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STUDIES OF SOME ASPECTS OF BEHAVIOUR IN THE AMBROSIA BEETLE TRYPODENDRON LINEATUM (OLIVIER)

ABSTRACT

Behaviour patterns of the ambrosia beetle Trypodendron lineatum (Olivier) were studied in relation to various influences of illumination, temperature, gravity, atmospheric pressure and host factors. The beetles were in the overwintered, reproductively mature state in which they are prepared for their normal functions of emergence, flight dispersal, host-discovery and attack. Experiments were confined to the study of the beetles in pedestrian situations. Their responses were studied both before and after being given flight experience.

Before flight the majority of individuals are strongly photopositive at temperatures in the range of 5°C to 36°C, the optimum being between 20°C and 26°C. They become progressively photonegative as temperatures rise above 26°C, until all individuals shun the light at 40°C. The effect is reversible as temperatures return to optimum. After a period of flight the photopositive reaction is weakened, nullified, or replaced by a negative reaction in some, but not all individuals. A change in threshold of response to light becomes most clearly manifest in the presence of attractive host odour. When a photopositive reaction occurs, it is retained regardless of the direction of the earth's gravitational field in relation to the light source. The photopositive response is not altered by two atmospheres pressure.

A response to host odour becomes manifest under three different situations: (1) Female beetles bore into wood which is itself attractive or is made so by application of attractive wood distillate. This reaction is displayed by flight-experienced beetles in illuminated or non-illuminated situations, or by non-flown beetles in darkness.

(2) Males or females display a centripetal response in a field of odour arising through a substratum. They trace a meandering path for a prolonged period, and repeatedly retrieve their general position when they transgress beyond the boundary of the odour field. This reaction is displayed under illuminated conditions by flight-experienced beetles.

(3) Males or females respond anemotactically to air streams carrying attractive host
odour. This reaction is displayed under illuminated conditions by flight-experienced beetles.

The effect of flight experience on photic responses is not all-or-none, but apparently involves a rise of threshold to light in the presence of attractive host odour, or a lowering of threshold to host odour in the presence of light.

The non-response of the beetles to green wood from a living tree, and the continued response to mixtures of green and attractive wood indicate that neither attractants nor repellents are present in the living tree. It is inferred that susceptibility of dying trees to this ambrosia beetle owes itself to chemical changes during the death process. Since both sexes react to the odours, it is inferred that initial attack on a tree involves a primary attractant from the host.

Implications are seen for the role of behaviour in the ecology of this insect. Other implications are seen for the use of the newly acquired information in bioassay techniques in which the insect will serve as a test instrument for chemical studies of host attractants.

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STUDIES OF SOME ASPECTS OF BEHAVIOUR IN THE AMBROSIA BEETLE

TRYPODENDRON LINEATUM (OLIVIER)

by

FAUSTINO G. FRANCIA

B.S.F., University of the Philippines, 1952

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A THESIS SUBMITTED IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE OF

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We accept this thesis as conforming to the required standard.

THE UNIVERSITY OF BRITISH COLUMBIA

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Department of Forestry

The University of British Columbia
Vancouver 8, Canada

Date July 16, 1965
ABSTRACT

The factors and mechanisms which consistently deliver newly over-wintered adults of the ambrosia beetle Trypodendron lineatum (Olivier) to specific host trees under specific conditions have been considered.

Studies and analyses of the behavioural patterns of the beetle in respect to light, host tree factors, and factors of the environment were made in recognition of the fact that preliminary research results demonstrated the predominant role that reactions to light played in the behaviour of the beetle.

The results of the studies showed that the beetles, before flight, were strongly phototactic at temperatures in the range of 5° to 36°C. Positive photic response was inhibited in an increasing percentage of individuals at temperatures above 36°C. At 38°C, positive response to light by the beetles ceased to exist.

The non-flown beetles reacted quickly to angular deviations of alignment in respect to a light source and turned with almost equal readiness toward the light regardless of its angle. The beetles' responses to light may be classified as follows: (1) not inhibited, the beetles immediately move toward the source of light; (2) initially inhibited positive response; (3) inhibited positive response, the beetles may or may not initially inhibited but the general movement toward the light source is not direct; (4) completely inhibited response, the beetles move with no apparent response to light.

The photopositive response was found to mask the other potential capabilities of the non-flown beetles. Exclusion of the photic stimulus from flight-inexperienced beetles resulted in response to host odour in an odour field. Flight experience was found to modify partially the simple photic reaction of some individuals in the absence of host odour, but the
majority of the beetles' responses remained unchanged.

The behaviour of Trypodendron is not strictly stereotyped in the sense that it follows a definite pattern. While flight may be normal as a conditioning mechanism preparatory to alighting and host finding, response to an "attractive" odour source and subsequent boring behaviour may be exhibited, in the absence of previous flight experience, under certain conditions.
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INTRODUCTION

Among the general problems concerning ambrosia beetles are those which pertain to their host tree relations. More specifically is the question as to the factors and mechanisms which consistently deliver these insects to host trees of specific kinds and conditions. The question is prompted by the fact that ambrosia beetles show remarkable ability in discovering felled, windthrown, or dying trees in a forest, or logs in water storage, "selecting" them as to botanical identity and state of morbidity in the sequence of changes between life and death. They are even able to detect these special requirements despite heavy coverage of the log surface with substances objectionable or confusing to human olfactory sensation, such as creosote and kerosene, or despite a residue of the insecticide lindane which ultimately kills those beetles as they crawl over the log surface.

Two associated problems are posed by the foregoing observations. One concerns the identity of the intrinsic and extrinsic factors and the behavioural patterns and mechanisms involved in the process of host discovery and discrimination. The other concerns the nature of the factors in a log and the mechanisms of their origin which account for the differential attack by these beetles on logs of different kinds and conditions. These problems are of both academic and practical importance.

Considerations of the general problems, in turn, pose subsidiary questions. Does attack involve random trial-and-error sampling by the beetles, or does the insect detect its host from a remote point? Of the various conceivable differences between living and dying trees, which of them should be capable of providing essential cues for the beetles?
detection is from remote points, which of the possible phenomena in a dying tree may act at a distance, and which of the conceivable senses in insects may take part in remote detection? If odours play an important role, as may be inferred from certain field studies (Chapman, 1962, 1965), are they absent from the healthy living tree, or merely occluded within the cells until mechanical alterations, such as permeability or hydrostatic pressure changes, release them when the tree begins to die, or does the change also involve the disappearance of chemical repellents? If attractants are normally absent, why do they not develop in the living tree, and why do they form as it begins to die? If a chemical process is involved, does it involve simple oxidation, simple cleavage, condensation, polymerization, molecular rearrangement, or abnormal metabolism? If abnormal metabolism is involved, how may normal and/or abnormal metabolism be artificially modified to accelerate or retard the formation of chemical attractants? If chemical attractants are formed, what are their group or specific chemical natures? Can their attractancy be obscured by other substances presented simultaneously with them to the insects?

The foregoing questions are of a factual and observational nature, some having practical implications. There is to be considered also the conceptual aspect which pertains to the relationships of ambrosia beetle behaviour to the general theory of animal behaviour. Kennedy (1956, 1958) refers to three types of hypothesis concerning the nature of instinctive behaviour. One is the simple physiological one such as Loeb favoured, according to which reflex and instinctive action do not differ in principle and changes of behaviour pattern are due primarily to changes in the reflex thresholds brought about by changes in the state of receptors and effectors.
A second hypothesis, based on the work of reflex physiologists, notably Sherrington, also recognizes no difference of principle between reflex and instinctive action but attributes changes of threshold primarily to the integrative activity of the central nervous system. A third hypothesis, advanced by the modern ethologists, draws a distinction of principle between reflex and instinctive action, the latter depending on an internal drive-generating mechanism which, even when triggered by an external stimulus, has nothing in common with reflex mechanisms.

The general study comprises several largely distinct but not entirely mutually exclusive tasks. These consist of analysis of behaviour in the insect, experimental modification of living and dying trees, and chemical and histochemical analysis of changes in chemical precursors and products of trees as they gradually die. The objective of the present phase of the undertaking is to investigate the behaviour of the insect, particularly in relation to the circumstances affecting its response to host tree factors.

The present investigations pertain to the ambrosia beetle species Trypodendron lineatum (Olivier) which has been an object of much concern and research in recent years. Earlier studies on this insect (Graham and Werner, 1956) revealed that the reproductively mature beetles, freshly removed from their overwintering quarters in spring, are entirely dominated by a strong photopositive response. In the presence of light, they do not bore into the kind of wood that is normally being attacked by non-captive individuals in the field. In darkness, they bore readily into attractive wood, or into non-attractive wood to which gas-distilled extracts of attractive wood are applied. This contrasts with events in the field
where attack takes place in broad daylight. Subsequent observations (Graham, 1959) showed that the ability of the beetles to bore into wood in daylight depends on their first having a period of flight. This appears to simulate one stage in the natural sequence of events in the field. Balfour and Paramonov (1962) contend that flight is not absolutely necessary. They found that under severe confinement, a small percentage of beetles will attack wood while exposed to light without having been preconditioned by flight. Further experience by Graham (1965), however, sustains the original basic conclusion that the initially strong photopositive response in overwintered adults of *Trypodendron* is a major obstacle to their boring-in activity until they have experienced flight. It is conceivable, however, that Balfour and Paramonov's observations signify that in certain populations or in certain samples of beetles from them different thresholds of responsiveness to host factors already exist among the various individuals and that the threshold is lowered for all individuals by the flight experience. It should be noted that in their caution of precluding the possibility of their beetles having had flight experience, Balfour and Paramonov used specimens which had been extracted artificially from brood logs and stored until spring. Thereby they denied the beetles the normal prehibernation flight.

Further investigations (Graham, 1961) indicated the importance of air-swallowing as a mechanism by which photic reactions are subdued to a point where responsiveness to host factors is released. Minimum periods of flight for this purpose were, however, not ascertained.

The discoveries to this point left various details of behaviour in *Trypodendron* untouched.
No evidence exists to indicate that *T. lineatum* discovers its host tree or log by a random, trial-and-error process. During the attacking phase of its life, it appears never to settle on hosts other than those of a particular species in a particular state between the living and the dead. These are the logs into which they will bore to establish their broods. It is thus evident that the mechanism of detection operates over an appreciable distance.

Entomologists are familiar with three forms of perception which enable insects to receive information at a distance, namely vision, audition, and olfaction. Certain evidence exists also for a sense of perception of bioelectric fields (Maw, 1961, 1962) even though no structure for their perception is known. Of the various properties of plants which emit information that is detectable at a distance, two classes of factors are well-known. One is odour; the other is of a visual nature, viz. contrast, form, and colour. Perhaps bioelectric fields should be considered as being a possible source of information to insects (Maw, 1961, 1962). As to the significance of voltage gradients (Parr, 1945) or bioelectric oscillations (Scott, 1962) as a source of signals for insects, nothing is known. It is not entirely inconceivable that movement of fluids and gases in a tree may be accompanied by subsonic or supersonic propagations of low intensity, but experimental evidence is lacking.

The fact that *Trypodendron*, during the attacking phase in its life cycle, appears not to settle on the "wrong" kind of logs or trees indicates that visual cues are not primarily or predominantly involved in host discovery. This is not to deny that sight is probably involved in their guidance mechanism. On the other hand, the important role of odour in the guidance of
insects is well-known. Furthermore, hidden log experiments in the field (Chapman, 1962, 1965) have demonstrated convincingly that odour must be a prime factor in host discovery by *Trypodendron*. With this evidence, it appears prudent to examine as far as possible the role of odours before testing for the operation of factors whose importance or existence for insects is uncertain.

The foregoing observations on *T. lineatum* accordingly indicated the initial dominance of the photic response and the release of a chemotactic response by exclusion of light, or by flight experience, the latter operating by inducing the swallowing of air. It was also evident that an olfactory guidance mechanism is involved, and volatile chemicals extracted from attractive wood are capable of inducing attack (boring-in) on otherwise non-attractive wood. An olfactory response to host factors was suggested by their tendency for an unstable aggregation about odour sources from attractive wood provided that light is excluded and that the air in the immediate surrounding of the beetles was not excessively dry (Graham and Werner, 1955).

The knowledge about *Trypodendron* now raised as many questions as it had answered. It was not known how long a period of flight is required for the appearance of a change in the response to host factors in the presence or absence of host factors. Neither was it known whether the effect of flight on the photic and host factor responses is all-or-none, or whether it involves a progressive change of thresholds. It was not known either whether the beetles could orientate to a stationary odour gradient or to an airstream carrying odour. The laboratory experiments implicating odour in behavioural effects were at this point quite meagre. By the same token, there were no satisfactory criteria by which olfactory responses
could be detected, assessed, or clearly segregated from the other responses which are incorporated into the more complex reaction of boring into wood.

The objectives of the present investigations were to explore factors and mechanisms of the orientation behaviour of *Trypodendron lineatum* (Olivier) during that stage in its life when it searches out, selects, and attacks logs. This period is in the overwintered reproductively mature adults. The immediate study is confined to pedestrian beetles because it appeared that much of their behaviour could best be gained under this circumstance. The study of photic reactions is here limited to the photopic (light adapted) state. Special attention is directed at photic reactions and factors which modify these.
The Experimental Insect

Trypodendron lineatum (Olivier) (Fig. 1) of the family Scolytidae was the species of ambrosia beetle used in these studies.

1. General considerations.

The species T. lineatum is, of all the thousand or more world species of ambrosia beetles, one of the most suitable for study. It occurs over an extremely wide geographic range, being found in the temperate coniferous forest of Europe, Asia, and North America (Hadorn, 1955; Chamberlin, 1939; Novak, 1965; Bletchly and White, 1962). A considerable body of literature is available as background information on its general habits, biology, physiology, and ecology (Hadorn, 1955; Chamberlin, 1939; Chapman, 1955, 1958, 1962, 1965; Chapman and Dyer, 1960; Chapman and Kinghorn, 1961; Dyer and Chapman, 1965; Graham, 1959, 1961; Graham and Werner, 1959; Nijholt and Chapman, 1964; Novak, 1963a, 1963b; Prebble and Graham, 1957; Rudinsky and Dateman, 1964a, 1964b). Its habit of overwintering during a period of its adult life in the forest litter, duff, or under flakes of bark on trees adjacent to logging or logged-over areas (Hadorn, 1955; Novak, 1965; Chapman, 1960; Chapman and Kinghorn, 1961; Dyer, 1962, 1965) permits collection of biologically uniform material in sufficient quantity for convenient experimentation in the laboratory. This contrasts with most other ambrosia beetles which are far less synchronous and do not accumulate in an intermediate storage medium, but search new logs almost directly following emergence from the brood log which nurtured them. Trypodendron adults are amenable to prolonged storage under refrigeration without showing marked loss of vigour or ability to fly or walk provided they are not exposed to desiccation of
Fig. 1. *Trypodendron lineatum* (Olivier) adult female beetle. 
Actual length 3 to 3.5 mm. (After Graham, 1965)
more than 25 per cent of their body weight (Nijholt and Chapman, 1964).

The visible differences between the sexes render them easy to define for the purpose of the experiments. The versatility of *Trypodendron* in accepting a wide range of genera of coniferous trees offers considerable freedom of choice in the kinds of wood which may satisfy certain needs of experimental convenience. The same diversity in respect to acceptable host species may provide increased opportunities for discovering the essential chemical attractants by correlative evidence.

2. **Source of experimental supply of beetles and methods of handling and storage.**

The source of the beetles was in the Cowichan Lake district of Vancouver Island, British Columbia. The time of collection was in late March and early April, 1964, just prior to the beetles' normal emergence as reproductively active adults from their overwintering quarters. Collections were obtained within a zone of about 100 meters inside the margins of standing forest adjacent to areas in which logging had been in progress about 18 months previously. Here the brood of new beetles, generated during the season preceding the collection, occurs in the duff layer near the base of standing trees, and under loose flakes of bark on the lower stem of very old Douglas fir trees. Old adults may occasionally be found among the population of overwintering new adults at a proportion of about 1 to 30 per cent (Chapman and Nijholt, 1965).

Bark flakes and forest duff containing the beetles were freed of coarse material and stored in plastic bags in a refrigerator at a temperature of about 0 to 5°C. Whenever beetles were required for the experiments, they were obtained by spreading the beetle-containing medium, a couple of handfuls
at a time, in a shallow pan floating on water at a temperature of about 50°C. As the beetles became activated, they were transferred to small jars containing moist crumpled paper towelling or bits of moist moss to prevent loss of body moisture and to minimize mutual contact among the beetles, as otherwise the beetles bite off each other’s front tarsi. Specimens thus mutilated are hardly able to walk normally and become useless for the purposes of the experiment. Care also had to be exercised in intercepting the beetles before they could take off in flight as it is known that this factor modifies their responses to light in the presence of odour from attractive wood (Graham, 1961) and to attractive odour in the presence of light.

3. Treatment of the beetles for testing.

The supply of beetles used in the experiments was segregated as to sexes. They were placed in jars with moist paper or moss. To prevent the beetles from becoming very active in the presence of light at room temperature, the jars containing them were kept in a thermos jug containing ice. Beetles were removed from the jars as needed in the experiments.

The beetles were tested for their photic behaviour immediately after removal from cold storage and without allowing them to experience flight. Later, the same beetles were given a period of captive flight by means of a procedure described by Chapman (1956). This was done for the purpose of studying details of the effect of flight experience on photic orientation as well as observing the time patterns of flight activity per se. Each beetle was glued by its pronotum to the underside of the tip of a cardboard insect-mounting point. The beetle was affixed in such a way that it was horizontal and that its wings were not obstructed in motion by the paper point or any glue. It was also noted that interference of glue with antenn-
nal movement suppressed all effort of flight. Four or five beetles individually affixed to separate points, each set on an entomological pin, were observed concurrently. At every one minute interval, the flight activity of each beetle was observed and recorded horizontally across graph paper ruled at ten lines per inch. Positive activity on each beetle was indicated by an "x" sign, while inactivity was represented by a blank square. Total flight as well as periodicity of intermittent flight were thus known.

The beetles were kept under these flight-testing conditions for various periods of time, from 5 minutes to 6 hours. To prevent possible loss of body moisture during the flight period and exposure to light, the piece of balsa wood to which the pins supporting the beetles were stuck was kept in a shallow pan of water.

After the prescribed period of flight, the beetles were removed from the card points to their respective vials, care being exercised so as not to cause injury to the beetles, and again tested for photic response, one at a time, or for responses to some other stimuli concurrently with the light factor.

Host Tree Factors

Like the beetles in being important as both objects and instruments in the study of behaviour is the host tree. The wood of the host tree is eventually to be investigated for products of biochemical changes, factors and mechanisms which are involved in rendering the wood attractive to ambrosia beetles. It is noteworthy that the attractive condition for the ambrosia beetles develops in a tree from the effects of injuries and exposure after a certain period of time. Before the attractant factors can be clearly interpreted preparatory to isolation and evaluation, it is necessary to
elucidate the accessory conditions required to induce an effective response of the insect to the host. For this purpose, portions of known attractive and non-attractive host materials were provided as reference standards of host factors.

1. General considerations.

The recorded host trees of *Trypodendron* are Douglas fir (*Pseudotsuga menziesii* Mirb., Franco), amabilis fir (*Abies amabilis* Dougl. & Forb.), grand fir (*A. grandis* Dougl. & Forb.), western hemlock (*Tsuga heterophylla* Raf. & Sarg.), spruce (*Picea* spp.), pine (*Pinus* spp.) in British Columbia (Frebble and Graham, 1957); noble fir (*Abies procera*), larch (*Larix leptolepis*), spruces (*Picea abies* and *P. sitchensis*), pines (*Pinus sylvestris* and *P. radiata*) in Scotland (Blethly and White, 1962), and several species of spruce in Europe (Novak, 1965b).

Host tree material of *Trypodendron* provides several different kinds of stimuli which may affect this insect in various ways. These include the tactile stimulus arising from contact with solid object. The solid surfaces may offer various topographic features varying from smooth plaques and deep narrow fissures as exist in bark texture to relatively flat and coarse surface as exists on the cut or sawn ends of logs. The colour may also vary considerably but its stimulating character is unknown. Odour is perhaps the most important stimulus to consider because most insects react to it in a very remarkable manner (Dadâ, 1963; Dethier, 1963; Buddenbrock, 1958; Kennedy and Booth, 1959a, 1959b, 1960; Roeder, 1965; Gara and Vité, 1962). In *Trypodendron*, the odour of a suitable host tree appears to be a guiding factor (Chapman, 1965). Taste is a factor to which most insects have a low threshold of sensitivity (Dethier, 1963) and which may
affect the reactions of the beetles as they begin to chew into wood. Another conceivable stimulating factor is the visual form or mass of the host (Dethier, 1957) but its influence on Trypodendron is not known.

As it is the purpose of the study to deal with factors involved in the attraction of the beetles to their host, material was chosen especially to provide a source of the odour stimulus. Accordingly, features of bark topography and colour and the property of taste played no part in the selection of the specific host for the preparation of the samples.

There were other considerations in the choice of wood. One is the choice of tree species among the potential or known host species of Trypodendron. For experimental convenience, certain preferences had to be made, since in the particular area where the experimental beetles were obtained, western hemlock and Douglas fir are not only the most commonly available trees but are also usually the most heavily attacked by Trypodendron (Graham and Werner, 1956). Of these two trees, Douglas fir is noteworthy for its white sapwood region which becomes attacked by the beetles and is easily differentiated from the reddish region which is immune to attack. Also, Douglas fir wood had been a subject of chemical investigation for its attractant properties (Graham and Werner, 1956). Douglas fir, however, possesses a limited sapwood layer which prohibits obtaining convenient size of tranverse slices for testing attack response of the beetles and, more important, appears to change from the non-attractive "green" condition to the attractive "ripe" condition in a shorter time than does hemlock. This instability is disadvantageous where alteration of host material condition during the course of the experiment is undesirable. For this reason, western hemlock appeared preferable as a source of wood in studies of
attack responses and as a source of odour in studies of orientation to light and air flow.

Another consideration in the choice of wood concerns its state of attractiveness. The state of attractiveness can be measured only by the response of the beetles. The chemical identity of the attractants is not yet known. In so far as attractiveness to the beetles is concerned, however, a host tree exists in several conditions ranging from a "green" state as exists in the wood of a newly felled tree to a "ripe" state which is highly favoured by the beetles and to a "spent" state in which the attractant factors are no longer present as in logs, wood, or finished dry lumber.

The attractive or "ripe" state develops during winter in the sapwood of the unconverted host trees felled during autumn and winter. Spring-felled trees with tops retained, or cut only into long log lengths remain unattractive to the beetles through the spring flight period of Trypodendron but become highly attractive if cut into short log sections at the time of felling (Johnson, 1964).

2. Source of host wood and preparation for testing.

The "ripe" and the "green" wood materials came from the same locality as the experimental beetles. The attractive state of the wood samples was assured by taking them from polyethylene-sheet-covered portions of logs of host trees felled in early winter and allowed to remain in the woods until attacks occurred on the uncovered portions. These "ripe" samples as well as "green" samples from spring-felled host trees were stored as thick slabs in plastic bags in a freezer at about \(-17.8^\circ\)C \((0^\circ\)F). Samples of both "ripe" and "green" wood for testing attack responses of the beetles were prepared by debarking the frozen slabs,
squaring the edges, and planing the surfaces with a woodworking "jointer" machine. The shavings obtained from the planing operation were saved in plastic bags and stored in the freezer.

5. Presentation of wood factors as stimuli to the beetles' responses.

The method used for evaluating the olfactory response consisted of testing for the retention of the beetles at an odour source while they were subjected to the potential attraction of a beam of horizontal light or a broad field of light whose source is overhead. A sheet of paper, finely perforated with pinholes at the center, was placed over a small section of either "ripe" or "green" wood, about 5.0 cm. by 7.0 cm. by 1.5 cm., as desired. The beetles were placed individually on the perforated area to examine the ability and behaviour of the beetles in orienting to a gradient of odour emanating from the wood beneath the paper without involving a stream of air.

Another condition under this series of tests consisted of associating wood with a stream of air alone or with "ripe" wood odour borne by a stream of air. The purpose of the test was to determine the possible occurrence of an anemotactic response prompted by the host odour. This would concern an alternative mechanism to the odour-gradient theory of host finding.

In another series of tests, the beetles were allowed physical contact with the piece of either "ripe" or "green" wood. This series would provide not only thigmotactic behaviour responses on physical contact with the piece of wood but also chemotactic behaviour responses as a result of tarsal contact and/or oral tasting of the host wood. In addition, the effect of contact with the source of the attractive wood odour may provide
a different response.

The Light Factors

In its most comprehensive aspects, the photic behaviour of an insect would be concerned with the directional changes and time patterns of its orientation reactions under diverse conditions of a photic environment. Light may be varied as to intensity level, specific wavelength, wavelength balance in mixed colours, degree and plane of polarization, discreteness or diffuseness, and angle and plane of incidence relative to the axis of the insect. Various contrast and colour patterns, both stationary and moving, in the visual field may influence the responses (Reichardt, 1961). All of these are possible elements and variables to which Trypodendron is subjected in its natural environment. In addition, the insect may be expected to respond differently in the dark-adapted and light-adapted states as demonstrated by Raymont (1959) with the beetle Dineutes. The present studies employed mainly a heat-filtered unidirectional white light of constant intensity and colour temperature, projected in a beam toward the beetles and a broad field of overhead light provided by ceiling fluorescent lamps.

1. General considerations.

Light is an important factor of the environment to which insects react either positively or negatively under certain conditions. Light is defined as that portion of the electro-magnetic spectrum ranging in wavelength from about 200 to 10,000 m\(\mu\) or about 2000 to 100,000 \(\AA\). The light visible to human eyes ranges from 4000 to 7500 \(\AA\) while that to a bee's eyes ranges from 3000 to 6500 \(\AA\) (Garthy, 1965). In terms of colour which the different wavelengths represent to human eyes, the bee's eyes can distinguish colour in the ultraviolet range and not in the far red range of the
spectrum. As a token stimulus, light is very effective in that its reflective and absorptive characteristics provide insects some kind of information about their environment. Changes in light intensity associated with shadows of moving objects notify the insects of the presence of prey or enemy. Because infrared wavelengths usually accompany visible light under aerial conditions, brighter illumination means a warmer, drier environment, and a lower illumination may mean a cooler, damper one (Brown and Prosser, 1962).

2. Description of the equipment used and methods of testing.

The source of white light was a Reichert microscope illuminator "Lux FNI" (Fig. 2) operating through a variable resistor with an amperage indicator. Its normal rating was 50 watts at 6 volts and 5 amperes. This equipment gave control over light in respect to focus, aperture, intensity, and to a certain extent, colour temperature. Because the wavelength balance (colour temperature) of light from a tungsten filament changes with voltage of input current, a fixed setting of the rheostat was adopted for an input of 4.0 amperes. The incident light to which the beetles were exposed was measured by a "Photovolt" photometer model 200 M as ranging from 25 to 50 footcandles. Colour temperature was judged to be similar to that of a 40-watt incandescent bulb operating at normal voltage, the value of which is rated at 2760° Kelvin. To insure that the responses to the horizontal beam of light were purely photic and not thermal, a heat filter from a Bausch and Lomb projector was interposed.

The overhead source of light was provided by four "General Electric" cool-white F40 CW fluorescent ceiling lamps at a distance of about two metres above the experimental table. The incident light furnished by these lamps ranged from 50 to 60 footcandles as measured by the
Fig. 2. A Reichert microscope illuminator "Lux SKI" operating through a variable resistor with an amperage indicator. It was used as the source of a horizontal beam of white light. A Bausch and Lomb heat filter is shown in front of the illuminator.
The simple photic reactions were tested by placing the beetles, one at a time, at a central point on a sheet of white writing paper. A narrow beam of heat-filtered light, as defined earlier, was projected horizontally across the surface of the paper. The beetle, its sex noted, was aligned with the axis of the beam. As the beetle was allowed to walk, a pencil line was traced behind it until it reached the edge of the paper, whereupon it was returned to the starting point. In some tests, the beetles were aligned in eight different directions, 45° apart, in respect to the light source. In other tests, only four directions at 90° intervals were tried. These starting points are illustrated in Fig. 5. The systematic testing of angular displacement was provided in recognition of the fact that certain insects react at different rates to different axial displacements relative to the light source (Buddenbrook, 1958; Fraenkel and Gunn, 1961). Besides the systematic tests which began with a fixed starting direction, other tests with different initial directions of alignment were tried in order to examine for possible adaptation of the insect during successive trials. After the beetles were each exposed to a horizontal beam of light, they were tested for their responses to a broad field of light. Essentially the same positions on the white sheet of paper were used in aligning the beetles.

The photic reactions were tested in the presence of other factors such as wood odours, air currents, increasing temperature, gravity, and atmospheric pressure. The beetles included both flight-experienced and flight-inexperienced individuals.

Previous observations indicated that the individual beetles
Fig. 3. Diagram illustrating plan of view of the initial starting points or angular displacements of the beetle *Trypodendron* in tests for its responses to white light.
walked toward a point source of a horizontal beam of light and began
attempts to fly when light was present in all directions as provided by the
ceiling lamps. These observations led to undertaking a test to determine
the responses of the beetles to light coming from below the horizontal
plane of sight of the beetles. For this purpose, the beetles were indi-
vidually placed on a sheet of transparent glass below which a light was
placed. Following this test, a combination of light coming from above
and below the beetle was tested to determine the responses of the beetles.

The orientation behaviour and responses to host wood factors were
also studied in the absence of light. The beetles were individually placed
in a cardboard box, about 50 cm. by 45 cm. by 15 cm., painted black inside.
The beetles were placed on a predetermined position on a piece of paper
inside the box which at times contained either an attractive or a "green" piece of wood as a particular test demanded; the box was afterwards covered
for a period of about five minutes; then it was opened to determine the posi-
tion of the beetles. Another condition of testing consisted of passing
wood odour through a hole in one side of the box.

Accessory Factors

The behaviour of insects under natural conditions is often stereo-
typed, described in terms of inborn pattern of behaviour commonly known as
instincts (Dethier and Stellar, 1964; Scott, 1963; Fraenkel and Gunn, 1961). Inborn reflexes, and reflexes "conditioned" by previous experience may
occur but are often masked by inhibitors and integrated in such a way that
they serve the needs and purposes of the insect as a whole. According to
Wigglesworth (1953), "stimuli which the insect can learn to associate with
the presence of food, or with the location of its nest, are judged to be
perceptible. Such experiments, of course, need the greatest care in their interpretation; for the insect may be guided by some other stimulus that has been overlooked by the experimenter; indeed, in the course of a single experiment, it may cease to be oriented by one stimulus and come to depend upon another; and there are many who hold that the whole perceptual experience of the organism is integrated, as it were, into a pattern, and not to the isolated stimuli of which it is composed."

While certain aspects of specific responses, or the aggregate behaviour of a species may be recognized as being peculiar to it in various ways, the component responses to internal (physiological) cues and external stimuli may show considerable flexibility as a result of modifying accessory factors. These factors have to be considered.

1. **Increasing temperature: its provision and use in the tests.**

   Earlier observations (Graham, 1959) indicated that photic reversal of *Trypodendron* occurred when the temperature was in the region of 55° to 58°C but it was desired to evaluate the effect in a more quantitative way. Several methods of test were employed. The first method made use of a glass tube, 2.0 cm. in diameter and 85 cm. in length, stoppered at the ends, placed in a temperature gradient apparatus (Fig. 4). The gradient apparatus consisted of a long shallow copper trough, to the under surface of which were soldered two lengths of copper tubing, one at either end of the trough and not intercommunicating. The tubing was folded in a zig-zag manner to give maximum contact with the trough. Hot water could be passed through one tube and cold through the other. Flow of the hot and cold water respectively was regulated to produce a temperature gradient from 15°C at one end and 40°C at the other. The glass tube into which the beetles
Fig. 4. Apparatus used for testing responses to light in a temperature gradient.
were placed was coated with a transparent red varnish, except for annular clear zones of about 2.0 cm. in width spaced about 15.0 cm. apart. The red zones were provided to create conditions which would constitute darkness to the insects, yet would enable the observer to see through. A strip of moist tissue paper was placed inside the glass tube to provide a crawling surface for the beetles. The beetles were put in groups of five, sexes noted, at the colder end of the tube; then, stoppered. A beam of white light was projected successively into each clear zone for five minutes at a time beginning at the colder end. The number of beetles aggregating at the lighted zone was recorded in relation to the temperature at the particular point in the gradient.

Another arrangement of apparatus was designed to relate the effect of temperature and of gravity to the photic responses of the beetle. This consisted of a water bath apparatus and a wide-mouth glass jar whose outer surface was painted flat black, except for two clear areas, each about three centimeters square. One of these clear areas was about two centimeters below the rim of the mouth of the jar. The other area was at the opposite side, near the base. A thermometer was fitted through the black rubber stopper and strips of moistened tissue paper, about 2.0 cm. in width and 11.0 cm. in length, were attached to the bottom surface of the rubber stopper so that when the jar was stoppered, the tip of the thermometer was halfway down the jar and the strips of paper touched the interior bottom surface. The apparatus is shown in Fig. 5.

Groups of five beetles, sexes noted, were put inside the jar. After being stoppered, the jar was immersed in a water bath. The water bath apparatus consisted of a cylindrical glass vessel containing warm
Fig. 5. Apparatus and set-up for testing responses of *Trypodendron* in relation to gravity and increasing temperature.
water whose temperature was varied from 15° to 40°C. A beam of white light was projected into the upper clear window so that the beetles had to climb or crawl up the paper strips (against gravity) to react to light. Once the number of the beetles responding positively to light had been recorded, the beam of white light was moved to the lower window. The beetles' movement would then be toward the force of gravity as they responded positively to light. The test was performed for every five-degree rise in temperature until 40°C.

2. Airstream with or without wood odour: its provision and use in the tests.

Anemotaxis is the term applied to reactions or orientation in an air current (Fraenkel and Gunn, 1961). Many species of insects, on taking to flight, head into the wind. *Drosophila* flies are known to walk and orientate very accurately into a wind containing the smell of mashed fruit. In *Trypodendron* beetles, the typical and characteristic flight orientation is against the wind (Chapman, 1962). Fraenkel and Gunn (1961) state that it is probable that many olfactory reactions are possible only with the air of air currents and that the means of reaching the source of odour is to go against the wind or air current. To test for the anemotactic and anemoolfactory effects on the photic reaction of the beetles, a gentle stream of air flowing at 0.5 meter per second (as measured by a "Wallac-Thermex GGA2C" thermo-anemometer), first without bearing wood odour, and then with odour in it, was directed to the beetles, its sex noted, as it was being tested for its reaction to light. The odour was provided by passing the airstream through a bottle containing either a mass of shavings from attractive wood or sawdust from unattractive "green" wood or various combinations of attractive shavings and "green" sawdust respectively.
Another test concerned the effect of air streaming in an odour-filled environment. The purpose was to test for the operation of anemotactic response that is prompted by the host odour. Accordingly, the beetles were brought into an odour field by placing them on perforated paper over attractive wood and exposing them to a stream of either non-odorous or wood-odour-carrying air flowing in the direction of the light source.

Tests of response to non-odorous and odour-bearing airstreams were also made with beetles placed inside a dark box. Non-flown as well as flown (flight-experienced) beetles were tested.

5. Increasing atmospheric pressure: its provision and use in the tests.

Experiments were devised to test for one of the possible mechanisms by which the air bubble in the ventriculus of the flight-experienced beetles (Graham, 1961) may function in the modification of the photic response. One possibility is that the gas bubble functions by crowding the internal space, thereby creating haemostatic pressure which in turn relays the effect as a signal to a pressure receptor centre. Another possibility is that a signal is received more directly by stretch receptors in the wall of the ventriculus in which the bubble occurs. A third possibility is that the crowding of internal space may stimulate stretch receptors in the body wall. In the absence of morphological evidence for stretch or pressure receptors in Trypodendron, the question must be approached experimentally.

In experiments with spruce budworm larvae, Wellington (1948) demonstrated that photic reversal in flaccid individuals could be brought about by such turgor-causing factors as feeding, injection of fluid into the gut or into the haemolymph, or the imposition of external pressure by means of ligaturing. It would be of both academic and practical experimental
interest to know whether the olfactory and other responses of *Trypodendron* can be studied while keeping the insect under pressure, in lieu of the otherwise necessary conditioning flight (Graham, 1961).

It was assumed that if pressure, and not stretch, is the mechanism involved in the change of photic response of *Trypodendron*, its effect could be made manifest in beetles placed under elevated atmospheric pressure. A compression chamber was constructed consisting of "Lucite" plastic tubing, 40.0 cm. long and 5.0 cm. in outside diameter and with a wall thickness of about 6.0 mm. It was fitted with a hose connection leading to a 4-way connector. The other passages in the connector were joined respectively to a pressure gauge, an air bleeder valve, and a nitrogen tank. Nitrogen was used as the compressed gas, on assumption that the normal quantity of atmospheric oxygen in the chamber was still available to the insects, whereas compressed air would have increased concentration of oxygen. This assumption follows that of Dalton's Law of partial pressure of gas mixtures.

In order to judge the effect of pressure on the photic response, it was necessary, in accordance with other findings of the investigation, to provide attractive host tree material as a source of an opposing stimulus to the photic one. Accordingly, a small sample of attractive wood was placed in one end of the compression chamber, non-flown beetles were introduced, the chamber sealed at the ends and placed in the retaining steel "cradle". Pressure was built up to a maximum of 50 psi (about two atmospheres). A beam of heat-filtered light was projected into the apparatus to cause the beetles to accumulate at the odour source, then the light was moved to the opposite end to compete with the odour for response of the beetles.
The apparatus for testing the response of the beetles to light under increasing atmospheric pressure is shown in Fig. 6.

**Methods of Observation**

The broadest problem of photic behaviour of *Trypodendron* may be considered to relate to the nature and strength of orientation and other responses under various conditions of light, alone, or in combination with other factors. The consideration should include the difference in sex and kind of conditioning of the insect.

For the study of behaviour, it was necessary to choose appropriate criteria by which responses could be interpreted. The responses of insects to effective external stimuli are variously manifest in changes of the state of activity or inactivity and in their spatial and temporal patterns. Manifestations of responses to stimuli are observable in movements of appendages or of regions of the body and displacement of the animals as a whole. *Trypodendron* is capable of slight movement of its head in a vertical plane, of extending, waving, and folding back its antennae, of manipulating its mouthparts for chewing or ingesting food, of waving its legs randomly if the beetle is held aloft, of coordinating them in walking on a surface, or of folding them against the body in feigned death, of elevating the elytra and unfolding its membranous wings, of restoring them to their resting position, of vibrating elytra and wings in flight movements, and of manipulating the external genitalia as occasion befits. Variables in these, conceivably include the dimensions of time, space and force, giving rise to such derived values of displacement of parts, or of the whole insect, such as rate of walking or of wing beat of flight, and various degrees of consistency in direction or activity in these. The variables would give rise also to such forms of
Fig. 6. Apparatus for testing photic responses of *Trypodendron* under increased atmospheric pressure.
measurement as rates of change, and periodicities in functions, change of orientation angle in respect to a direction stimulus, and observations on the assumption of postures such as feigned death or preparatory stance for flight, boring into wood, feeding and mating.

Preliminary experience in handling the beetles suggested that certain of the foregoing manifestations of response to stimuli would be most meaningful of the single or integrated reactions of the insect to light, darkness, contact, pressure, gravity, air flow, temperature, and chemical and physical factors in the host tree. The kinds of response that were sought included the beetles' alignment and directed movement in respect to directional stimuli, turning activity, retention at an odour centre or other centres of stimuli, attempts to fly or actual flight and the compound responses of the whole insect which are manifest in its attempt to bore into wood. Group responses were observed quantitatively in the aggregation of beetles when a number of them were exposed simultaneously to an experimental situation as in a temperature gradient apparatus.

The experiments were conducted in a darkened room. The primary purpose of the darkness in these studies was not with the intention of adapting the insect to the condition of scotopic vision, which would involve the use of beam intensities far below the present photopic requirements, but to avoid extraneous sources of light that might interfere with the normal response of the beetle to a given stimulus.

The experiments were conducted in a series which started in May, 1964. The scheme of the programme of experiments conducted in these studies of the behaviour Trypodendron is presented in Fig. 7.
Fig. 7. Scheme of the programme of experiments on the photic responses of *Trypodendron lineatum* in relation to various host wood factors and conditions of the environment.
OVERWINTERED ADULTS (♂&♀) OF *Trypodendron lineatum* Oliv. (COLEOPTERA: SCOLYTIDAE)

- Programme of Experiments -

1. WHITE LIGHT PRESENT

   NORMAL LABORATORY CONDITIONS

   OVERHEAD FIELD OF LIGHT  \ HorIZONTAL BEAM OF LIGHT

   Wood Factors Absent  
   Without Air Stream  
   Air Source Antipodal to Light  
   No Odour in Stream  
   Attractive Wood Odour in Stream

   "Green" Wood Present  
   Insect Not in Contact  Insect in Contact  
   Without Air Stream  
   Air Source Antipodal to Light  
   No Odour in Stream  
   Attractive Wood Odour in Stream

   "Attractive" Wood Present  
   Insect Not in Contact  Insect in Contact  
   Without Air Stream  
   Air Source Antipodal to Light  
   No Odour in Stream  
   Attractive Wood Odour in Stream

   INCREASING TEMPERATURE

   DIRECTIONAL BEAM OF LIGHT

   GRAVITY ANTIPODAL TO LIGHT  \ GRAVITY SYMPODAL WITH LIGHT

   INCREASING ATMOS. PRESSURE

   HORIZONTAL BEAM OF LIGHT

   Attractive Wood Factors
2. IN DARKNESS

NORMAL LABORATORY CONDITIONS

Wood Factors Absent

- Without Air Stream
- Air Source Across Insect
  - No Odour in Stream
  - Attractive Wood Odour in Stream

"Green" Wood Present

- Insect not in Contact
- Insect in Contact
  - Without Air Stream
  - Air Source Across Insect
    - No Odour in Stream
    - Attractive Wood Odour in Stream

"Attractive" Wood Present

- Insect Not in Contact
- Insect in Contact
  - Without Air Stream
  - Air Source Across Insect
    - No Odour in Stream
    - Attractive Wood Odour in Stream
EXPERIMENTAL RESULTS.

1. Responses to white light under normal laboratory conditions.-

Both male and female Trypodendron adult beetles which had no previous flight experience showed strong positive phototaxis to a horizontal beam of white light. There was no observable difference in response between the sexes as indicated by the several tracings of their paths of response to light. Response varied from immediate orientation followed by movement directly toward the light to feigned death and sluggish orientation followed by a circuitous or compassing movement which may or may not lead to the source of light. Examples of paths taken by the beetles in response to a horizontal beam of white light are shown in Fig. 8 (A to H) and Fig. 9 (A to H). The responses of the beetles to the horizontal beam of white light may be divided into four categories: (1) not inhibited, the beetles immediately orient themselves and move toward the source of light. This category of response is exemplified in Fig. 8 D and Fig. 9 A, 9 B, 9 C, 9 D, 9 F, and 9 H (especially by the paths of the non-flown beetles, represented by thin lines); (2) initially inhibited positive response, the beetles move away for some distance from the source of light at the start of orientation, then gradually recovering and moving toward the source of light. An example of this particular category of response is indicated by lines P2 in Fig. 8 A and U2 in Fig. 8 D; (3) inhibited positive response, the beetles may or may not be inhibited at the start of orientation but the general movement, though toward the general direction of the source of light, is oblique and not direct. Examples of this category of response are indicated by lines U5 and F5 in Figs. 8 B and 8 C; (4) completely inhibited response, the beetles ignoring the presence of light and the general direction of movement is away from the source of light. This particular type or category
of response is indicated by lines U4 and F4 in Fig. 8 B.

In successive trials of the same individual beetle, different degrees of consistency of response occurred. The majority of the beetles oriented positively toward light in every trial (Figs. 8 D, 9 A, 9 B, 9 C, 9 D, 9 F, and 9 H. Note especially the paths taken by the non-flown beetles). Some beetles reacted positively in nearly every trial (Figs. 8 A, 8 C, 8 E, 8 F, 8 G, and 8 H). Others showed no consistent orientation to light, and thereby demonstrated a consistency of randomness (Figs. 8 B and 9 E).

A summary of the responses of the non-flown beetles to a horizontal beam of white light is presented in table 1.

Table 1. Summary of responses of non-flown Trypodendron adult beetles to a horizontal beam of white light under normal laboratory conditions.

<table>
<thead>
<tr>
<th>Type of response</th>
<th>Proportion of responses (% of total) 1/</th>
<th>Male</th>
<th>Female</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Not inhibited, movement direct to light</td>
<td></td>
<td>47</td>
<td>52</td>
</tr>
<tr>
<td>2. Initially inhibited positive response</td>
<td></td>
<td>26</td>
<td>23</td>
</tr>
<tr>
<td>3. Inhibited positive response</td>
<td></td>
<td>21</td>
<td>15</td>
</tr>
<tr>
<td>4. Completely inhibited, negative response</td>
<td></td>
<td>16</td>
<td>10</td>
</tr>
</tbody>
</table>

1/ Total number of observations = 98
Fig. 8 (A to H). Representative paths of response to a horizontal beam of light by newly overwintered adult males of *Trypodendron lineatum* (Olivier). Thin lines, marked "U", represent paths of flight-inexperienced beetle; thick lines, marked "E", represent paths of the same beetle after flight exercise. Numbers represent type of response (see table 1).
Figure 8 A.
Specimen: male beetle
Ammeter at 4.0 amperes
Light, heat filtered
Duration of flight: 10 min.
Figure 8B
Specimen: male beetle
Ammeter at 4.0 amperes
Light, heat filtered
Duration of flight:
30 min.
Figure 8 C.
Specimen: male beetle
Ammeter at 4.0 amperes
Light, heat filtered
Duration of flight:
50 min.
Direction of light

Figure 8 D
Specimen: male beetle
Ammeter at 4.0 amperes
Light, heat filtered
Duration of flight:
50 min.
Figure 8 E.
Specimen: male beetle
Ammeter at 4.0 amperes
Light, heat filtered
Duration of flight:
1 hour
Figure 8 F.
Specimen: male beetle
Ammeter at 4.0 amperes
Light, heat filtered
Duration of flight: 1 hour
Direction of light.

Figure 8 G.
Specimen: male beetle
Ammeter at 4.0 amperes
Light, heat filtered
Duration of flight: 2 hours
Figure 8 H.
Specimen: male beetle
Ammeter at 4.0 amperes
Light, heat filtered
Duration of flight: 50 min.
Fig. 9 (A to H). Representative paths of response to a horizontal beam of white light by newly overwintered adult females of *Trypodendron lineatum* (Olivier). Thin lines, marked by "U", represent paths of flight-inexperienced beetle; thick lines, marked "P", represent paths of the same beetle after flight exercise. Numbers represent types of response (see table 1).
Figure 9 A.
Specimen: female beetle
Ammeter at 4.0 amperes
Light, heat filtered
Duration of flight: 15 min.
Figure 9 B.
Specimen: female beetle
Ammeter at 4.0 amperes
Light, heat filtered
Duration of flight:
30 min.
Figure 9 C.
Specimen: female beetle
Ammeter at 4.0 amperes
Light, heat filtered
Duration of flight:
1.0 hour.
Figure 9 D.
Specimen: female beetle
Ammeter at 4.0 amperes
Light, heat filtered
Duration of flight: 40 min.
Direction of light

Figure 9 E.
Specimen: female beetle
Ammeter at 4.0 amperes
Light, heat filtered
Duration of flight:
30 min.
Figure 9 F.

Specimen: female beetle
Ammeter at 4.0 amperes
Light, heat filtered
Duration of flight: 3.0 hours.
Figure 9 G.
Specimen: female beetle
Ammeter at 4.0 amperes
Light, heat filtered
Duration of flight:
2.0 hours
Figure 9 H.
Specimen: female beetle
Ammeter at 4.0 amperes
Light, heat filtered
Duration of flight:
50 min.
The beetles that were given flight experience varying from five minutes to six hours showed various degrees of inhibition of their response to a horizontal beam of white light. Inhibition was more apparent in the female beetles than in the males which behaved as if they had not flown. Examples of the path taken by the flight-experienced beetles in response to a horizontal beam of white light are shown in thick lines in Figs. 8 (A to H) and 9 (A to H). Responsiveness to light in the female beetles is not, however, completely lost or totally inhibited as a result of flight experience even when the duration of flight experience is increased. Several beetles which had been given flight experience of more than six hours still exhibited positive response to light.

A summary of the responses of the flight-experienced beetles is shown in table 2.

Table 2. Summary of responses of flight-experienced Trypodendron adult beetles to a horizontal beam of light under normal laboratory conditions.

<table>
<thead>
<tr>
<th>Type of response</th>
<th>Proportion of responses (% of total)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Male  : Female</td>
</tr>
<tr>
<td>1. Not inhibited, movement direct to light</td>
<td>45 : 22</td>
</tr>
<tr>
<td>2. Initially inhibited positive response</td>
<td>25 : 16</td>
</tr>
<tr>
<td>3. Inhibited positive response</td>
<td>21 : 30</td>
</tr>
<tr>
<td>4. Completely inhibited, negative response</td>
<td>13 : 32</td>
</tr>
</tbody>
</table>

1/ Total number of observations = 95
After the tests for the simple photic responses of flight-inexperienced and flight-experienced beetles to a horizontal beam of white light, another set of beetles was exposed, under normal laboratory conditions, to overhead light.

The beetles took to flight in the presence of a broad field of light from above. The time differences between setting (putting the beetles on a fixed position at the center of the piece of paper) and taking to flight was not determined, although it was noted that previous flight experience did not inhibit the beetles from taking to flight again.

Representative samples of response of the beetles to an overhead source of light are shown in Fig. 10 (A to D). The paths of the flight-experienced beetles were in several instances punctuated by pauses or rests. Orientation was consistently random.

2. Photic response in the presence of air current with or without wood odour.

The introduction of a gentle stream of air flowing at the rate of about 0.5 meter per second did not alter the response of the beetles to light. Neither did an airstream passed through sawdust of "green" host wood. However, when the airstream was passed through a mass of shavings from "attractive" host wood, both non-flown and flown beetles immediately abandoned their course toward light in favor of the odorous airstream. Samples of these responses are illustrated in Fig. 11 (A to D).

In the presence of an overhead source of light, the beetles also responded positively to the airstream carrying odor from the mass of shavings of attractive host wood. The response, however, of the flight-inexperienced beetles was of short duration and was readily overcome by the positive response to light. The flight-experienced beetles took much longer time in
Fig. 10 (A to D). Representative paths of response to an overhead source of light by newly overwintered adults of *Trypodendron lineatum* (Olivier). Thin lines represent paths before flight and thick lines after flight.
Figure 10 A.
Specimen: female beetle
Lighting: ceiling fluorescent lamps
Duration of flight:
10 min.
Figure 10 B.
Specimen: female beetle
Lighting: ceiling fluorescent lamps
Duration of flight: 1.0 hour.
Figure 10 C.
Specimen: male beetle
Lighting: ceiling fluorescent lamps
Duration of flight: 20 min.
Figure 10 D.
Specimen: male beetle
Lighting: ceiling fluorescent lamps
Duration of flight: 50 min.
Fig. 11 (A to D). Representative paths of flight-inexperienced (represented by thin lines) and flight-experienced (represented by thick lines) adult *Trypodendron* in response to a gentle stream of air (x) without odour, and (o) with attractive wood odour.
Figure 11
A. Before flight
B. After flight
Specimen: male beetle
Light, heat filtered
Duration of flight: 1.0 hr.

\( y = \) course taken in still air
\( x = \) course taken while odour-free air flowed from behind.
\( o = \) course taken while attractant was blown toward light.
Club of light

Figure 11.

C. Before flight
D. After flight
Specimen: female beetle
Light, heat filtered
Duration of flight: 30 min.

y = course taken in still air
x = course taken while odour-free air flowed from behind.
o = course taken while attractant was blown toward light.
investigating the source of the air carrying the attractive host odour. They, too, however, eventually abandoned the source of the airstream and became positively attracted to light.

5. Photic response in the presence of "green" wood factors.

The presence of the various stimuli provided by "green" wood such as odour or contact did not alter the response of the beetles to either a horizontal beam of white light or an overhead light source. The responses of the flight-inexperienced and flight-experienced beetles were similar to previously observed responses of the beetles where "green" wood host factors were absent. A slight change in the behaviour of a few flight-experienced beetles was noted when the beetles were individually placed in contact with a "green" piece of wood. The change was characterized by some indication of investigative behaviour; the beetles occasionally hesitated in their movements, paused, manipulated their antennae while still on the surface of the wood. The exhibition of investigative behaviour was not, however, of long duration, whereas attraction to light or to an airstream carrying attractive wood odour was pronounced. Representative paths of response exhibited by the beetles in contact with "green" wood or in the presence of "green" wood and other factors involved with it are illustrated in Figs. 12 (A to D) and 15 (A to D).

4. Photic response in the presence of attractive wood factors.

Response of the flight-inexperienced male or female Trypodendron to either a horizontal beam of white light or an overhead light source was invariably inhibited by the presence of an attractive piece of wood under the perforated area at the center of the sheet of paper where the beetles were individually set for observations. In some instances the beetles were only
Fig. 12 (A to D). Representative paths of response to light and to an airstream with (marked "o") or without (marked "x") attractive wood odour by flight-inexperienced (U) as well as flight-experienced (F) adults of *Trypodendron* placed on a perforated area on a sheet of paper above a piece of "green" wood.
Figure 12 A
Specimen: male beetle
Ammeter at 4.0 amperes
Light, heat filtered
Duration of flight:
50 min.
Direction of light

Figure 12 B.
Specimen: male beetle
Ammeter at 4.0 amperes
Light, heat filtered
Duration of flight: 1 hour.

Direction of air stream
Direction of light

Figure 12 C.
Specimen: female beetle
Ammeter at 4.0 amperes
Light, heat filtered
Duration of flight:
10 min.

Direction of air stream
Direction of light

Figure 12 D.
Specimen: female beetle
Ammeter at 4.0 amperes
Light, heat filtered
Duration of flight:
30 min.

Direction of air stream
Fig. 15 (A to D). Representative paths of response to light and to an airstream with (marked "o") or without (marked "x") attractive wood odour by flight-inexperienced (U) as well as flight-experienced (F) adults of *Trypodendron* in direct contact with a piece of "green" wood. The course taken by the beetle on the wood was not recorded.
Direction of light

Figure 13 A.
Specimen: female beetle
Ammeter at 4.0 amperes
Light, heat filtered
Duration of flight: 30 min.

Direction of air stream
Figure 13 B.
Specimen: female beetle
Ammeter at 4.0 amperes
Light, heat filtered
Duration of flight: 1 hr.

Direction of light

"Green"-wood

Direction of air stream
Figure 13 C.
Specimen: male beetle
Ammeter at 4.0 amperes
Light, heat filtered
Duration of flight: 30 min.

Direction of light

"Green" wood

Direction of air stream
Figure 13 D.
Specimen: male beetle
Ammeter at 4.0 amperes
Light, heat filtered
Duration of flight:
1.0 hour

Direction of air stream
initially inhibited for a very brief period of time before they moved toward the source of light or attempted to fly away. In other instances, they lingered on the perforated area, moved slowly, and took a convoluted course (see Fig. 14 A and B). Investigative behaviour was exhibited but not pronounced.

Response of the flight-experienced male or female Trypodendron to such conditions as mentioned in the preceding paragraph was characterized by an apparent initial indifference to light and by a certain high level of excitability in the display of investigative behaviour. Investigative behaviour took the form of very convoluted paths of movement on the perforated area of the paper above the attractive piece of wood. The time spent by the beetles walking on the perforated area varied from a few minutes to more than half an hour (a period of time set arbitrarily as the limit for the purpose of the test). After a period of time on the perforated area, the beetles wandered away or became attracted to light.

Examples of the path of response of the flight-experienced and flight-inexperienced beetles to light in the presence of attractive wood underneath a perforated paper are shown in Figs. 14 (A and B), 15 (A and B) and 16. It was noted that the flight-experienced beetles were far more reactive than the flight-inexperienced individuals to a source of attractive wood odour. In still air, there was a consistent display of investigative behaviour especially on the perforated area of the sheet of paper just about the region where the sapwood portion of the piece of attractive wood lied underneath (see Fig. 14 A).

One observable effect of directing a stream of non-odour-bearing air to the perforated area was a dissipation of wood odour as manifested
by a decrease in the density of responses to a particular area (see Fig. 15 A) or by back-and-forth paths of responses (see Fig. 15 B).

The introduction of an airstream conveying an attractive wood odour had about the same effect as a non-odorous airstream. One notable difference, however, was the presence of minor concentrated responses and inclinations to approach the source of the stream of odour (see Fig. 16).

The responses of the flight-inexperienced beetles to light when they were individually placed in contact with the piece of attractive wood varied from a very brief period of retention by the wood to a few positive-negative responses to it but finally attraction to light predominated. Response to a non-odorous air current was nil; to an airstream conveying the attractive odour, it was positive.

The flight-experienced beetles exhibited a very strong investigative behaviour when they were individually placed in contact with attractive wood. They were excited, active, and mobile. They explored all sides of the wood, at times moving away from it but returning again. This type of behaviour was exhibited for a variable period of time before the beetles finally moved away or became attracted to light. An introduction of an airstream to the area on the piece of wood where the beetle was located did not alter its response as it did when the beetle was not in contact with the wood. The response to an airstream conveying attractive wood odour was variable; many of the beetles tested did not move away from the attractive piece of wood, while others were drawn to the source of the airstream for a short period of time.

Representative paths of response of the beetles in contact with an attractive piece of wood in the presence of white light are illustrated in
5. **Response to background black-and-white patterns.**

The series of tests using (1) horizontal black-and-white broad lines, (2) vertical black-and-white broad lines, (3) diagonal black-and-white broad lines, (4) all black, or (5) all white background pattern while the beetles were individually exposed to a horizontal beam of white light did not produce results which showed any marked preference or tendency by the beetles to respond to any of the patterns.

6. **Responses to white light under increasing temperature.**

Tests of the photic responses of flight-inexperienced adult *Trypodendron* at temperatures ranging from 14° to 40°C, with the beetles inside a painted glass tubing placed on a temperature gradient apparatus, indicated that the peak of activity characterized by excitability, positive phototaxis, and attempts to fly occurred between 26° and 28°C. At 38°C the beetles ceased to become attracted to light entirely. The results of 10 tests, using 10 beetles in each test, are shown in Table 5.

In the tests for responses of the beetles to light, antipodal to gravity, under increasing temperature, the range of temperature under which the responses of the beetles were studied was from 23° to 40°C. In these tests, the peak of activity of the beetles was noted at about 29°C. The maximum temperature which registered a positive photic response by the beetles was 56°C. In only one instance out of 10 tests did a beetle appear at the lighted window at 56°C. Mating occurred occasionally between 25° and 35°C. These pairs were indifferent to light.

In the tests for responses of the beetles to light positioned sympodally with gravity, the range of temperature registering the highest
Fig. 14 (A and B). Representative paths of responses to light and to an attractive piece of wood under perforated area on sheet of paper by flight-inexperienced (indicated by thin line) as well as flight-experienced (indicated by thick line) *Trypodendron lineatum*. 
Figure 14 A.
Specimen: female beetle
Ammeter at 4.0 amperes
Light, heat filtered
Duration of flight: 30 min.
Figure 14 B.
Specimen: female beetle
Ammeter at 4.0 amperes
Light, heat filtered
Duration of flight: 30 min.
Fig. 15 (A and B). Types of response to light and to an airstream without attractive wood odour by flight-inexperienced (indicated by thin line) and flight-experienced *Trypodendron* beetle on a perforated sheet of paper above an attractive host wood.
Figure 15 A.
Specimen: female beetle
Ammeter at 4.0 amperes
Light, heat filtered
Duration of flight: 30 min.
Figure 15 B.
Specimen: Female beetle
Ammeter at 4.0 amperes
Light, heat filtered
Duration of flight:
15 min.

Direction of air stream
without wood odour
Fig. 16. Representative paths of response to light by flight-inexperienced (thin line) and flight-experienced (thick line) adult *Trypodendron* beetle placed on a perforated sheet of paper above attractive host wood and subjected to a gentle stream of air with attractive wood odour.
Figure 16.
Specimen: female beetle
Ammeter at 4.0 amperes
Light, heat filtered
Duration of flight: 10 min.

Direction of air stream
with "ripe" wood odour
Fig. 17 (A and B). Representative paths of response to light by the flight-inexperienced (thin line) or by the flight-experienced (thick line) Trypodendron beetle in contact with a piece of attractive host wood. Tracings were made of paths as beetle wandered away from the wood.
Figure 17 A.

Specimen: female beetle
Ammeter at 4.0 amperes
Light, heat filtered
Duration of flight:
3 hours
Figure 17 B.
Specimen: male beetle
Ammeter at 4.0 amperes
Light, heat filtered
Duration of flight:
1.0 hour
Fig. 18 (A and B). Representative paths of response of flight-inexperienced (indicated by thin broken line) and of flight-experienced (indicated by thick broken line) adult Trypodendron beetle to light and to a stream of air with attractive wood odour. Beetle was in contact with wood and its path was traced whenever it left the wood.
Direction of light

Figure 18 A.
Specimen: female beetle
Ammeter at 4.0 amperes
Light, heat filtered
Duration of flight:
5 hours

Direction of air stream
with attractive wood odour
Direction of light

Direction of air stream with attractive wood odour

Figure 18 B.
Specimen: male beetle
Ammeter at 4.0 amperes
Light, heat filtered
Duration of flight: 40 min.
Fig. 19. Representative paths of response of the flight-experienced *Trypodendron* beetle placed in contact with a piece of attractive wood in relation to light in the presence of an airstream without (indicated by dotted line) or with attractive host wood odour (indicated by dashed line).
Figure 19
Specimen: female beetle
Ammeter at 4.0 amperes
Light, heat filtered
Duration of flight: 45 min.
........ = response to air without odour.
---- = response to air with attractive wood odour
percentage of beetles responding to light was 25° to 28°C. The maximum temperature registering the least number of beetles responding positively to light was 56°C. In some tests, increasing temperature caused the beetles to become very active or "excited". Attempts to fly were noted in many instances. Thermal paralysis and death of several beetles occurred between 56°C and 58°C.

The summarized data on the responses of the beetles to light in relation to gravity and increasing temperatures are shown in table 4. They are also illustrated in Figs. 20 and 21.

Table 5. Photic responses of adult Trypodendron under increasing temperature in a glass tubing on a gradient apparatus.

<table>
<thead>
<tr>
<th>Temperature range (°C)</th>
<th>Per cent of beetles responding positively to light</th>
</tr>
</thead>
<tbody>
<tr>
<td>14 - 16</td>
<td>55</td>
</tr>
<tr>
<td>17 - 19</td>
<td>75</td>
</tr>
<tr>
<td>20 - 22</td>
<td>83</td>
</tr>
<tr>
<td>23 - 25</td>
<td>83</td>
</tr>
<tr>
<td>26 - 28</td>
<td>85</td>
</tr>
<tr>
<td>29 - 31</td>
<td>61</td>
</tr>
<tr>
<td>32 - 34</td>
<td>52</td>
</tr>
<tr>
<td>35 - 37</td>
<td>36</td>
</tr>
<tr>
<td>38 - 40</td>
<td>0</td>
</tr>
</tbody>
</table>
Table 4. Photic responses of adult *Trypodendron* as influenced by gravity and increasing temperature. 1/

<table>
<thead>
<tr>
<th>Temperature range</th>
<th>Per cent of beetles responding positively to light</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>a. Light antipodal : b. Light symphodal</td>
</tr>
<tr>
<td></td>
<td>to gravity with gravity</td>
</tr>
<tr>
<td>25 - 25</td>
<td>81 : 85</td>
</tr>
<tr>
<td>26 - 28</td>
<td>85 : 85</td>
</tr>
<tr>
<td>29 - 31</td>
<td>86 : 70</td>
</tr>
<tr>
<td>32 - 34</td>
<td>58 : 44</td>
</tr>
<tr>
<td>35 - 37</td>
<td>18 : 17</td>
</tr>
<tr>
<td>38 - 40</td>
<td>0 : 0</td>
</tr>
</tbody>
</table>

1/ Average of 10 tests per temperature range; 10 beetles per test.

7. Responses of Trypodendron to various stimuli in the dark.-

Under normal laboratory conditions, newly overwintered *Trypodendron* adults, having flight experience or not, moved about in a random manner when placed inside a dark box. The same results were obtained when a stream of air was allowed in and out of the box through tiny holes. However, when the airstream carried attractive wood odour, the beetles tended to approach the hole through which the air stream was introduced.

Physical contact with a piece of "green" wood placed inside the box did not cause an aggregation or positive response of the beetles. The majority of the beetles had moved away from the piece of wood after the allotted time of five minutes allowed for each test. Again the introduction of an airstream without wood odour did not change the initial behaviour of the beetles. Positive response, however, was observed when the airstream carried attractive wood odour.
Fig. 20. Effect of increasing temperature on the photic responses of *Trypodendron lineatum* (Olivier).

Fig. 21. Comparison of effects of gravity and increasing temperature on the photic responses of *Trypodendron lineatum* (Olivier).
Temper at tare range in degree centigrade

Beetles responding to light

%  100
90  80  70  60  50  40  30  20  10  0

16  19  22  25  28  31  34  37  40
Temperature range in degree centigrade

Beetles responding to light

%  100
90  80  70  60  50  40  30  20  10  0

16  19  22  25  28  31  34  37  40
Temperature range in degree centigrade

. light antipodal to gravity
+ light sympodal with gravity
Attractive wood inside the box caused an aggregation of the beetles on or near the wood. During the period of observation, some of the beetles crawled under the wood while others were either away from it or at the base of contact of the wood with the sheet of paper. No boring behaviour was observed during the period allowed for each test. However, in a test in which the beetles were confined to a piece of wood covering it with a suitable stacking dish and left overnight, preliminary borings were observed.

The response of Trypodendron adults to light at the end of their overwintering period has been shown by these studies and by previous other observations (Graham, 1959) to be strongly photopositive. Furthermore, the tests have shown that the beetles' ability to orientate to the source of light is in no way affected by their initial angular displacement. The expression of positive phototaxis appears essential at this particular stage of the life cycle of the beetles. After overwintering, residence in the forest litter or loose bark not only ceases to function advantageously for the insect, but would frustrate its survival if special sequences in behaviour did not cause it to disperse and react to host factors.

The presence of a narrow horizontal beam of light attracts Trypodendron. Positive response is often characterized by an increase in the locomotory speed toward the source of light. At some point in the expression of positive phototaxis or at a certain distance from the source of light, the beetles may be stimulated to fly. Another condition which stimulates flight is the presence of a broad overhead field of light as provided by ceiling lamps or by skylight. The importance of an overhead source of light is shown by the fact that when the beetles were exposed to light coming from below their horizontal plane of sight, flight did not occur. Restoration of an overhead source of light caused initiation of flights.

In the laboratory, escaped beetles were observed flying continuously about the ceiling lights, at times even when their heads in touch with the fluorescent light tubes. The light intensity close to the light tube was
of the order of 500 footcandles. In nature, ordinary sunlight produces an illuminance of some 10,000 to 14,000 footcandles (Platt and Griffiths, 1964). Under field conditions, the beetles do not fly upward into the sky. At most, they have been observed flying up to about six to seven meters from the ground in forest areas with an elevation of about 400 meters above sea level (Chapman, 1962). One conceivable explanation for the beetles' not flying toward the sun may be that they fly, like many other insects, at a certain angle to the rays of light. This type of light reaction is termed light compass reaction (Fraenkel and Gunn, 1961). It is also possible that there is an upper limit in the threshold of light intensity which the photoreceptors of the beetles can tolerate.

The occasional negative phototactic response among positively phototactic beetles has been observed (see table 1). Why it should exist among flight-inexperienced beetles which generally are positive in their light responses remains among other questions to be answered. It is conceivable that in these individuals, diapause influences are still partly operative, or reproductive maturity is delayed.

Positive phototaxis in Trypodendron is not a unique behaviour. Photic attraction is involved in various activities among different insects. Fireflies, for instance, though nocturnal in activity also exhibit positive phototaxis in attracting or locating a mate (McElroy, 1964). In the moths, however, it is still unexplained as to why these nocturnal insects are attracted to light at night but not to sunlight in the day. Winged termites, on the other hand, utilize their brief positive phototactic behaviour as a means to disperse and possibly interbreed with members from different termite colonies of the same species.
Little is known directly of the mechanisms which trigger light attraction in *Trypodendron* although much has already been studied and written about photoreception in many species of insects (Birukow, 1961; Booth, 1965; Burtt and Catton, 1956, 1962; Crescitelli and Jahn, 1959, 1942; Dethier, 1953d; Fingerman, 1952; Goldsmith, 1964; Rogers, 1962; Ruck, 1965; de Vries, 1956; de Wilde, 1962). One of the factors known to influence the expression of phototaxis in some insects is hormone concentration. Beetsma *et al* (1962) found that injections of an extract of the abdomen of male cecropia moth into fourth and fifth instar larvae of a hawk moth shifted the balance between photopositive and photonegative tendencies towards a definite photopositive response. In the Colorado potato beetle, activity of the corpora allata has been correlated with positive phototaxis (de Wilde, 1959). Photonegative response was also demonstrated by implantation of active prothoracic glands into the body cavity of the caterpillars. It is conceivable that in some of the newly overwintered *Trypodendron* adults the prothoracic gland still exerts an inhibiting influence on the photic behaviour of the beetle.

In some other insects, light attraction is tied with homeostatic processes which regulate the physiological and biochemical functions of the various internal organs. Thus the larvae of several species of tent caterpillars, *Malacosoma distria*, *M. pluviale* and of the fall webworm *Hyphantria textor* on becoming hungry are attracted to light and crawl up to the top branches where there is young foliage to feed on (Sullivan and Wellington, 1955; Wellington *et al*, 1954). A similar light attraction enables the adults of white pine weevil, *Pissodes strobi*, to climb to the terminal shoots or leaders which they infest (Sullivan, 1959). These observations
suggest possible approaches to the study of physiological mechanisms in photic responses in *Trypodendron*.

One important observation on the behaviour of *Trypodendron* that needs derivation from known physiological characteristics of organ systems in insects is the mechanisms which stimulate the beetle to fly. It appears that the amount and intensity of light falling on its photoreceptors may be involved in the flight-initiating mechanisms. It is also possible that the photoreceptors have a threshold number which triggers the flight response. Pielou (1940) believes that in the beetle *Tenebrio molitor*, there is a relation between threshold of response and the number of sensilla stimulated.

The failure by a broad field of light coming from below the horizontal plane of sight of the beetles to stimulate the beetles to fly seems to support the foregoing statement. Another explanation relevant to the beetle's failure to fly in the presence of "sunken" light involves differences in the thresholds of stimulation or in the ability to discriminate light between the dorsal and ventral part of the eyes of insects whose eyes are divided into two portions (Burkhardt, 1964). *Trypodendron* has divided eyes.

2. **The modifiers of photic behaviour: their relation to host-finding.**

The failure of a non-odour-bearing airstream to modify the activity of *Trypodendron* beetles moving toward the source of light indicates that the airstream alone has no inhibiting effect on the phototactic behaviour of the beetles, nor does it elicit a positive anemotactic response. This conforms with statements by Dethier (1957) in his review on the orientation by some flying insects that air current alone does not initiate
orientation. This statement was supported by observations made on the behaviour of diverse kinds of insects such as *Drosophila*, a fly; *Geotrupes stercorarius*, a beetle; and *Bombyx mori*, a moth. In these insects, it is odour which initiates orientation to air currents. In our own studies, pedestrian *Trypodendron* adults responded to an airstream carrying attractive wood odour. Their positive phototactic behaviour was immediately inhibited on their being exposed to an airstream carrying attractive wood odour. Their response, however, was variable in the duration of time they stayed at the odour source. The beetles approached the orifice of the air source but eventually left it to proceed toward light. On the basis of this observation, one may postulate the need for other kinds of stimuli that must be present in order to retain the beetles at the odour source.

The failure of the beetles to react to an airstream when they are already surrounded by odour appears at first to be contrary to expectations. It does not appear to correlate with their response to an odorous airstream brought into an odour-free "field". It also tends to contradict the suggestion that an anemotactic response occurs. It should be remembered, however, that these studies pertain to a pedestrian situation in which the tactile stimulus of the insect in contact with a surface may under certain conditions inhibit an anemotactic response. If the beetles reacted otherwise, they would be biological failures, abandoning attractive host material every time a breeze blew across it.

At least two considerations might be discussed in connection with the foregoing statements: (1) conditions within the beetles and (2) conditions within the host materials.
Granting that all conditions within the host material meet the requirements of the beetles, it seems that the beetles still must go through a series of stereotyped responses starting with positive phototaxis, flight, orientation to an airstream carrying attractive wood odour, approach to the source of the odour, settling and crawling before being able to bore into the host material.

Graham (1959) indicated that flight exercise could effect an inhibition of the phototactic response of the beetles. Flight-exercised beetles were no longer strongly photopositive, and when put in contact with an attractive piece of wood, the beetles behaved normally by exploring the bark contours and eventually boring into wood.

While the present study did confirm that flight and the presence of attractive wood inhibit the positive phototactic behaviour of *Trypodendron*, it did not, however, show such strong depression of the phototactic reaction, nor the strong tendency to bore into attractive wood. The reason for the disparity of results is not clear. It may have to be sought in differences in the population stock, conditions of storage or unrecognized differences in the environmental conditions during the experiments.

There appears to be present in the behaviour pattern of *Trypodendron* another mechanism of responses leading to the boring into wood. For instance, Graham (1959) observed that beetles which had no previous flight experience when kept in the dark with a piece of attractive wood exhibited the boring behaviour. Chapman (1959) and Dyer and Chapman (1965) reported that newly overwintered, flight-inexperienced beetles could be forced to bore into attractive logs but not into "green" logs when confined to the upper surface of logs in small aluminum rings partly imbedded in the
surface of the logs. While Graham's observations noted borings made in the dark, Chapman and Dyer's did not note whether the borings were made during the day or during the night. Neither, however, excluded the possible effect of locomotion by prolonged walking or crawling on responsiveness to light or to its host as observed by Johnson (1958) in connection with the settling responses in aphids.

The importance of flight experience preparatory to host attraction under normal conditions has been noted in insects other than Trypodendron. In aphids, Kennedy (1955, 1958) and Kennedy and Booth (1965a, 1965b) observed that flight experience "primes" or promotes the settling response on a host leaf. A suitable host leaf itself was considered to possess an inhibitory stimulus that would cause the aphid to remain. If the leaf were unsuitable, the insect would take to flight again. The "excitability of the settling responses increased as an aftereffect of flight in which the excitability of flight itself (measured by the rate of climb) was not falling and was even increasing."

As regards the effect of flight on phototaxis, Kennedy (1965) believes that, in aphids, "at first the phototaxis is positive to all light intensities, but that as flight proceeds it becomes negative to bright light while still remaining positive to weaker light, until finally it becomes negative even to the dimmest light and the reversal can then be said to be complete."

Several suggestions have been advanced to explain the underlying mechanisms which cause the settling and feeding behaviour as an aftereffect of flight. Evans and Dethier (1957) and Hudson (1958) are of the opinion that flight, especially in the blowfly and the honeybee, causes a diminution
of blood trehalose and glucose levels resulting in the lowering of the threshold for feeding. Johnson (1958) also suggests that respiratory metabolism has an effect on the settling responses as he found that aphids increased readiness to settle after a brief anaesthesia with carbon dioxide but not with ether. These suggestions appear to come under the "peripheral" hypotheses which, according to Kennedy and Booth (1963b), are "versions of the chain-reflex theory of behaviour assuming that the link lies not in the central nervous system but in some cumulative physiological consequence of the locomotor activity which provides 'feed-back'." Kennedy (1965) believes, however, that the mechanism lies in the central nervous system and is controlled by it, "over and above any peripheral feed-back from flight such as air swallowing and gut distension seem to provide."

As to the composition and make-up of the set of stimuli that must be present in the host material before a "conditioned" or "primed" insect could show a favorable response, Beck (1965) suggests that they are biochemical and biophysical in nature. He gives the following classification of stimuli which influence different feeding responses:

<table>
<thead>
<tr>
<th>Type of response</th>
<th>Evoking stimulus</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Positive</td>
</tr>
<tr>
<td>Orientation</td>
<td>Attractant</td>
</tr>
<tr>
<td>Orientation</td>
<td>Arrestant</td>
</tr>
<tr>
<td>Biting or piercing</td>
<td>Incitant</td>
</tr>
<tr>
<td>Maintenance of feeding</td>
<td>Stimulant</td>
</tr>
</tbody>
</table>

Beck defines an "attractant" as any stimulus which attracts the insect by orienting movement toward the source. An "arrestant" is said to cause an insect to cease locomotion in close contact with the source, while
an "incitant" is a stimulus which evokes a biting or piercing response. The negative responses are caused by a set of stimuli, termed differently, which prevent or inhibit the positive responses.


In Trypodendron, neither the nature of the so-called "incitant" which would cause the beetle to begin boring, nor the other sets of stimuli in the series, nor their corresponding inhibitory counterparts are known.

The effect of increasing temperature in the environment on the phototactic behaviour of various insects has always been that of reversal (Jack and Williams, 1937; Green, 1954; Pertunnen, 1959; Pertunnen and Paloheimo, 1965, 1964; Rudinsky and Vité, 1956; Wellington, 1948; Wellington et al, 1951, 1954). The results of the tests on Trypodendron show that the beetles shun the light at temperatures above 58°C.

The term "photonic reversal" in the sense of a permanent change from photopositive to photonegative or vice versa as a result of high temperature may not be an applicable term for Trypodendron. Photonic inhibition may be a more appropriate term because the beetle does not really become negatively
phototactic as indicated by the fact that they still respond positively to light when returned to ordinary temperatures. The apparent effect of high temperature under field conditions on the photic response of insects may not actually be a reversal of phototaxis but a different response which prompts the insects to escape from heat which is correlated with the most intensely illuminated condition. Should, however, the temperature in the shaded area be higher than or equal to that in the exposed area, the insect would likely, as does Trypodendron move about, even venturing to light, in search of a favorable temperature.

Photonic reversal seems to persist, as is manifest in flown termites or in Trypodendron as it begins to bore a tunnel into wood, or in the last instar larva of the hawk moth as it digs into the ground in order to pupate (Gilbert, 1964).

Positive geotaxis is often correlated with negative phototaxis, especially in many plant-climbing insects. This is particularly true of the larvae of lepidopterous and of hymenopterous insects. However, many of the non-plant-climbing insects may become photonegative in their response to light without becoming positively geotactic. This is indicated by the photonegative responses of the beetles at high temperatures (up to 57°C) when light was symiodal with gravity (see table 4).

The failure of the elevated atmospheric pressure to simulate the effect of the swallowed gas bubble in reducing the photic response showed that pressure per se is not involved. One must therefore contemplate the possibility that stretch effects on the gut wall or on the body wall are involved (Finlayson and Lowenstein, 1955).
Insects are generally classified as either diurnal, crepuscular, or nocturnal in habits depending on the time of the day they are most active. While *Trypodendron* is definitely diurnal in habits, especially in so far as emergence and flight are concerned, they are nevertheless active in the absence of light. The activities of these beetles in the dark include copulation, orientation by crawling toward and attractive odour source, boring into a suitable piece of wood, feeding and oviposition.

While the behaviour of the beetles in the dark in relation to a suitable piece of wood or to an attractive odour is similar to the behaviour of the flight-experienced beetle in the presence of light, the intrinsic motivating stimulus acting on the beetle in the dark may be entirely different from the "priming" effect of flight. As already reported, flight results in the expenditure of energy by the insect (Pringle, 1965; Sacktor, 1965), accumulation of a gas bubble in the ventriculus (Graham, 1961), and consequent physiological and/or physical effects (Chapman, 1956) responsible for lowering some thresholds which permit the beetle to settle on and bore into a suitable piece of wood. What "primes" the beetle in the dark is not known. It appears that the physiological, biochemical, and physical changes brought about by flight are too much for the flight-inexperienced beetle to attain or obtain in the dark. These observations suggest that there must be other mechanisms involved and that the importance of the central nervous system as stipulated by Kennedy (1965) in governing the behaviour of the beetles is not to be overlooked.

The retention of beetles on perforated surfaces separated from attractive wood by a shallow space, as well as their ready response to a stream of air passing over attractive wood but not over green wood can be
explained only on the assumption that odour is the prime factor involved.

The similarity of responses of males and females to the odour from attractive but non-attacked wood demonstrates the existence of an effective primary attractant originating from the wood alone. This is not to say, however, that secondary attractants may not play an important role in increasing subsequent frequency of attack (Rudinsky and Daterman, 1964a, 1964b).

The retention of the flown beetles in a field of odour above attractive wood is characterized by their decisive return to the field of odour after transgressing the boundary of that field into an odourless area (see Fig. 15). This reaction suggests either a memory for position, or a direction-reversal when the olfactory stimulus diminishes or fails, or an ability to detect a gradient within a very short radius. Dethier (1957) mentions that in Bombyx mori a strong drop in odour concentration while the insect is responding to an odour stream results in elimination of stream orientation.

The continued photopositive response of T. lineatum even when placed in contact with green wood, or in a field of odour from it, or in a directed stream of odour from it allows several possible inferences. Either attractants are not present in stimulating concentrations or they are present but are obscured or rendered ineffective by repellents or olfactory inhibitors. Now the inhibition of the photic response of flight-experienced beetles when brought into contact with attractive wood or odour from it may signify the formation de novo of olfactory attractants from non-attractive or even from repellent precursors, or it may signify the disappearance of repellents which prohibit the action of pre-formed attractants, or it may mean that repellents are initially present which convert
to attractants. The questions are largely resolved by consideration of the fact that olfactory attraction of attractive wood was retained even when it was admixed with a large proportion of "green" wood. This indicates that if repellents or olfactory inhibitors exist, they are not present in significant quantities in "green" wood. This being so, one may then conclude that attractants are not present in "green" wood, for if they were, their effect would have been manifest because there is evidently nothing in "green" wood to prohibit any attractants in it from eliciting a response.

5. Aspects of behaviour of Trypodendron which are useful in bioassay techniques

Previous investigations on attractancy of materials for *T. lineatum* depended on the beetle boring into wood. The technique consisted of placing female beetles in darkness on either bark-covered slabs of wood or half-inch thick transverse sections of wood which were treated in various ways with test chemicals. It may be assumed that a boring-in response depends not only upon attractancy for the olfactory sense, but also upon factors of texture and taste. The boring-in test is therefore not ideally suited for detecting purely olfactory stimuli. It has other disadvantages. It is suitable only for female beetles, since it is only the females of this species which initiate and carry out tunnelling. It is therefore costly of potential experimental specimens. Furthermore, for statistical reasons, each trial should be based on the proportional responses of at least 10 individuals introduced simultaneously. Another disadvantage is that there is a considerable time lag in obtaining a decisive indication of response, and this interval of lag varies considerably between individuals. A period of about 24 hours is often required before the responses of the beetles can be decided. During this interval, pronounced chemical changes
may occur in the material being tested. If texture, taste, and other factors as yet not understood, are unsatisfactory, olfactory attractants may not yield a response. On the other hand, the test has the advantage of not requiring close and constant observation of the beetles. It has a further advantage in that the holes bored by the beetles provide a permanent record of their response. This type of test can be set up with non-flown females confined in the dark with the test material. This bypassing of the need for flight that would be required for study of responses in the light simplifies the procedure and ensures more uniformity of the test population of beetles.

The present researches have opened up two new possibilities of experimental situations for testing olfactory attractants for _T. lineatum_. One depends upon the centripetal response of beetles in a field of odour. The other depends upon anemo-olfactory orientation and locomotion of beetles in an odour-laden airstream. Both have the advantage of a briefer period of observation than the boring-in response.

The centripetal response is the one which is characterized by the beetles repeatedly retrieving their position within a field of odour originating in the substratum. This reaction would serve the purposes of a bioassay technique in which unknowns are introduced into the substratum. The length of the meandering path and/or the duration of contact with the odour field would be compared with values obtained with the insect in an odour-free field. This technique would have the economical feature of permitting the utilization of both sexes for studies of the primary host attractant. It also would yield information from specimens studied individually. Tracings of the path travelled by a beetle and/or the duration of contact with the odour field provide one possible quantitative measure of attractiveness. This study must be carried
out either with flight-experienced beetles illuminated with a horizontal beam of light, or with non-flown beetles observed under a dark red light to which they are insensitive.

The anemo-olfactory response would provide an immediate measure of attractiveness. A test would depend upon directing an odour-laden airstream toward flown or flight-experienced beetles in the presence of an opposing illumination source, or toward non-flown beetles under a dark red light. The method would permit the utilization of both sexes when primary host attractants are to be studied. This method would be the least time-consuming of all. It is conceivable that with this type of test, the manipulation of intensity of the opposing light source would provide a means for quantitative expression of olfactory attraction. Strength of olfactory attraction would be measured in terms of the strength of light necessary to inhibit the olfactory influence. In practice, however, the test might consist of the converse manipulation in which the odour is attenuated while the light is kept constant.
CONCLUSIONS

The present researches have cleared away some of the primary obstacles to a comprehensive understanding of the behaviour of *T. lineatum* (Oliv.). In turn, the patterns of its behaviour assume importance in terms of its biology and ecology. These studies have also removed the primary obstacles to the use of the insect as an instrument for bioassaying the attractant nature of chemical substances isolated from the host trees. This laying of foundations for bioassaying techniques also opens up opportunities for the study of factors affecting the formation of attractants in wood in as much as tests for attractancy will no longer depend on the beetles boring into intact wood. Now it should be possible to experiment with wood that is in a mechanically disintegrated state, which is more amenable to chemical procedures.

The following conclusions pertain to the pedestrian situation for the beetles in their non-diapausing condition as they occur in spring, prepared for normal emergence, flight and attack. Males and females were similar in responses except in those situations which involve boring into wood, as only the females perform this operation.

1. The beetles, before flight, are strongly photopositive at temperatures in the range of 5° to 36°C. Positive phototactic response is inhibited in an increasing percentage of individuals at temperatures above 36°. At 38°C, positive response to light by the beetles ceases to exist.

2. The non-flown beetles react quickly to angular deviations of alignment in respect to a light source and turn with almost equal readiness toward the light regardless of its angle.

3. The beetles' responses to light, before flight, may be classified as follows: 1) not inhibited— the beetles immediately move or even
run toward the source of light; 2) initially inhibited positive response—the beetles may head away from light at the start of movement, but immediately turns about and move toward the source of light; 3) inhibited positive response—the beetles may or may not at the start of movement be inhibited by light but the general direction of movement toward the source of light is oblique; and 4) completely inhibited response—the beetles move with no apparent response to light.

4. The photopositive response largely masks the other potential capabilities of the non-flown beetles. A photopositive response is retained regardless of the relative direction of light in respect to the earth's gravitational field. Its effect is retained, albeit delayed, despite proximity of the insect to a host odour source.

5. Exclusion of the photic stimulus from flight-inexperienced beetles unmasks their capabilities of responding to host odour in an odour field.

6. Flight experience partially modifies the simple photic reaction of some individuals in the absence of host odour, but the majority remain unchanged.

7. Flight experience prepares the beetles for a response to host factors in the presence of light. As brief a flight as five minutes has produced this effect in some individuals.

8. A response to odour from attractive wood becomes manifest under various conditions:

(a) Non-flown beetles display a response in darkness in the form of a "fluid" aggregation of part of a population free to move in an area containing an odour field caused by either the presence of a piece of
attractive wood or the introduction of a stream of air carrying attractive wood odour.

(b) Flight-experienced beetles display a positive olfactory response under white light by lingering for an extended period of time over an odour field in opposition to a beam of light.

(c) Flight-experienced beetles display a positive olfactory response under white light by heading upstream in a current of air carrying that odour in opposition to a beam of light.

(d) Non-flown beetles display an inhibited olfactory response under white light but exhibit a positive olfactory response in darkness.

9. Non-flown and flight-experienced beetles take to flight in the presence of a broad overhead field of light. They do not take to flight when light arrives from below the horizontal plane of vision of the beetles but they do so in the presence of a combination of lights above and below.

10. As pedestrians, the beetles do not respond to patterns of black-and-white lines in their immediate background as they do to a source of attractive wood odour. This fact implies that vision is not employed as much as olfaction in host-finding.

11. Non-flown beetles under pressure of 50 psi do not respond to host odour while exposed to white light. The implication is that the presence of gas bubble in the ventriculus accumulated during flight does not produce the change of photic response in the presence of odour by a pressure effect. This conclusion leaves the possibility of its acting by stimulating stretch receptors in the gut wall. It also denies the experimenter this condition for studying olfactory responses in non-flown beetles.
12. When odour already surrounds a beetle, the latter generally does not react to an airstream. Some of the beetles which behave otherwise may not have the threshold of response sufficiently lowered.

13. The responses of this insect to the conditions studied here explain some of the important mechanisms of its ecology. The initial strong positive response to light sponsors dispersal of the adult population in spring and empowers the insects with the capacity for territorial coverage.

14. The behaviour of *Trypodendron* is not strictly stereotyped in the sense that it follows a definite pattern. While flight, for instance, may be a normal conditioning or priming mechanism for the alighting or olfactory response, response to odour sources and the subsequent boring behaviour may be accomplished, in the absence of previous flight experience, in the dark.

15. The response of the flight-experienced beetle to an odour-bearing airstream probably provides a simple mechanism for host discovery, in which the host odour may act merely as a releaser of an anemotactic response. This mechanism would lead the insect almost inevitably to the source of the odour, without the necessity of one attributing to it the memory in a trial-and-error search, and without assuming the ability of a three-millimeter insect to recognize direction in an odour gradient which may extend over hundreds of meters. The non-reaction of the pedestrian beetle to air flow when it is in an odour field suggests a mechanism for restraining or inhibiting its departure from an attractive log once it has established contact.
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