in critical size, meaning that critical size (development time) could be achieved at the same time under constant temperature conditions.

Growth rate under fluctuating temperature effect may lead to achieve critical size early or late if this rate not dependent on temperature.

Fluctuating Temp. and Increased Fecundity:

Egg masses are formed not only increasing depending on growth rate but metamorphosis is influenced by temperature affecting ovarian branches and number of eggs and egg size and duration of the mature eggs is complete, this mean increased fertility under fluctuating temperature conditions as in black field cockroach.

- **Photoperiod and Thermo period Action:**

Long day causes shortness of development in most insects, already stated that development and body size in insect *Chaoborus* is similar under different conditions of light period and constant temperature, with constant lighting conditions and fluctuating temperatures.

Sequence of the thermal cycle and its association with periodic light hour have an effect on the metamorphosis and these processes are mediated by a nervous glandular.

- **Temporal Programming of Adult Emergence and Oviposition:**

Emergence of adult and laying eggs is a daily and laying eggs is a daily pattern shows that there are operations directed to that controlled by hours photoperiod and nervous glandular.

It time development consists of today's unit, and this illustrates that development period can be finely regulated with different environmental situation.

Double action theory of temperature on development time and adult size and fertility produce events for temperature on the rate of growth is responsible for all growing operations, as well as accumulated effect of temperature controlled nervous glandular how especially type.

Lecture: 3

Host-Plant Selection: How to Find a Host Plant.

Most species of insects 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. For several insect species it has been shown that they may even prefer particular individuals within a host-plant population. Selection behaviour indicate that, the host plant-range of a certain insect species dose not necessarily include all plant species that appear under laboratory testing conditions behaviourally acceptable or nutritionally adequate; under natural circumstance 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 a small body size and consequently possess limited energy reserves, they are capable of leaving the plant on which they hatched if they appear to judge it unsuitable. There are a number of 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. The arrival in a novel habitat after migration or dispersal and local exhaustion of food plants are other examples of such circumstances. Food specialization requires the ability to find and recognize host plants, which in natural habitats often grow in mixed and complex vegetations.

Host-Plant Selection: How to Find a Host Plant.

Terminology:

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

- **Searching:** when an insect is remote from a potential food plant, it needs to search for and find that plant. To locate a host plant, it needs to move towards it and contact it, or at least to arrive and stay in the proximity of it in order to further examine its characteristics. 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 synonym, may rather be the end result of searching.

Selection: In the strict sense of the word, to select' means to choose from among alternative. In order to do this, it is necessary that differential sensory perception of alternative food plant occurs. Selection thus implies a weighting of alternatives. From a methodological point of view it is difficult to prove that comparison of alternatives is being behaviour, especially if contacts with potential hosts occur sequentially. Sequential contacting occurs more frequently than simultaneous contacting .In case 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 assumptions implied by the term selection. For example, when a beetle is released in the middle of a monoculture 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, since no alternatives were available. It can only be said that the bean plant is accepted by the insect.

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 sought for. This image is present in one or another from in the central nervous system of the insect. The profile of incoming sensory information on plant cues is compared to 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 quite some extent.

From the above it appears that the term 'acceptance' is the most straightforward one, while searching, selection, preference and recognition implicitly refer to complex behavioural processes, the neural mechanisms of which are being elucidated. It is also important at this point to relate the behavioural terms defined above to the classification of semiochemicals that may effect host-plant selection behaviour, this terminology is summarized in following table.

TABLE: CHEMICAL DESIGNATION IN TERMS OF INSECT RESPONSES

Attractant: A chemical that causes insects to make oriented movements towards its source.

Repellent: A chemical that causes insects to make oriented movements away from its source.

Arrestant: A chemical that may slow the linear progression of an insect by reducing actual speed of locomotion or increasing turning.

Feeding or ovipositional stimulant: A chemical that elicits feeding or oviposition in insects (feeding stimulant is synonymous with phagostimulant).

Deterrent: A chemical that inhibits feeding or oviposition when present in a place where insects would, in its absence, feed or oviposit.

Host-Plant Selection:

A catenary process:

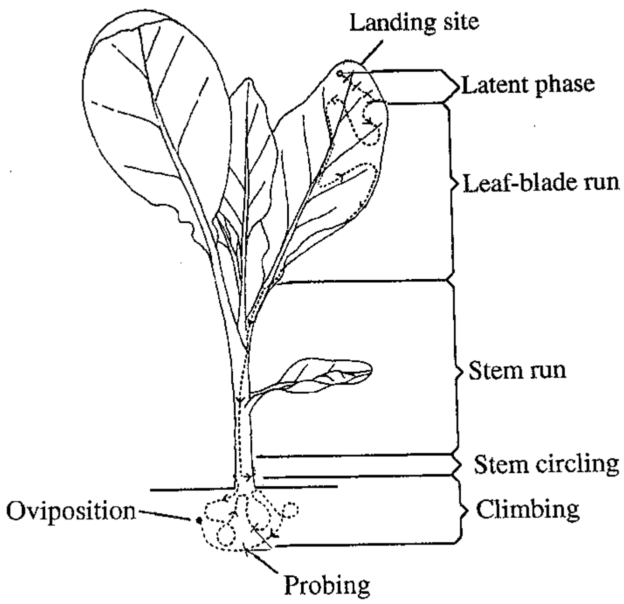
Insects are often said to show' programmed behaviour' and stereotype, predictable sequences of behavioural acts, so-called reaction chains. This means that more or less distinct behavioural elements follow each other in a fixed order. The insect shows appropriate reactions to a succession of stimuli.

When the outcome of a sensory evaluation is rejection of a particular plant or plant part as food or oviposition site, the insect jump back to one of earlier steps in the reaction sequence. Modification of selection behaviour as a result of previous experience leads to faster decision making or to changes in preference, but the sequence remains the same.

In the process of host-plant selection two main consecutive phases may be distinguished, delimited by the intermittent decision to stay in contact with plant: 1- searching and 2- contact-testing; the first phase may end with the event of finding; the second phase ends by acceptance or rejection.

FIGURE A EVIDENCE THE COMPLEX BEHAVIOUR PATTERNS INVOLVE A SEQUENCE OF STIMULATION AND RESPONSE STEPS, AS EXEMPLIFIED BY OVIPOSITION BEHAVIOUR IN THE CABBAGE ROOT FLY (*DELIA RADICUM*).

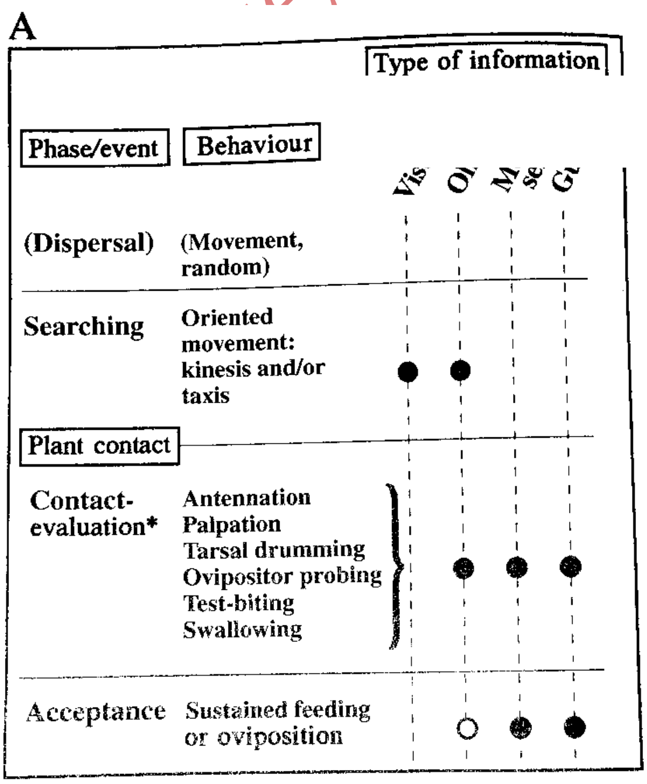
An airborne gravid female fly may land in response to yellow-green wavelengths (500-600nm), as reflected by green foliage. During the 'latent phase' she walks along the leaf, pausing now and then to groom or to make short flight. During the next phase, the leaf-blade run' she walks continuously, often 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 stem or a midrib of a leaf, which is quickly followed. 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 centimeters. 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.

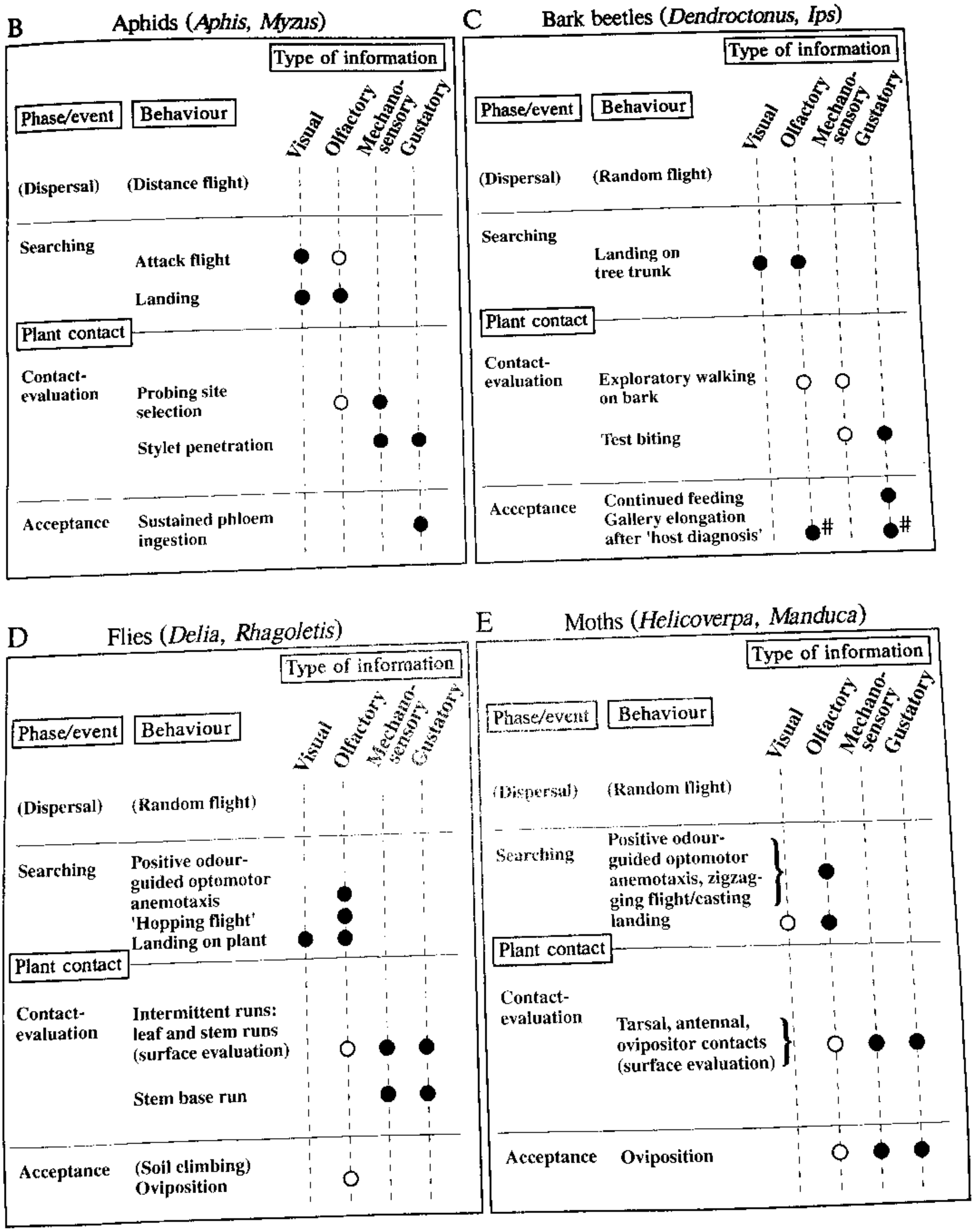


ACCEPTANCE IS A CRUCIAL BEHAVIOURAL DECISION AS IT RESULTS IN INGESTION OF PLANT MATERIAL OR DEPOSITION OF EGGS, WITH POSSIBLE NEGATIVE CONSEQUENCE FOR FITNESS. A HOST-PLANT SELECTION SEQUENCE IS SCHEMATICALLY DEPICTED IN FIGURE (A).

Generalized sequence of host-plant selection behaviour of 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. ●: well documented plant cues for several species; ○: Suggested or probable; *: examples of behavioural elements displayed by many species, not all elements occur in a particular species and not necessarily in this sequence. Between brackets at the top, dispersal is indicated as a preceding behavioural phase with its behavioural elements.

B–E HOST SELECTION BEHAVIOUR SEQUENCE OF REPRESENTATIVES OF THE MAJOR INSECT ORDERS.




B
Aphids (Aphis, Myzus)
Type of information
Phase/event
Behaviour
Visual
Olfactory
Mechano-sensory
Gustatory
(Dispersal)
(Distance flight)
Searching
Attack flight
Landing
Plant contact
Contact-evaluation
Probing site selection
Stylet penetration
Acceptance
Sustained phloem ingestion
C
Bark beetles (Dendroctonus, Ips)
Type of information
Phase/event
Behaviour
Visual
Olfactory
Mechano-sensory
Gustatory
(Dispersal)
(Random flight)
Searching
Landing on tree trunk
Plant contact
Contact-evaluation
Exploratory walking on bark
Test biting
Acceptance
Continued feeding
Gallery elongation
after 'host diagnosis'
#
#
D
Flies (Delia, Rhagoletis)
Type of information
Phase/event
Behaviour
Visual
Olfactory
Mechano-sensory
Gustatory
(Dispersal)
(Random flight)
Searching
Positive odour-guided optomotor anemotaxis
'Hopping flight'
Landing on plant
Plant contact
Contact-evaluation
Intermittent runs: leaf and stem runs (surface evaluation)
Stem base run
Acceptance
(Soil climbing)
Oviposition
E
Moths (Helicoverpa, Manduca)
Type of information
Phase/event
Behaviour
Visual
Olfactory
Mechano-sensory
Gustatory
(Dispersal)
(Random flight)
Searching
Positive odour-guided optomotor anemotaxis, zigzagging flight/casting
landing
Plant contact
Contact-evaluation
Tarsal, antennal, ovipositor contacts (surface evaluation)
Acceptance
Oviposition

Going through the sequence, the number and intensity of the cues the plant offers to the insect increase and thereby also potentially the intensity and modalities of sensory information 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 plants is found, i.e. it is contacted by either touching or climbing it or 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 (chewing species), probing (sucking species) or puncturing with the ovipositor.

7-The plant is accepted (eggs being laid or continued feeding) or is rejected, resulting in the insect's departure.

HOST-PLANT SELECTION: A CATENARY PROCESS

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. 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 physiology status.

Host-Plant Selection: Search Mechanisms

To understand the ways in which insects search, it is necessary to present a description of searching behaviour as well as a discussion of possible causal mechanisms involved.(Random search or highly directed search patterns)

In the field, random search has been described for various insects, such as polyphagous caterpillars, immature and mature polyphagous locusts, and adult oliphagous Colorado potato beetles. In these cases, frequency, rate and direction of movement appear unrelated to the suitability of plants within their perceptual range, i.e. the range in which host-plant derived cues are detectable by the sensory system.

Host-Plant Selection: Search Mechanisms

The generation of random movements can be explained by the functioning of so-called’ central motor programmes' located in CNS . When an insect becomes motivated to search for food, e.g. because blood trehalose levels fall below a certain level, these programmes are activated and as a result the insect may start a random walk.

During random search, several types of orientation response may be performed upon stimulation by plant-derived cues. These responses may be either non-directed or directed.

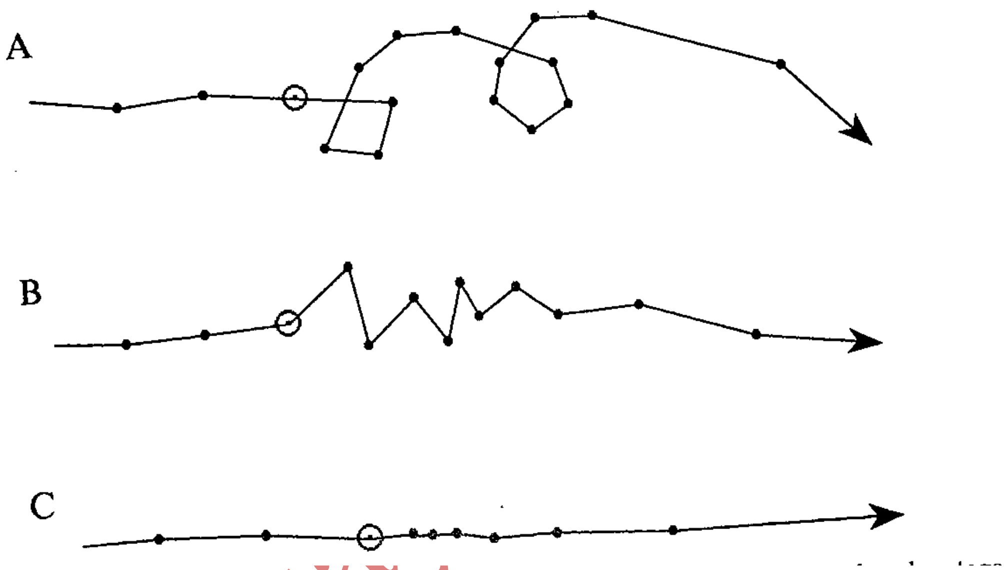
The non-directed in random movement are classified as kinesis. The insect may change its linear speed of movement or it may change rate or frequency of turning.

These kinetic responses often lead to area-restricted search, i.e. an intensified search in a small area. They are most prominent close to a host plant or upon contact **(figure b and c).** Rate of linear movement often decreases and turning rates increase.

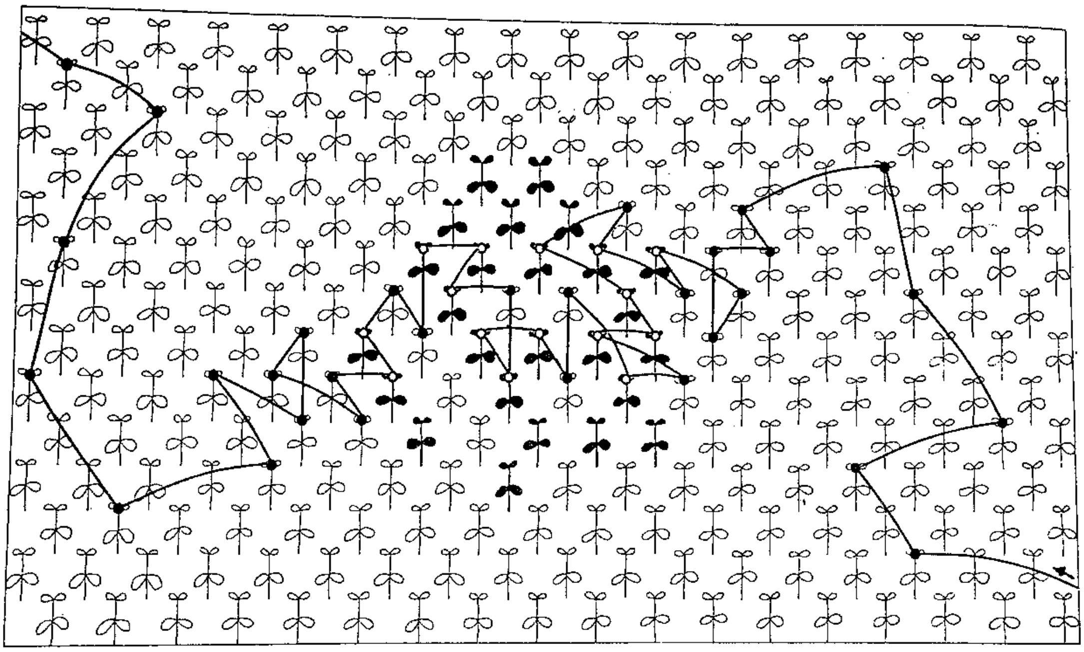
HOST-PLANT SELECTION: SEARCH MECHANISMS

Directed movement in random movement becomes possible when the host plant emits signals that, either alone or in combination with a second cue, allow directionality to perceive 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 influence of central motor programmes. Wind or light direction, perceived as air flow by mechanoreceptors or photo 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. Light compass orientation, is a main mechanism for insects walking on the ground.

Directed orientation is often viewed as adaptive, as it improves the efficiency of search, i.e. it produces a higher success ratio per unit of time and energy invested in searching behaviour.



Searching patterns used where resources are aggregated. In these cases it may be advantageous for an insect to search an 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 length of moves between stops.
Dots indicate landing, circled dots represent landing on host plants followed by egg lying.



Behaviour search in egg laying females of *Cidaria albulata* , a specialist on *Rhinanthus spp*. The moths fly shorter distances between alighting's and show more turning flight near a host-plant, thereby increasing the chance of alighting on a host plant. Turning of flight path and alighting are stimulated by host-plant odour. Total number of plants=252; no. of *Rhinanthus* plant=25 total no. of alighting =45; number of alighting on *Rhinanthus*= 15

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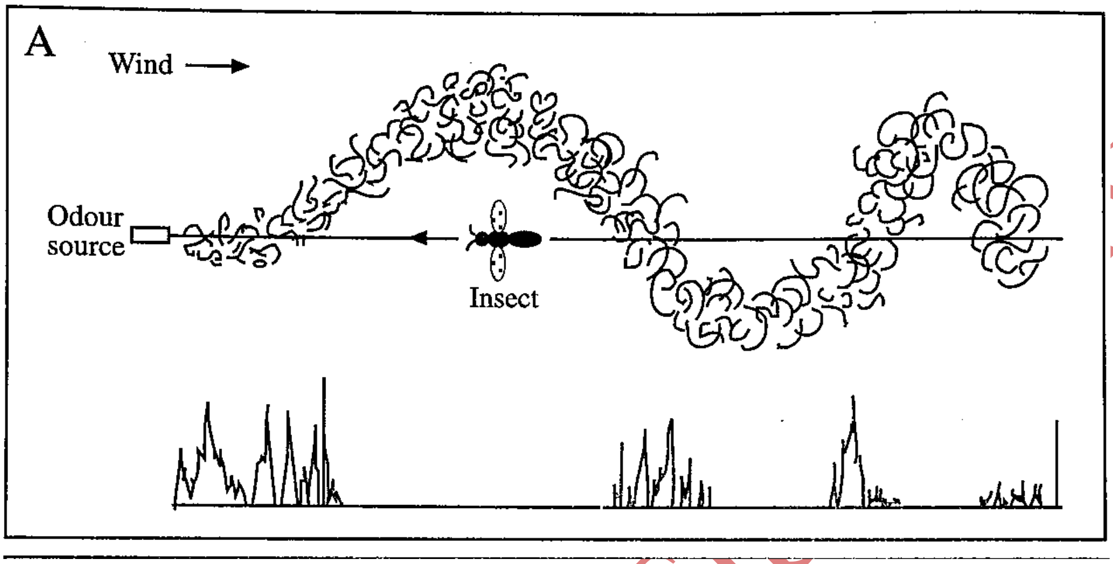
ORIENTATION TO HOST-PLANT:

- **Optical versus chemical cues :**

Two important types of stimulus that could be used as directionality cues by 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 nature of optical and chemical plant derived cues differs in some important aspects. 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. 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 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.



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.

ORIENTATION TO HOST-PLANT:

- **Optical versus chemical cues :**
  When considering abiotic factors, optical plant characteristics are relatively constant with respect to their distribution and largely in dependent of temperature and wind speed, but of course they depended on light intensity. Odours emanating from plants have a spatially highly variable distribution and concentration, which depends on wind speed, on temperature

and to some extent also on light intensity. Moreover, the quality and quantity of emitted plant volatiles may vary with the plant's physiological state and wounding effects. 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.

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 the threshold for a behavioural response. In the absence of visual cues, behavioural responses to plant odours have been demonstrated at distances of 5-30m for several oligophagous species, with a maximum of 100m reported for the onion fly , *Delia antiqua.*

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 50m, even if these odours have passed non-host plant. Optical contrasts in a mixed plant stand may be perceived over distances of a few meters especially in flying insects.

Table 5.2 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		
Leptinotarsa decemlineata	0.6	54
	6	33
Ceutorhynchus assimilis	20	38
Delia radicum	24	41
Dendroctonus spp.	30	127
Pegomya betae	50	2
Delia antiqua	100	55
Optical cues		
Delia brassicae	2	87
Empoasca devastans	3.6	95
Leptinotarsa decemlineata	8	115
Rhagoletis pomonella	10	4

Visual responses to host-plant characteristics:

Three optical characteristics of plants may influence host selection behaviour: spectral quality, dimensions and pattern. The spectral sensitivity of insect compound eyes range from 350-650nm (near ultraviolet to red) and thus includes shorter wavelengths than that of the human eye. 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 while at greater distances perception of shape is poor.

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 visual discrimination some examples of insect responses to optical host-plant cues, such as shape and color, will be presented.

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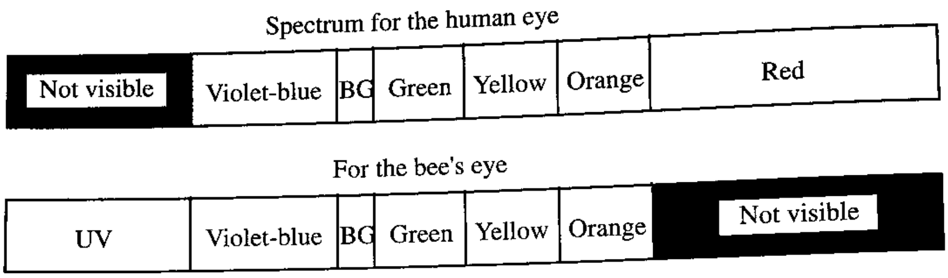


Lepidoptera:

The responsiveness of day-foraging butterflies to colours has been relatively well studies. When artificial green paper leaves are offered to oligophagous cabbage white butterflies, *P. rapae and P. brassicae,* naive individuals show landing responses, albeit at much lower frequencies than with cabbage leaves. Immediately upon alighting on the substrate they start to drum it for a few seconds, even through specific host-plant chemicals are absent.

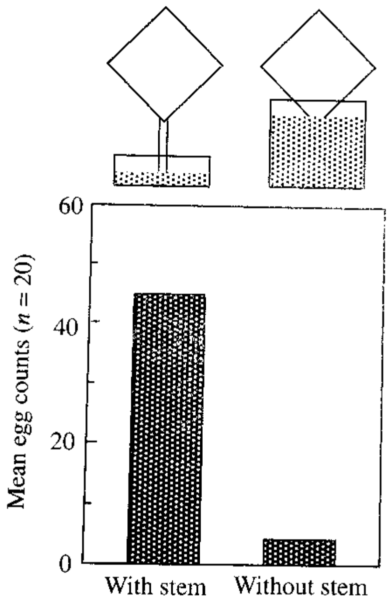
These butterflies switch their colour preference for landing responses from green leaf colour to flower colours (yellow, blue and violet), depending on their motivation for oviposition or nectar feeding respectively.

Diptera:

Females of *Rhagoletis pomonella* in searching 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 10m, 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 meters 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 e.g. foliage, fruits or trunk. At still closer range (1m or less), as a third step, detailed discrimination on the basis of size or shape becomes possible.

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.

Artificial leaves (green paper dipped in paraffin and sprayed with a surface extract of cabbage leaves) with a stem of cabbage or not, were tested for oviposition preference of cabbage root flies. The type with a stem is significantly preferred for oviposition. Clearly plant colour, shape and size play important roles in the host selection behaviour of these flies.



Homotera:

The attraction to the colour of foliage has been studied extensively in aphids and whiteflies. *Brevicoryne brassicae* and *Myzus persicae* alight in the field preferentially on leaves reflecting a greater proportion of long-wave energy, with little or no regard for the taxonomic status of the plants. Since sugar beet leaves have a higher long/short-wave ratio than cabbage leaves, more cabbage aphids alight on sugar beet leaves than on cabbage, although the former is not one of its hosts. Long/short-reflectance ratio 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. In fact, most diurnal insect are attracted to yellow. In many cases yellow surfaces act as a supernormal stimulus, because they emit peak energy in the same bandwidth as foliage, but at greater intensity.

Whiteflies avoid setting in the presence of short-wavelength illumination (400nm), but will alight on green light (550nm).

Olfactory Responses to Host-plants:

We will discuss two examples of orientation to odours as demonstrated under laboratory circumstances, one of flying insect and one of a walking insect.

Flying insect:

When a flying female tobacco hornworm moth is searching for a host plant, she displays positive anemotaxis ,i.e. she flies upwind using the prevailing direction of air flow as a cue. Mechanoreceptors located on her antenna and serving as anemoreceptors provide this directional information. Her flight path can be described as a regular zigzag of limited amplitude. How does the odour emitted by the tobacco plant come into play? Firstly, the host-plant odour may have acted as an activator 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 mainly determined by trying to prevent loss of the odour plume.

Olfactory Responses to Host-plants:

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 positive anemotaxis. The female's host-plant searching behaviour is in fact similar to odour-modulated upwind of male moths in search of females. 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 central nervous system that is set in motion by olfactory activity, but afterwards is continued automatically.

OLFACTORY RESPONSES TO HOST-PLANTS:

Walking insect:

One of the best studied cases of the ability of a walking insect to orient to host-plant odours is the Colorado potato beetle.

This specialist on solanaceous plants has a strong preference for the cultivated potato on which it is one of the most devasting insect pests. During the first 7 days of adult life the beetles need to feed in order to fully develop their flight muscles and as a consequence. Host-plant location is done by walking. To quantify its walking behaviour a locomotion compensator in combination with wind a wind tunnel has been used. This instrument allows detailed and automated recording of walking tracks without the insect contacting any obstacles.

When clean air is blown over a hungry beetle, it shows a menotactic response to the wind, maintaining a relatively constant angle to the wind direction. The walking track shows circling by making turns of 360 °. When the airstream carries the odour of intact potato plants, the straightness of the path increases dramatically.

OLFACTORY RESPONSES TO HOST-PLANTS:

Walking insect:

Now circling is absent, average walking speed is increased and the beetles spend more time walking upwind.

This response can be classified as positive odour conditioned anemotaxis. When the odour of non-host, 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.

Somewhat unexpectedly. Similar effects were found when odour of another Solanaceous plant, wild tomato was offered. This plant is an unsuitable food for the beetle.

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Chemosensory basis of host-plant odour detection:

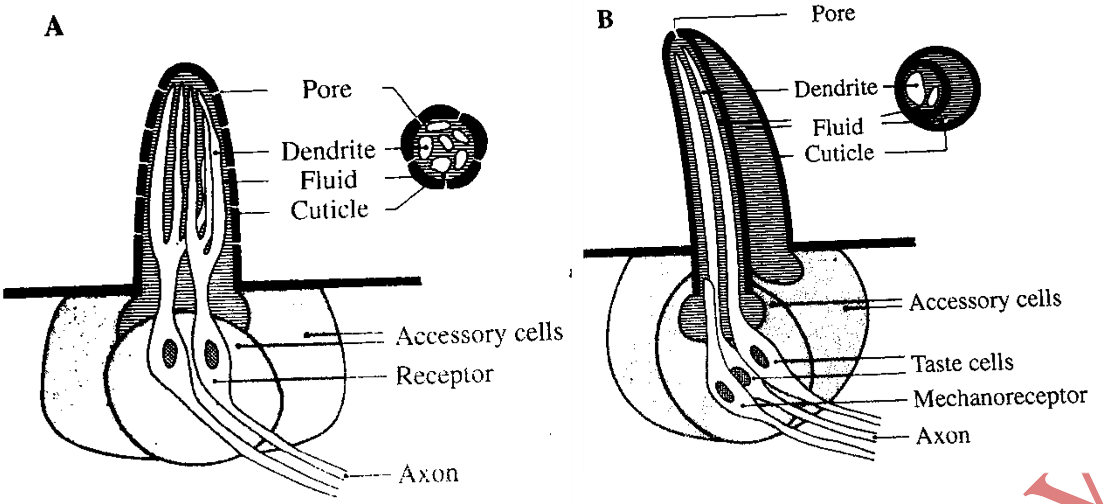
Insects heavily rely upon chemoreception when searching for food, oviposition sites and mating partners, as well as for social communication. In this context it is often stated that insects live in a chemical world. Chemoreception refers to the classical senses of small (olfaction, organs for detecting volatile chemical stimuli) and taste (gustation, or contact chemoreception for the detection of dissolved or solid chemicals. The distinction between the two is not absolute as insect taste sensilla have occasionally been found to respond also to odours.

Morphology of olfactory sensilla:

Olfactory chemoreceptor cells are associated with so-called sensills (singular: sensillum), organs consisting of neurons, accessory cells and a cuticular structure. The cell bodies of neurons are located at the base of the sensillum. Typically there are two to three neurons per sensillum, but examples of more (up to 30) neurons innervating one sensillum have also been reported. The dendrites are usually located in specialized cuticular structure, which are classified on the basis of external form. They include hairlike varieties, pegs and cones. Pegs or cones sunk in shallow depressions and pore plate organs. Chemosensory neurons are mostly bipolar and their axons run to the CNS via peripheral nerves without intermittent synapses. A filament-like extension of the neuron that protrudes into the sensillum cavity, the dendrite, is specialized to respond to the chemical stimulus with a graded potential called the receptor potential. When the potential reaches a value above a certain threshold, it gives rise to a train of action potentials.

Morphology of olfactory sensilla:

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 10-50nm) and dendrites are often branched. In contrast, gustatory sensilla are uniporous, the pore (diameter 200-400nm) mostly being located at the very tip of a peg- hair, or papilla-like sensillum. 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 limen by the tormogen and trichogen cells at the sensillum base. Olfactory sensilla are predominantly present on antennae but may also occur on palpi and ovipositor.



SCHEMATIC DRAWING OF A LONGITUDINAL AND A TRANSVERSE SECTION OF (A) AN INSECT OLFACTORY HAIR AND (B) AN INSECT TASTE HAIR.

Sensitivity of olfactory sensilla :

Like most sensory cells, chemoreceptors are especially responsive to changes in stimulus intensity, i.e. change in the concentrations of chemicals. Olfactory cells have been shown to handle up to ten odour pulses per second, which means that they can resolve the temporal pattern of odour bursts in a plume quite well. Responses to constant stimuli generally show sigmoid concentration response relationships at the level of electroantennogram (summated receptor potential) as well as single cell recordings.

Upon increasing the odour concentration by one order of magnitude, EAG amplitude and frequency of action potential 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. This in principle enables the insect to sense odour gradients, on the basis of which it may perform tropotactic behaviour.

Sensitivity of olfactory sensilla :

Sensitivity of detection is enhanced enormously by the neural phenomenon of convergence. The axons running from olfactory receptor cells make synaptic contacts with a limited number of first-order interneurons in the antennal lobe of the brain. Which means that they converge? This leads to an amplification of the signal (an interneuron receives inputs from many receptor cells simultaneously and its threshold may therefore be reached at a lower concentration than that necessary to depolarize a receptor cell) and improved signal-noise ratio by separating background activity from the presence of a volatile signal. Thus, a 100-1000-fold amplification of the signal can be measured in the deuterocerebral internneurons responding to green leaf volatiles in the Colorado potato beetle, as compared to the sensitivity of its antennal receptors. The interneurons are organized in so-called glomeruli.

Specificity and olfactory coding:

Summated receptor potential (EAG) recordings from several species of insects have shown that generally occurring plant volatiles, such as green leaf alcohols, aldehydes, acetates and terpenoids evoke different response. The responses increase in amplitude with increasing carbon-chain lengths of the alcohols and aldehydes until an optimum is reached at or near C 6 -compounds, which at the same time are the most abundant chemicals in leaf headspaces.

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?. Rather than total antennal responses electrophysiological studies based on recordings of the activity of individual olfactory neurons, so-called single-cell recording, offer the possibility to determine which individual plant chemicals evoke changes in chemosensory activity (excitation or inhabitation), and how mixtures of chemicals are coded.

Specificity and olfactory coding:

The olfactory system functions as a filter because olfactory receptors are sensitive to only a limited array of stimuli. For each olfactory and gustatory receptors two main categories are recognized: specialist and generalist chemoreceptors. A specialist cell responds to only a small number of structurally related compounds. Among olfactory receptors, sex pheromone receptors are the classical example of specialist receptors. Recordings of neural responses evoked in single olfactory cells, obtained from some oligophagous species, have revealed the presence of specialist-type olfactory neurons that are sensitive to certain host-plant specific volatiles only. Such specialist receptors have been found, among others, in coleoptera, lepidoptera larvae and aphids, but not in all species studied. Volatiles emanating from plants in most cases excite generalist-type odour receptors. The response spectra of generalist receptors are by definition fairly broad and vary from cell, often with overlapping patterns.

Specificity and olfactory coding:

Sex pheromones, genes coding for carrier proteins that bind the pheromone molecules and transport them to the dendritic membrane have been cloned. In a addition genes coding for carrier proteins binding to general odourants have been characterized in several moth species.

The existence o68f specialist and generalist olfactory receptors are reflected in present ideas on the processing of sensory information in the CNS. Labelled-line codes have been inferred to operate in oligophagous species, in which the activity of such specialized chemoreceptors will trigger kinetic responses or odour-induced anemotaxis either positive or negative.

Host-plant searching in nature:

When insect is searching in the field, it meets a multitude of stimuli, which are distributed heterogeneously. Inherent to the field situation is a lack of control over abiotic parameters and the stimulus situation. It is therefore difficult to assess the relative importance of the two main stimulus modalities, optical and odorous plant cues. 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 stimuli may change with distance to the plant. Apple maggot fly is one of the causes of stimuli interaction, its visually-guided host searching behaviour has been described; 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. 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.

Host-plant searching in nature:

, 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. In contrast , host selection behaviour of bark beetles in forest ecosystems is largely governed 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 microorganism, and interspecific inhibitory semiochemicals.