SOME ASPECTS OF THE HOST PLANT RELATIONSHIPS OF POTATO TUBER MOTH, *PHTHORIMAEA OPERCULELLA* ZELL. (LEPIDOPTERA: GELECHIIDAE)

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ABSTRACT

Aspects of the behaviour and biology of potato tuber moth (Phthorimaea operculella Zell.) relevant to host-plant selection and utilization were investigated. Literature of relevance concerning this and other insects is reviewed.

Oviposition behaviour

To provide a basis for later experimental work the fecundity and oviposition behaviour of individual potato tuber moths was investigated. Fecundity ranged from 0 to 236 eggs deposited per female for moths provided with sugar solution and muslin over filter paper as an oviposition substrate. Fecundity under these conditions was not correlated with pupal weight but the number of mature eggs in the ovaries on emergence from the pupa was related to pupal weight. This initial egg complement accounted for slightly more than half the total number of eggs laid, so that further egg maturation must take place during adult life. Females kept with males throughout their lifespan did not lay more eggs than those separated from males after an initial mating, but unmated females laid very few eggs all of which were infertile. Peak oviposition (of mated females) occurred 2 to 5 days after adult emergence.

Mated moths were offered a range of materials in a series of experiments in order to define physically optimum substrates for oviposition. Surface depressions just large enough to accommodate eggs (0.2 - 0.5 mm^2) were preferred, but in addition hairy substrates were much more attractive than smooth. Mechanical stimulation of tactile hairs on the ovipositor, which was examined by scanning electron microscopy, may account for these effects. Moist substrates were highly deterrent for egg laying and also reduced the total number of eggs laid during the experimental period.

Four host plants (potato, egg plant, tobacco and tomato) and five non-host plants (silver beet, bean, pea, radish and ryegrass) were evaluated with respect to oviposition behaviour in a series of experiments. It was concluded that acceptable plants contain oviposition stimulant factors whilst unacceptable plants contain deterrent factors. Neither of these are however volatile and act for the most part only on contact. Active extracts were prepared from most plants but no attempt was made to identify individual active constituents. As these factors were released in experimental situations for the most part only when plant tissue was ruptured, it is uncertain how they are detected by the insect in the intact leaf. Strongly stimulative plants such as potato, egg plant and tobacco, induced greater total egg deposition as well as influencing the location of eggs.

Factors affecting fecundity

Anaesthetization with carbon dioxide as practised to facilitate handling of moths, had no effect on fecundity. Starved moths laid only slightly more eggs than the complement of fully developed eggs in the ovaries at eclosion from the pupa. Moths provided with water laid almost twice as many eggs but provision of 5% sucrose solution did not increase fecundity further.

Moths kept in the presence of potato tubers laid up to twice as many eggs over their life span compared to moths not so exposed. Isolated pieces of potato peel did not produce this effect. The factor(s) responsible for this stimulation of fecundity appears to be one of odour as tubers covered with muslin produced a similar effect compared to those to which moths had access to the surface.

Larval behaviour

Newly hatched first instar larvae move vigorously and continually in the absence of plant material and would be able to travel several metres before requiring to locate a suitable host plant if eggs were laid away from the plant. Mean life span of starved first instar larvae was 3-4 days at 20^{o}C and was not greatly influenced by relative humidity at this temperature.

First instar larvae tend to be positively phototactic but do not respond to moisture. Their ability to locate host plant material is poor and no strongly directional response was detected. Movement is arrested after contact is made with leaf tissue of host plants but not to any extent with non-host plants. Newly hatched first instar larvae begin to feed soon after coming into contact with leaves of host plants but will not feed to any extent on non-host plant tissue. Discriminatory ability is thus inherited.

Relative susceptibility of potato cultivars

Twelve named potato cultivars were compared for degree of tuber infestation in two small plot trials, one under glass and the other outdoors. Tuber moths were artificially seeded into the experimental areas in each case. Significant differences in degree of infestation were obtained between cultivars in the outdoor trial but not in that under glass.

In laboratory tests, differences in oviposition preference were detected between tubers of different cultivars but less so with foliage. Differences were also found between cultivars in the numbers of pupae recovered following the seeding of known numbers of first instar larvae onto tubers. Pricking the surface of tubers resulted in better percentage recovery of pupae for all cultivars. No close correlation was found between percentage pupation and resistance of tuber skin to rupture or with the number of eyes per tuber. Significant differences in fecundity were recorded according to the cultivar on which the larvae were fed.

When cultivars were ranked according to oviposition preference (bare tubers), percentage pupation and fecundity, there was a close correlation with ranking based on degree of infestation in the field, suggesting that such factors are largely responsible for the differences in levels of infestation found between cultivars under field conditions.

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Chapter I

INTRODUCTION

It is common knowledge that phytophagous insects discriminate as to the kinds of plants on which they feed, and that for each insect species there is a reasonably well defined list of plants that are acceptable. In some cases the list of acceptable species is long and they come from diverse plant groups (polyphagous habit), whereas in other cases host plants are confined to a few closely related genera or species within a single plant family (oligophagous habit). The extreme of selectivity is presented by insects that feed on a single species of plant (monophagous habit).

In the process of selection of plants by phytophagous insects, the stages of obvious importance are the ovipositing adult and the feeding larva and most investigations of the bases of host plant specificity have involved one or both of these stages (e.g. Gupta and Thorsteinson 1960a, and b, for Diamond Back Moth). The influence of the host plant on the insect may be much more subtle and intimate however, than merely guiding oviposition and feeding behaviour. Riddiford (1969) has for instance shown that, in the case of the Polyphemus moth, the female will release her sex pheromone, and hence mating will take place, only in the presence of leaves of the host plant (oak). Similarly, there are instances reported of host plant presence stimulating fecundity of adult Lepidoptera though feeding on the plant does not take place at this stage. (Deseö 1970[69], Hillyer and Thorsteinson 1969). Nutritional effects of different host plants on fecundity are well known both directly on the adult stage (e.g. for Colorado Beetle, Hsiao and Fraenkel 1968d) and indirectly via the larval stage (e.g. for Potato Tuber Moth, Meisner et al. 1974b).

The following theoretical framework (Table 1) is proposed as a basis for analysis of the possible influences of host (and non-host) plants on insect behaviour, development and reproduction. A similar scheme has been proposed by Saxena (1969). Although the sequence of

Table 1. Theoretical analysis of possible effects of plants on insect behaviour, development and reproduction

Developmental stage	Behavioural or physiological step	Possible plant influence
1. Mature virgin adult (♂ and ♀)	host plant location	attraction and/or arrestance by host plant, repellence by non-host plant
2. Mature virgin adult (♂ and ♀)	copulation	presence of host plant required or not
3. Mated female	oviposition	stimulation by host plant, deterrence by non-host plant
4. Mature female (mated or virgin)	fecundity	stimulation by host plant
5. Newly hatched 1st instar larva	plant location (if eggs not laid directly on host plant)	attraction and/or arrestance by host plant, repellence by non-host plant
6. 1st instar larva	plant recognition and feeding (preference inherited or induced?)	stimulation by host plant, deterrence by non-host plant
7. 1st instar larva	ability to penetrate plant surface and establish	possible presence of physical barrier to establishment
8. Developing larva	larval growth and development	nutritional adequacy, presence/absence of toxicants affecting survival, growth rate and size at maturity
9. Adult	fecundity	influence through quality of larval food.

events listed is consecutive, the detailed order could vary somewhat, e.g. mating could precede host plant location or vice versa.

Potato Tuber Moth is an oligophagous insect with host plants restricted to certain genera within the plant family Solanaceae (Attia and Mattar 1939, Cunningham 1969, Picard 1913a,b).

Although literature concerning Potato Tuber Moth is extensive (Haines 1977, lists 121 references mostly from the last decade), remarkably little has been published concerning the basis of host plant selection and that only in recent years (Meisner et al. 1974a, b, Traynier 1975).

The theoretical scheme proposed in Table 1 has formed the basis of this thesis, the main objectives of which have been:

1. To investigate the nature of the host plant relationship of Potato Tuber Moth with particular reference to:
   (a) oviposition behaviour;
   (b) host plant influence on fecundity via the adult stage;
   and (c) behaviour of newly hatched first instar larvae;

and

2. To examine a range of potato cultivars for possible differences in susceptibility, and to analyse the basis of any such differences.

Chapter II

REVIEW OF THE LITERATURE

Major reviews of literature concerning mechanisms of host plant selection by phytophagous insects have been provided by Thorsteinson (1960), Kennedy (1965) and Schoonhoven (1968). The review of Beck (1965), although concerned primarily with insect resistance in crop plants, is also valuable and provides definitions of a number of terms relating to insect behaviour (e.g. arrestant, stimulant). In addition, a number of important symposia have been organized on the subject of insect/host plant relationships in recent years, several of which have been published in separate volumes (National Academy of Sciences (Anon. 1969), Van Emden 1973, Jermy 1976, Wallace and Mansell 1976, Chapman and Bernays 1978).

Although there has been much controversy about the relative roles of various factors in mediating insect behaviour with respect to plants, there is general agreement on the dominant role that chemical plant constituents play. This aspect of the chemical interaction between living organisms generally has recently been considered by Whittaker and Feeney (1971) and places insect/host plant relationships in a broader biological perspective.

Much of the published information in this field, and a great deal of the discussion, deals with the feeding stage of insects, i.e. with the larval stage in holometabolous insects (other than Coleoptera, which are also often plant feeding in the adult stage). It is however, almost invariably the adult that is the most mobile stage in the life cycle, so that location and selection of host plants (for the ensuing generation) is largely made by the ovipositing female rather than by the subsequent larvae.

For convenience of discussion in this review, and to permit consideration of individual aspects, literature is considered under the major headings of 1. Adult behaviour and oviposition; 2. Plant location, recognition and feeding behaviour; and

3. Plant suitability. With individual publications there is of course often overlap between one aspect and another, though for the most part oviposition and feeding have been investigated separately.

1. ADULT BEHAVIOUR AND OVIPOSITION

(a) Plant location by the adult

Although this is a crucial step in the life cycle of phytophagous insects, especially for monophagous species, it is probably the least understood aspect of the whole insect/plant interaction. Two possibilities are obvious and have been proposed (Kennedy 1965, Saxena 1969). Either the insect makes orientated movements towards suitable plants (by visual and/or chemical stimuli) or its movement is random and host plant location is a matter of chance. The latter must involve some arrestant mechanism so that the insect stays on a suitable plant but takes off again from one that is unsuitable. Plant recognition on contact must therefore take place. There is also the possibility that some non-host plants may be repellent so that the insect never makes contact with them. Factual information to substantiate the type of mechanism for individual insect species is sparse, and unfortunately there are many instances of workers failing to distinguish between attraction (i.e. orientated movement at a distance) and stimulation of oviposition, which may only take place on contact (e.g. Gokhale and Srivastava 1973, Meisner et al. 1974b).

Yamamoto et al. (1969) proposed three phases in the selection of plants for oviposition by adults of the Tobacco Hornworm; (i) approach to the plant (non-discriminatory); (ii) landing (discriminatory due to olfactory stimuli); and (iii) oviposition (due to contact chemo-stimulation). Chemical odours emanating from host plants are known to act as attractants for some insect species, e.g. for Melon Fly (Keiser et al. 1973) and for White Butterfly (Hovanitz and Chang 1964) but in both these cases visual stimuli also play a part (loc. cit.) The same is true of Rhagoletis pomonella (Moericke et al. 1975). There are some instances where host plant odour has been shown to stimulate activity of gravid females but not to evoke attraction (e.g. for Erioischia brassicae, Traynier 1967a). This may be due to

the experimental difficulty of demonstrating attractive behaviour with some insects, rather than to actual lack of response.

In the case of insects which are nocturnal or crepuscular, as is the case with Potato Tuber Moth, it could be theorized that olfactory stimuli are likely to be more important than visual in guiding adults to host plants. Olfactory attraction has not however been adequately established for Potato Tuber Moth. Meisner et al. (1974b) showed that oviposition is stimulated by certain chemical components of potato, in particular L-glutamic acid, but their experimental design did not permit conclusions as to whether attraction had also taken place or not. Goldson (1976) produced evidence that a steam distillate of potato foliage stimulated moth activity, but was not able to demonstrate attraction under laboratory conditions.

(b) Mating

Specific environmental requirements, in particular of temperature and light, are known to be essential for mating to occur with many insects, but are considered to be outside the scope of this review, which is confined to the influence of plants. In general, phytophagous insects do not seem to require any stimulus from their host plants for mating to take place, provided other environmental conditions are met, if lack of references in the literature to this aspect is any measure. However, in the case of the Polyphemus moth Riddiford (1969) has shown, as already mentioned, that the presence of host plant leaves is essential if mating is to occur. Similarly, Schroeder (1969) found that, for another Lepidopteran (Laspeyresia caryna) mating occurred at only a low level (25%) in the absence of host plant material but at a high level (84%) in its presence. Possibly, with further investigation, similar effects may be shown for other species. No accounts of rearing of Potato Tuber Moth (e.g. Platner and Oatman 1968) mention any difficulty in obtaining mating or benefit to be derived from the presence of host plant material. It appears to be unimportant for this species.

(c) Regulation of oviposition

Much work has been done on the factors which regulate oviposition in phytophagous insects and the following discussion includes only a selection of references to illustrate particular points.

Surface texture is important in choice of oviposition site for many insects and relates to the selection of plant species and site on the plant for egg laying. For instance Pedigo (1971) found that the Noctuid Plathypena scabra chose pubescent leaf surfaces for oviposition. Similarly the Carpenter Worm Moth (Solomon 1967) selects cracks and crevices in the bark of trees into which to lay its eggs. Further work (Solomon and Neel 1974) confirmed that stimulation of oviposition in this insect is primarily tactile, the ovipositor being covered with prominent mechano-receptor hairs. The moth does not distinguish between host and non-host trees, or between natural and artificial substrates provided they present similar surfaces. Mechanical stimulation of the ovipositor is also known to be important for the Eastern Spruce Budworm (Stadler 1974) though in this case chemical factors are also involved.

For some species, the requirement is for a smooth rather than a rough surface e.g. for the Fruit Fly Rhagoletis cerasi (Prokopy and Boller 1971) and this clearly relates to the natural oviposition site (cherry fruits). In addition, other physical properties of the fruit (convex shape, size and colour) are important for this and other Rhagoletis species (Prokopy and Boller 1971, Prokopy and Bush 1973). In at least one instance (Yamaoka et al. 1971, Yamaoka and Hirao 1973) mechanosensory hairs on the hind part of the abdomen (but not on the ovipositor itself) have been shown to control oviposition (Bombyx mori). The preference of Potato Tuber Moth for rough surfaces over smooth for oviposition was early observed (Picard 1913a). Traynier (1975) has provided a more critical evaluation of oviposition preference with respect to texture, moisture and light. He concludes that the most preferred surfaces are shaded, dry and with indentations large enough to accommodate eggs.

Different coloured surfaces may be differentially attractive for oviposition for some species (Callahan 1957, Prokopy 1967).

For the Citrus Moth (Prays citri) the most preferred colour was blue and the least preferred red (Sternlicht 1974).

For many phytophagous insects (perhaps for most) the dominant factor in selection of oviposition site is the correct chemical stimulus from the host plant. Some species in fact will not lay eggs at all unless they receive it. Perception may be olfactory, by contact, or both. Deseö (1969) examined three species of Lepidoptera and found that for the Plum Fruit Moth (Grapholitha funebrana) odour of the host plant was essential for egg laying. Without it, the moths showed follicle absorption and died prematurely. Similar effects were reported for another moth (Zeiraphera dimana) by Benz (1969). The other two species examined by Deseö (1969) however, Codling Moth (Laspeyresia pomonella) and the Indian Meal Moth (Plodia interpunctella) both laid eggs without stimulus from plant material, though P. interpunctella laid more eggs when exposed to odours of food material. It has since been shown (Wearing and Hutchins 1973, Sutherland et al. 1974) that Codling Moth is influenced in choice of oviposition site by a volatile chemical (α-farnesene) emanating from apple fruits.

Chemical odours are also known to influence oviposition of Fruit Flies. Fletcher and Watson (1974) showed for instance that Dacus tryoni is stimulated to oviposit by 2-chloro-ethanol. Anthomyid Root Flies usually lay their eggs in the soil adjacent to the base of host plants rather than on the plants themselves. Hylemyia cilicrura, which attacks seedlings rather than larger plants, is stimulated to oviposit by moist soil and the presence of certain seeds beneath the surface. Detection is clearly olfactory (Barlow 1965). In the case of the Onion Maggot (H. antiqua) organic sulphur compounds (n-propyl disulphide and n-propyl mercaptan) have been identified as oviposition stimulants (Matsumoto and Thorsteinson 1968a, Pierce et al. 1978), but it is interesting to note that high concentrations of n-propyl disulphide depressed oviposition rather than stimulated it. Again, in the case of H. brassicae, which attacks Cruciferous plants, chemicals from host plants which stimulate oviposition have been identified (Nair and McEwen 1976); in this case sinigrin and four other glucosinolates. Traynier (1967b) considered that contact with host plants was necessary for oviposition by this species.

Unmated female insects normally lay few, if any eggs, but Huignard (1976) has shown that virgin female Acanthoscelides obtectus will lay eggs if stimulated by the presence of the host plant. Factors influencing oviposition by Potato Tuber Moth, including chemical plant constituents, have been examined by Meisner et al. (1974b) as referred to under Section (a) plant location by the adult, and also by Traynier (1975). In addition to the presence of oviposition stimulants in host plants, Traynier's work suggests that some non-host plants contain oviposition deterrents.

Although physical or chemical factors may be dominant in the regulation of oviposition for some insects, there are many instances where maximum oviposition is not obtained unless a combination of favourable factors occurs. This may prove to be the case for most insects when adequately investigated. For the Diamond Back Moth, Gupta and Thorsteinson (1960b) found that both plant odour (identified as allyl isothiocyanate) and a rough surface were required. Similarly for Trichoplusia ni combinations of host plant odour, moisture, colour (especially yellow) and a smooth surface were necessary for optimum egg lay (Shorey, 1964). Again, for Manduca sexta, Sparks (1973) noted that touch, odour and moisture together were more stimulating than any one element alone.

Negative stimuli, acting as oviposition deterrents, could be just as important as positive stimuli in nature in guiding choice of oviposition site, but have not been extensively studied. There are however, several instances reported of the occurrence of oviposition deterrent substances in non-host plants. An extract of tomato was found by Gupta and Thorsteinson (1960b) to inhibit oviposition of Diamond Back Moth on normally acceptable surfaces. The substance(s) responsible was not identified. Similar reports exist for Pieris brassicae (Lundgren 1975), for Scrobipalpa ocellatella (Robert 1976) and for Hylemyia antiqua (Wiens et al. 1978). In the latter case it was shown that the oviposition deterrent factor was non-volatile and operated by contact. The likely significant role of inhibitory stimuli for phytophagous insects has recently been considered by Jermy and Szentesi (1978). As already indicated, Traynier (1975) has produced evidence that oviposition deterrents are present in some non-host plants of Potato Tuber Moth.

Where olfactory clues guide oviposition behaviour, the sense receptors concerned are likely to be located on the insect's antennae, being the normal site of olfactory perception. With tactile and contact chemo-sensory responses however, a more likely location is the insect's ovipositor. Where they have been looked for receptors have usually been found on the ovipositor. Van Lenteren (1972) described contact chemoreceptors on the ovipositor of the Cynipid wasp, Pseudocoila bochei. They were revealed only by SEM study and had not been observed under light microscope examination. Sensory receptors have been more recently described from the ovipositor of Carrot Fly and of Cabbage Root Fly by Behan and Ryan (1977), and on the ovipositor of Acanthoscelides obtectus (Szentesi 1976). Such sensory receptors on the ovipositor of insects are not confined to phytophagous species. Hooper et al. (1972) described six morphologically distinct types on the ovipositor of the Face Fly, Musca autumnalis and Greany et al. (1977) found them present on the ovipositor of an insect parasitoid, Biosteres longicaudatus.

(d) Modification of ovipositional preference

It should not be assumed that ovipositional preference of an insect for one species or group of plants is fixed and immutable. Hopkins (1917) suggested that adult oviposition preference is modified by larval feeding experience. This has since become known as Hopkins' host selection principle, and may be stated as "females of phytophagous insects prefer to oviposit upon the same plant species as that upon which they themselves had fed as larvae". However, as Wiklund (1974) points out, the principle has never been validated for any insect species despite numerous attempts. What does seem certain though is that oviposition preference can be modified by selection over a number of generations (Hovanitz and Chang 1963), and that strains within species with different oviposition preferences may naturally exist in some cases (Takata 1961). Such differences are clearly brought about by genetic modification and are not induced within the lifetime of an individual as the Hopkins' host selection principle requires. Wiklund (1974) considered that, for the species with which he worked (Papilio machaon), separate genetic mechanisms were responsible for controlling adult oviposition and larval feeding preference.

(e) Ovipositional "errors"

Dethier (1959) has pointed out that adult Lepidoptera sometimes lay eggs on plant species which are incapable of supporting larval development. Similar behaviour has been reported by Straatman (1962) and by Yamamoto and Fraenkel (1960b). All these reported instances involve Lepidoptera but the same phenomenon probably occurs with other phytophagous groups. The explanation for this anomolous behaviour is probably that the insect species have not co-evolved with the plants concerned. This is certainly the case with the instances reported by Straatman (1962) as all the unsuitable plants (which were poisonous to the larvae) were introduced (into Australia) and the Lepidopterous species were all indigenous. If the oviposition behaviour of most phytophagous insects is guided by secondary plant substances, as seems to be the case, then it is likely that the plant species concerned, though unsuitable to the larvae, contain the necessary attractant/stimulant factors for adult oviposition, but this appears not to have been examined experimentally.

(f) Effects on fecundity

The quality and quantity of food available to insects from their host plants have important effects on fecundity. In the case of phytophagous insect groups which feed little (and for some species not at all) in the adult stage (Lepidoptera, Diptera), the main effect is through food quality and availability for the larval stage so that fecundity of the adult female is commonly influenced by the species of plant on which the larva fed. For instance, Meisner et al. (1974a) reported that the mean total numbers of eggs laid by Potato Tuber Moth varied from 10.7 for adults derived from larvae fed on tobacco leaves to 75.4 for adults derived from larvae fed on potato tubers.

With Coleoptera, which mostly feed to a considerable extent as adults, quality and quantity of adult food may be just as important in influencing fecundity as that of the larva e.g. for Colorado Beetle as reported by Hsiao and Fraenkel (1968d).

Though, as pointed out above, most adult Lepidoptera do not feed to any great extent, availability of food, or even of water only, may nevertheless affect fecundity. In the case of Potato Tuber Moth

Labeyrie (1957) found that moths provided with water laid twice as many eggs as those denied it and those provided with honey as well as water, laid three times as many.

Effects of host plants on fecundity are not necessarily due solely to nutritional factors however. Hillyer (1965) reported that the mere presence of the host plant, without feeding taking place, stimulated ovarian development in the Frit Fly and increased the total number of eggs laid. This was also found to be the case with Diamond Back Moth (Hillyer and Thorsteinson 1969) and the effect in this case could be simulated by allyl isothiocyanate, (a constituent of host plants for this species). These authors showed that contact with the host plant was required for full response, but that odour alone produced some effect. Deseö (1976) working with the Indian Meal Moth, reported a similar effect induced by the odour of food material. Response could be eliminated by removal of the distal half of the antennae, showing clearly that perception was olfactory in this case. 50 per cent antennectomy did not however eliminate discrimination by the moth of location of the oviposition site, suggesting that for this species at least, there are two separate mechanisms (both olfactory) governing stimulation of ovarian development and choice of oviposition site.

This phenomenon of stimulation of fecundity by chemical factors emanating from the host plant may be more common than these reports suggest, as it appears to have been investigated for a few species only.

2. PLANT LOCATION, RECOGNITION AND FEEDING BEHAVIOUR

Although initial selection of a plant is often made by the ovipositing female for her offspring, most of the literature dealing with insect/plant relationships and mechanisms of plant selection concerns feeding by the larval stage, and additionally by the adult in those instances where it occurs.

A pioneer in this field was Fraenkel who published a series of papers in the 1950s and '60s (Fraenkel 1951, 1958, 1959, 1969; Fraenkel et al. 1960). He put forward the theory that all plants are

of similar nutritional value to insects, and attributed host plant selection to "secondary plant substances" (i.e. of no known physiological role in plants) of no nutritional significance. These he considered could be either stimulatory or inhibitory and that the balance of such properties for a particular plant determined whether it was accepted or not. In particular, he stressed that repellant and deterrent substances were important in determining plant acceptance or rejection.

The importance of rejective stimuli has been confirmed by Jermy (1965, 1966) who considered them to be the main mechanism of host plant selection. That they are indeed important is no longer in doubt as a recent review of chemical inhibition of feeding by phytophagous insects by Chapman (1974) shows. (Further reference to feeding deterrence is given in the section concerned with this below). Other factors have however been shown to play a role. Thorsteinson (1958, 1960) showed that positive stimulation of feeding was usually necessary and that for some insects, especially polyphagous species, soluble nutrients may serve this function. Waldbauer (1962) demonstrated that growth and development of an insect were not satisfactory when induced to eat normally rejected plants.

Fraenkel's original proposals, though providing stimulus for research, have therefore required considerable amendment. The more modern concept of host plant selection mechanisms has been put by Dethier (1970a, b, 1976) who stresses the importance of the total stimulus pattern perceived by the insect. He considers individual chemical stimuli, whether positive or negative in terms of response, to be important in contributing to plant acceptance or rejection, but stresses that they should be considered within the context of total sensory input. With this general introduction to theories of host plant selection, specific aspects are reviewed in more detail below.

(a) Attraction and arrestment

The degree of development of host plant location mechanisms in the larval stage of insects is likely to vary with the normal location of the eggs (on or away from the host plant), the mobility of the larvae, and also the degree of polyphagy exhibited. Some degree of

host plant finding ability is however always likely to be present even if limited to host plant recognition after contact. As pointed out for ovipositing adults, only two possibilities exist as to plant location mechanisms; random movement with chance location of suitable plants, or orientated movement in response to a directional stimulus. There is evidence for both types of mechanism in plant feeding insects.

The best example of a chance location mechanism is probably that of aphids which seem for the most part to land on plants at random followed by either acceptance and initiation of feeding or take off and repeat of the process (Kennedy 1976). Many other insects however appear to orientate to volatiles from their host plants as evidenced for Colorado Beetle by de Wilde (1976) and Visser and Nielsen (1977), Silkworm larvae (Watanabe 1958), larvae of the weevil Listroderes (Matsumoto 1970), larvae of Codling Moth (Sutherland 1972), larvae of Rice Stem Borer (Saito and Munakata 1970) and larvae of Carrot Fly (Jones and Coaker 1977). In some cases the chemical substances involved have been identified e.g. allyl and phenyl isothiocyanates for Listroderes (Matsumoto 1970), α-farnesene for Codling Moth (Sutherland and Hutchins 1972), p-methyl acetophenone for Rice Stem Borer (Saito and Munakata 1970). The distance over which such attractant behaviour is exhibited may be quite small; in the case of larvae of the Onion Maggot only about 1 cm (Matsumoto and Thorsteinsen 1968b).

Live plant tissue produces other volatile substances besides organic compounds of the type referred to above; in particular carbon dioxide and water vapour. It is possible that attraction of plant material could be due in part to such substances rather than to more specific attractants. Jones and Coaker (1977) however have shown that carbon dioxide is not attractive for Carrot Fly larvae, but Sutherland (1975) reported a positive response to water vapour in the case of newly hatched Codling Moth larvae. Response to such volatile substances of universal occurrence could not of course provide selective plant location.

(b) Feeding stimulation and deterrence

These aspects, though involving opposite behavioural responses, may be considered as two sides of one coin. In feeding studies of individual insect species they have often both been examined and are therefore jointly dealt with here. The literature concerning regulation of feeding in insects is extensive and a selection of references only is considered here to underline particular points. A general review of the chemical control of feeding behaviour in the Animal Kingdom has been provided by Lindstedt (1971).

Although the initiation of feeding depends partly on internal physiological state, most phytophagous insects require some external chemical stimulus before feeding will take place. In polyphagous species, such as locusts and armyworms, this stimulus seems to be provided by nutrient chemicals of general occurrence in plants, in particular certain sugars and amino-acids (Goodhue 1963, Cook 1977, Ma and Kubo 1977). Insects that have a more restricted plant host range (oligophagous species) appear to require a rather more specific chemical stimulus of limited botanical occurrence, e.g. mustard oil glucosides in the case of Diamond Back Moth larvae (Thorsteinson 1953, Nayar and Thorsteinson 1963). Other oligophagous species follow a similar pattern (Nayar and Fraenkel 1963a, b, Yamamoto and Fraenkel 1960a, Hsiao and Fraenkel 1968b), though the chemical substances involved have not been identified in all cases. In the silkworm, a monophagous species, separate chemical factors stimulating biting and swallowing have been identified (Hamamura 1970). In these cases (oligophagous and monophagous species) common nutrients may reinforce the more specific feeding stimulants, e.g. for Colorado Beetle (Hsiao and Fraenkel 1968a) so that combinations of chemicals may be necessary for maximum food intake. For the silkworm, Nayar and Fraenkel (1962) report that specific phagostimulants operate only in the presence of sucrose. Meisner et al. (1974a) investigated the feeding behaviour of potato tuber moth larvae and found that feeding was strongly stimulated by sucrose and by certain amino acids, in particular α-amino butyric. Their work suggests however that a further unidentified substance may be responsible for host plant specificity. The possible occurrence of feeding deterrents in non-host plants was not examined.

If polyphagous insects are stimulated to feed by common nutrient chemicals of universal distribution in plants, some other factor(s) must be responsible for determining those plants that are not fed on (there are always some). This seems to be provided mainly by chemicals which act as feeding deterrents as has been shown for locusts (Bernays and Chapman 1975, 1977) and an armyworm (Granich et al. 1974). Although many oligophagous and monophagous insects are known to require specific feeding stimuli restricted to their host plants, deterrent chemicals in non-acceptable plants also seem to play a role in defining plant host range. This is certainly the case for Colorado Beetle (de Wilde 1958, Jermy 1958, Hsiao and Fraenkel 1968c, Hsiao 1969, 1976) and probably for Diamond Back Moth (Gupta and Thorsteinson 1960a). Even in the case of a strictly monophagous species (silkworm) positive feeding stimulants in the host plant species seem to be reinforced by deterrent chemicals in many non-host plants (Ishikawa et al. 1969). Chapman (1974) in his review of chemical inhibition of feeding in phytophagous insects, points out that the chemical nature of feeding deterrents is very diverse. Also, as insects exhibit a great deal of differential susceptibility to them, interactions are extremely complex.

It may be concluded that distribution of feeding stimulant and feeding deterrent chemicals between species of plants is a major factor (probably the major factor) in determining the host range of phytophagous insects, but other properties of plants may also be important (see Sections (c) and 3. below).

(c) Modification of feeding preference

It seems to have been assumed by most workers that feeding preference of phytophagous insects is a fixed and genetically determined feature. This view has been challenged by some investigators who have shown that preference for particular species of plants can be modified (i.e. induced) by previous feeding experience (Jermy et al. 1968, Hanson 1976). The phenomenon appears to be most common amongst Lepidoptera, but perhaps only because they have been studied most. Hanson (1976) suggests that it is more common in polyphagous species. The fact that host plant preference is not entirely inherited is also shown by the fact that some insects lose specificity after a period of rearing on an artificial diet (Schoonhoven 1967) and by the fact that

newly hatched first instar larvae may be more polyphagous in habit than later instars (Yamamoto 1974). The limits of such modification appear to be quite narrow so that the host range of the insect concerned is unlikely to be drastically altered. A certain amount of flexibility is clearly a biological advantage in many situations.

(d) Physical factors

Although chemical factors seem to be the dominant ones in determining plant host range, physical properties of plant tissues may also be important in some cases. If toughness of epidermal layers prevents newly hatched first instar larvae from establishing for instance, the plant concerned will not be an effective host plant no matter how suitable in other ways. Some physical characteristics of plants may have therefore evolved as defence mechanisms against phytophagous insects. Physical factors have been recognized as contributing to insect resistance in crop plants in some cases (Painter 1951, Beck 1965, Agarwal 1969) but appear to have received little detailed investigation. Tanton (1962) has shown that feeding by larvae of the Mustard Beetle is reduced by leaf "toughness" and that this in turn is reflected in reduced growth rate. Leaf pubescence has been described as a feeding deterrent for the Cereal Leaf Beetle (Schillinger and Gallun 1968). The ability of some plant hairs to physically trap insects has recently been described by Gibson and Turner (1977), and in some cases leaf hairs may contain toxic chemicals besides providing a physical barrier (Thurston 1970).

It seems possible that in some instances phytophagous insects are able to discriminate between plants on the basis of chemical/physical properties of the plant surface without taking a test bite, as indicated by the ability of locusts to perceive plant surface waxes (Bernays and Chapman 1970, Bernays et al. 1976).

3. PLANT SUITABILITY

(a) Toxic effects

There seems little doubt that insect feeding deterrent chemicals are part of the armoury that plants have evolved as protection against herbivores, which may of course include animals other than insects (Feeny 1976, Rhoades and Cates 1976). Where herbivores are not deterred from feeding, there is still the possibility of toxic substances within the plant tissues acting as a second line of defence. This probably accounts for the large number of chemicals with insecticidal activity reported from plants (Jacobsen 1975). Species of plants containing such materials are not however necessarily immune to insect attack, as insects may have the biochemical ability to evolve detoxication mechanisms to overcome the plant's defences. Recent work by Reese and Beck (1976a, b, c, d and by Schoonhoven and Derksen-Koppers (1976) has shown that toxic substances in plants may not necessarily exert rapid effects. More subtle properties may be present which are only revealed by feeding to insects over a period of time, and are expressed in such parameters as reduced growth rate, smaller size at maturity and lowered fecundity, rather than by acute mortality.

(b) Nutritional adequacy

Differences in larval growth rates, size at maturity and adult fecundity according to host plant species, may be due to differences in nutritional value as much as to presence of chronic toxicants. Although much is now known about the nutritional requirements of phytophagous insects, inadequate information is available in most instances to determine the relative importance of this factor in cases of insect resistant crop plants (Maxwell 1972).

A further complication is that digestibility may vary from one plant to another as has been shown to be the case even for highly polyphagous insects such as Southern Armyworm (See Hoo and Fraenkel 1966). Similar variation was also obtained for an oligophagous species (Tobacco Hornworm) by Waldbauer (1968).

Nutritional differences may also occur between cultivated varieties of plants within a single plant species and contribute to differences in biological performance of the insect concerned as has been shown for aphids by Auclair *et al*. (1957) and Van Emden and Bashford (1971).

Nutritional requirements of larvae of potato tuber moth have not been studied and no information is available to assess whether differences in nutritional values could contribute towards reported differences in susceptibility of potato cultivars to this insect (Bald and Helson 1944, Helson 1949, Abdel-Salam *et al*. 1972, Bedi 1974, Foot 1976).

Chapter III

REARING

To provide a regular supply of insects for experimental work a programme of laboratory rearing was undertaken based on the method of Platner and Oatman (1968) using potato tubers as larval food, but scaled down to produce smaller numbers. Although an artificial diet for larvae of Potato Tuber Moth has recently been described (Singh and Charles 1977), this was not available at the time studies were commenced and in any case seems to provide little advantage over potato tubers for general rearing.

MATERIALS AND METHODS

The colony was started from a nucleus stock obtained from Entomology Division, Department of Scientific and Industrial Research, Auckland. Small potato tubers of cv. "Ilam Hardy" were used as larval food. To assist larval penetration, tubers were perforated superficially by rolling them over a board with spikes at approximately 1 cm^2 spacing. Groups of 4 or 5 such tubers were placed on a shallow layer of fine river sand in plastic boxes 17 x 17 x 10 cm. Filter papers bearing eggs close to hatching were placed on a layer of muslin laid over the top of the tubers. The boxes were then closed with perforated lids and kept at 25°C and 60-70% RH for 18 days. The muslin, and filter paper bearing any unhatched eggs, were removed after 2 or 3 days. The rearing containers were kept in darkness except for daily attention to the colony. The number of eggs seeded into each container was adjusted so that the larval density did not exceed 1 per 3 g of fresh tuber weight.

After 18 days most larvae had emerged from the tubers and pupated in the sand. To retrieve the majority of pupae the tubers were removed, any adhering pupae scraped off, and the sand passed through a sieve. Pupae (within their cocoon and adhering sand covering) were

held in a refrigerator at 5-6°C for up to 4 weeks, for use as required.

Containers for adult moths consisted of glass preserving jars of approximately 500 ml capacity into which batches of pupae were placed for emergence. The mouth of each jar was covered with terylene gauze of approximately 0.5 mm mesh. Filter paper (7.0 cm diameter) placed over the gauze and held down with a small petri dish provided a suitable oviposition site. Five per cent sucrose solution was provided for the moths. Containers of adult moths were kept in an incubator at 25°C, uncontrolled humidity, and in darkness except for daily attention.

As soon as oviposition commenced, the filter paper, on which almost all eggs were laid, was renewed daily. Individual containers of moths were kept for about a week and then discarded, since by this time egg production had declined sharply.

Papers bearing eggs were held at 25°C for 2-3 days to allow embryonic development to proceed. At the end of this time the eggs were orange in colour, as opposed to pearly white soon after laying. Eggs of this age could be stored for at least 4 weeks in a refrigerator at 5-6°C without serious loss of viability. Eggs required for rearing were transferred to 25°C and held at that temperature until hatching was imminent (indicated by dark grey to black colouration) or had already commenced. They were then seeded into rearing containers of potato tubers prepared as described.

RESULTS AND DISCUSSION

The method described proved convenient and reliable in supplying insects of known age and rearing history for experimental purposes. The separation of the four life stages of eggs, larvae, pupae and adult moths into distinct phases of the rearing cycle provided precise control over age and quality of insects used for experiments.

In artificial rearing of any insect species there is always the possibility of genetic modification through selection imposed by the rearing conditions (Chambers 1977). Some workers have suggested periodic addition of field collected insects to the rearing stock to minimize this problem. Such a procedure was considered in the present instance but was discarded because of the possibility of accidental introduction of a disease organism such as the virulent virus disease of Potato Tuber Moth described by Reed and Springett (1971). No problems of pathogen infection were encountered in the laboratory rearing of Potato Tuber Moth as described over approximately 40 generations.

Chapter IV

STUDIES ON OVIPOSITION

1. PRELIMINARY EXPERIMENTS

To provide essential base line data on the pattern of egg laying in time and on individual variation in fecundity, a series of preliminary experiments was conducted. Opportunity was also taken to obtain information on the relationship between fecundity and mated state and between fecundity and pupal weight.

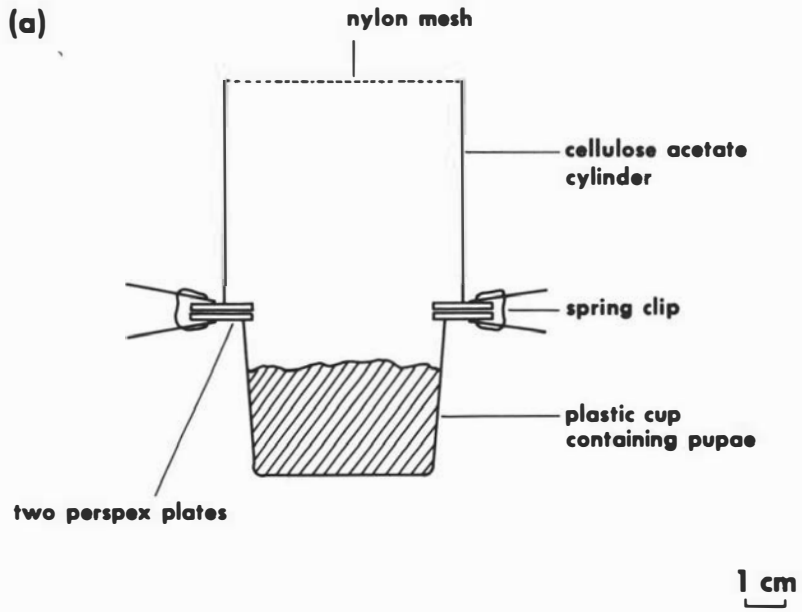
MATERIALS AND METHODS

To facilitate separation of emerging moths from pupae, and hence to provide adults of known age, small emergence cages of the type illustrated in Fig. 1 (a) were used. On emergence, most moths moved into the upper part of the container; a sheet of cellulose acetate was then slid between the upper and lower halves. Moths were removed daily in this way, anaesthetized lightly with CO_2 to facilitate handling, sexed, and set up in experimental containers. When unmated moths were required, pupae were separated individually into small glass tubes and emerged moths were removed daily.

All experiments were conducted in temperature controlled cabinets at 25°C, uncontrolled humidity and in darkness except for daily attention to the containers. 5% sucrose solution was provided on cotton wicks, which were re-moistened daily.

(a) Individual variation in fecundity and relationship to pupal weight

Pupae were dissected free from their silken cocoon and weighed to the nearest 0.1 mg. They were then placed individually into small tubes and held at 25°C until adult emergence. Within 24 h of emergence moths were sexed and placed into plastic cups of approximately 55 ml capacity. The mouths of the cups were closed with fine terylene



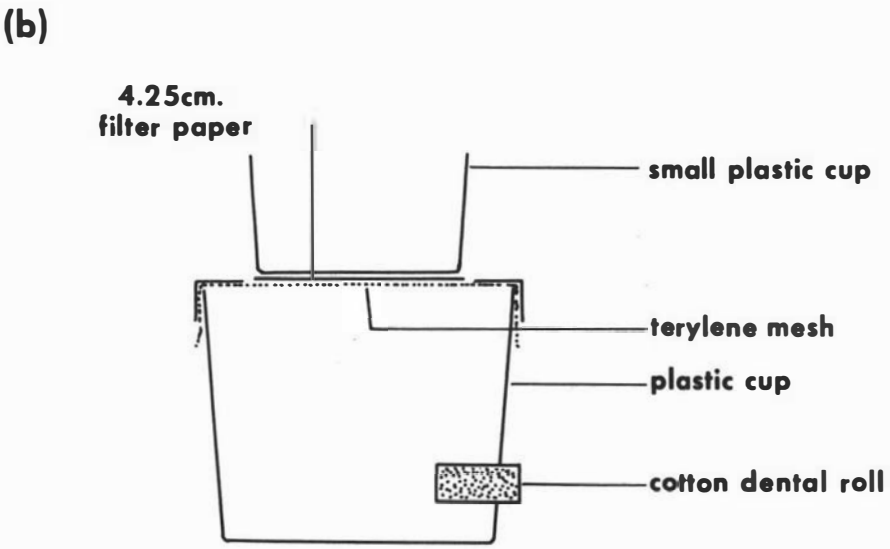


Fig. 1. Designs of containers for experiments on fecundity in relation to mated state, age and pupal weight:
(a) for moth emergence and separation from pupae;
(b) for collection of eggs from moths held singly or in groups.

net (approximately 0.5 mm^2 mesh) secured by the cut-out rim of the plastic lid. A 4.25 cm diameter filter paper was placed in close contact with the terylene net and held down by a second plastic cup. Cotton feeding wicks were inserted through the sides of the cups near the base. In addition to allowing replenishment of the sugar solution from the outside, this arrangement allowed the wicks to act as removable plugs so that dead moths could be removed from the containers daily. The design of the experimental containers is shown in Fig.1(b).

Two males and one female were initially placed into each cup. Any males which died were replaced until the death of the female. Almost all eggs were laid through the terylene mesh onto the filter paper, thus the number of eggs laid per container per day was readily assessed by daily replacement of the filter papers. The very few eggs laid elsewhere in the containers were ignored.

(b) Relationship of egg number in ovaries at emergence to pupal weight

Pupae were weighed and held individually in small tubes for emergence, as described above. Female moths emerging from these pupae were dissected within 4-16 h of emergence and the number of fully developed eggs within the ovaries determined. Dissection was undertaken by removing the abdomen, and tearing it open gently with fine forceps in a drop of water on a microscope slide. The total number of fully developed eggs (based on size) within the ovaries was then counted. Smaller eggs were not recorded.

(c) Relationship between eggs laid and mated state and the pattern of egg laying in time

Moths less than 24 h old were placed in 120 ml plastic cups of the same pattern as those used for holding moths individually. Batches of 5 females per container were used and each treatment was replicated in 5 separate units.

Treatments were as follows:

(i) Single mated

Seven males were placed into each container together with 5 females. After 48 h the moths were lightly anaesthetized

with CO_2 and the males were removed. Preliminary experiments showed that females were almost invariably mated after this period.

(ii) Multiple mated

The term multiple-mated is used in reference to females confined with males throughout life, and probably correctly describes their condition in most instances, since copulations additional to the first were observed on numerous occasions. Dissections to determine the presence of more than one spermatophore were not undertaken. Containers were set up with 7 males plus 5 females as for the single mating treatment. In this experiment however the males were not removed but were replenished with fresh males as required, so that a minimum sex ratio of 1:1 was maintained throughout the life span of the females.

(iii) Unmated females

Five females that had emerged individually in separate tubes were placed in each container.

For all treatments, eggs were collected daily as described above. Dead moths were removed from the containers daily, and all females of suitable condition were dissected. The number of fully developed eggs that each contained was recorded.

RESULTS AND DISCUSSION

(a) Individual variation in fecundity and relationship to pupal weight

The variation in totals of eggs laid by individual moths was extremely high, with a coefficient of variation in excess of 50%. Of the 45 examined 4 did not oviposit and 1 laid only 1 egg. These individuals may have failed to mate, but this was not investigated. The remaining 40 moths laid from 46 to 236 eggs each. Broodryk (1971) reported almost identical figures (0 - 232 per moth). There was no significant correlation between total eggs laid and pupal weight, or between pupal weight and lifespan.

(b) Relationship of egg number in ovaries at emergence to pupal weight

Dissection of 39 females 4-16 h after emergence showed that they contained a mean of 68.7 ± S.E. 4.1 fully developed eggs. Mean pupal weight was 11.6 ± 0.25 mg and was positively correlated ($r = 0.78$, $p < 0.01$) with the number of eggs in the ovaries. The complement of fully developed eggs at emergence was thus less than the mean total number of eggs laid by mated females. Further maturation of eggs must therefore take place during adult life and may in part explain the lack of correlation found between fecundity (in terms of total eggs laid) and pupal weight.

(c) Relationship between eggs laid and mated state; the pattern of egg laying in time

Data on total eggs laid, mature eggs remaining within the ovaries at death, and minimum of days to commencement of oviposition for groups of (i) single mated; (ii) multiple mated; and (iii) unmated females are given in Table 2. Mean life span is also included together with the life span of males held with them during the experiment.

With moths held in groups, no significant difference occurred between the total number of eggs laid by single-mated females (with males for first 48 h) and multiple-mated females (with males throughout life). A single mating therefore seems to serve the female's full ovipositional potential, but fertility of eggs was not examined. Unmated females laid a small number of eggs (mean 7.7) as reported by Picard (1913a) and Attia and Mattar (1939). All such eggs laid by virgin females collapsed within a day or two and failed to develop.

Dissection at death of as many females as possible showed that some apparently mature eggs remained within the ovaries of most; up to 4 per ovariole (mean 5.6 per moth) for single-mated females, up to 12 (mean 16.5) for multiple-mated females, and up to 11 (mean 27.5) for virgin females. Experimental conditions for oviposition may therefore have been less than optimum, and this may have additionally contributed to lack of correlation between fecundity and pupal weight. This was later confirmed in experiments on the influence of host plant tissue on fecundity (see Chapter V).

For virgin females, the mean number of mature eggs within the ovaries at death plus the mean number laid (27.5 + 7.7 = 35.2) was less than the number of eggs in females shortly after emergence from the pupa (68.7). Some resorbence of eggs must therefore take place in virgin moths during their life time.

The lifespan of multiple-mated females was significantly shorter than that of females mated only once (mean 8.5 days cf. 14.4 days). Virgin females did not live significantly longer than females mated once. This difference in lifespan between single- and multiple-mated females may explain some of the variability previously reported for this insect. Salama et al. (1972) reported a mean life span of 16.2 days (at 25°C), close to the 14.4 days in the present study; Attia and Mattar (1939) obtained a mean of 8.7 days, which agrees closely with the present figure of 8.5 days for multiple-mated moths.

The extreme longevity of males in the present study (23.6 days and significantly greater than for all groups of females) is at variance with most previous findings since Salama et al. (1972) and Attia and Mattar (1939) reported males to be shorter-lived than females. Nabi (1978) has however confirmed the greater longevity of males of Potato Tuber Moths from the same source as the author's culture.

The patterns of egg laying in time for the groups of single-mated, multiple-mated and unmated females are presented in Fig. 2(a), (b) and (c) respectively. The patterns for single-mated and multiple-mated females were closely similar with a slight suggestion that oviposition may be more concentrated into the earlier part of life with multiple mating. In both groups peak oviposition occurred at age 2-5 days and declined to low levels after 7 days. Oviposition by virgin females (Fig. 2(c)) did not commence until at least 5 days later than mated females. Numbers of eggs laid were small, and showed no well defined peak.

On the basis of the patterns of egg laying obtained in these experiments, the procedure was adopted for further experimentation on oviposition behaviour of holding moths for 24 h after emergence then running the experiment for 48 h to cover the peak oviposition period.

Table 2. Relationship between mated state, number of eggs laid and lifespan for groups of potato tuber moths

Group	n	Days to commencement of oviposition (per container)	Total eggs laid per container ± S.E.	Mature eggs in ovaries at death	Life span (days) ± S.E.
♀♀:					
(i) single-mated	25	< 1	455 ± 46.8 (91.0 per ♀)	5.6 (0-4 per ovariole) (n = 20)	14.4 ± 1.1
(ii) multiple-mated	25	< 1	492 ± 95.3 (98.4 per ♀)	†16.5 (0-12 per ovariole) (n = 15)	‡8.5 ± 0.6
(iii) unmated	25	5	*38.4 ± 12.1 (7.7 per ♀)	27.5 (0-11 per ovariole) (n = 23)	16.9 ± 1.5
♂♂:	32	-	-	-	ϕ23.6 ± 1.9

* Significantly different from single- or multiple mated ($p < 0.01$)

† One individual with 96 mature eggs

‡ Significantly less than single-mated ♀♀ ($p < 0.01$)

ϕ Significantly more than virgin ♀♀ ($p < 0.05$)

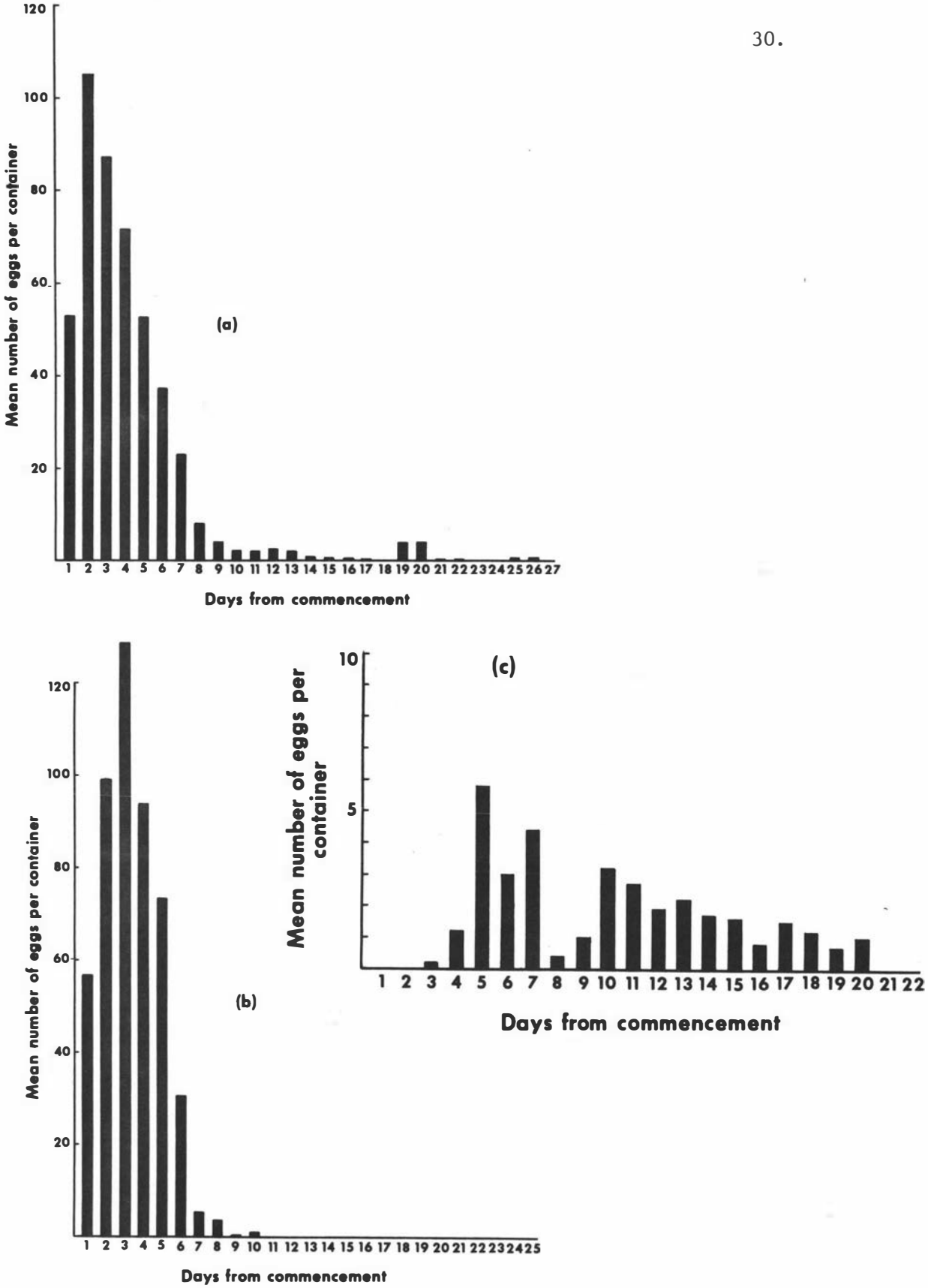


Fig. 2. Patterns of egg laying for groups of 5 female moths: (a) single-mated; (b) multiple-mated; (c) unmated.

2. THE PHYSICAL NATURE OF THE OVIPOSITION SUBSTRATE

Although potato tuber moth deposits its eggs freely in the absence of host plant material, it is apparent that egg laying is not indiscriminate and that some selection of oviposition site takes place. One factor that seems to be important in this respect is the physical nature of surfaces available to the moths. Picard (1913a) stated that tuber moth oviposited on rugose surfaces rather than on smooth, and in cracks and depressions, and that oviposition was stimulated by contact of the tip of the abdomen with rough surfaces such as muslin cloth. Attia and Mattar (1939) commented that the female is "not at all particular" about egg laying, and that "eggs may be deposited on any part of the green plant and perhaps in the soil". However they also stated that eggs are laid on the tubers, especially in and around the eyes.

Various materials have been used effectively as oviposition substrates in artificial rearing. Marvin (1944) used paper with a rough surface held closely against 20-mesh wire screen (coated with paraffin wax to prevent eggs from adhering); moths laid through the mesh openings on to the paper. Platner and Oatman (1968) used unbleached muslin cloth stretched over the mouths of jars containing moths.

Meisner *et al*. (1974b) compared cheesecloth, foamed polystyrene, silk, nylon sponge, filter paper, and glass in multi-choice tests and found that cheesecloth was very strongly favoured. Traynier (1975) found that organdie of mesh size 0.25 mm^2 was suitable for oviposition, especially when backed with plastic, but that abrasive paper of various grit sizes was not acceptable. He also showed that under field conditions, a considerable proportion of eggs was laid in soil adjacent to host plants rather than on the plants themselves. Traynier concluded that "preferred oviposition substrates provided irregularities that were large enough to accommodate eggs" and considered surface texture to predominate over light/shade, moisture, and presence of host-plant juices. The object in the present instance was to try and define optimal surfaces more precisely by examining a number of physical features of possible oviposition substrates. Since it appears that the stimulus for oviposition in this insect is primarily tactile, the external structure of the ovipositor was examined by scanning electron microscopy.

MATERIALS AND METHODS

A series of experiments was conducted as described below. Five, 10 or 20 pairs of moths were used per container, depending on its size and the number of oviposition sites provided. Each treatment was replicated five times in separate containers. All experiments were conducted in temperature controlled cabinets at 25°C and in continual darkness over a 48 h period using moths 24-48 h old at the commencement of each experiment. Five per cent sucrose solution on cotton dental rolls was provided for the moths in all cases. Eggs were counted using a zoom stereomicroscope with a magnification range of x 10-20.

(a) Nature of material backing a standard mesh size

Gloss paper, waxed paper, paper towelling, polythene sheet, and aluminium foil were compared with filter paper as backing to a 0.5 mm^2 terylene mesh, in a non-choice situation (single oviposition site per container). Experimental containers consisted of 120 ml plastic cups with the terylene mesh stretched over the mouth by means of the cut-out lid. Five pairs of moths were placed in each unit. Sample materials were cut into 4.25 cm diameter discs to match the filter paper standard, and were held tightly against the upper surface of the terylene mesh with thin polythene film held down by the lid. In a second series the sample discs were offered below the terylene mesh, and were held in place by double-sided sticky tape.

Eggs were counted in the following categories: (a) on the sample disc; (b) on the gauze; (c) elsewhere in the container. In addition, for the series with test discs below the mesh, a fourth category, (d) eggs "behind" sample disc, was recognized, because many eggs were found inserted between the disc and the terylene mesh layer, around the edges of the samples.

(b) Smooth compared to hairy surface

The comparative suitability of smooth and hairy substrates was evaluated in two experiments. In the first, a mesh composed of smooth fibres (terylene) was compared with a mesh composed of hairy fibres (muslin), each with an opening of approximately 0.5 mm^2, both with and

without filter paper backing. In the second experiment, hairy fibred mesh (muslin) was compared with a hairy surface without mesh openings (felt carpeting - "Feltex"). A further treatment was included in which no oviposition site was provided within the containers. The experimental containers were 500 g glass preserving jars closed with a glass petri dish half. Ten pairs of moths were placed in each jar.

Terylene net and muslin samples were prepared by stretching the material across a 5.0 cm diameter plastic ring. Filter paper (4.25 cm) backing was held closely against the mesh by means of a cardboard disc. For samples of mesh without backing, the material was held stretched in place by a second ring which fitted within the rim of the first. Discs of felt carpet were cut to 5.0 cm diameter and fitted in rings as for the mesh samples. Samples were presented in pairs (choice situation) or singly (non-choice situation), and were fastened on opposite walls of the containers with adhesive tape.

(c) Dimensions of mesh openings and surface grooves

Two experiments were conducted, one using a graded series of eight different mesh openings provided by samples of nylon bolting cloth; the second employing four widths of grooves prepared on the surface of thin card. Experimental containers consisted of 500 g glass preserving jars each with 10 pairs of moths.

The nylon bolting cloth (Monyl brand, D. Hourigan Ltd., Auckland) mesh apertures were 120, 170, 220, 270, 320, 450, 525 and 650 microns (manufacturer's specifications). Muslin mesh was also included for comparison. Samples were prepared on 5.0 cm diameter rings as described in the previous section. Each mesh size was offered both with and without filter paper backing, using a single sample per container (non-choice situation).

Smooth white card 1 mm in thickness was used to prepare grooves of various widths. Strips of card of appropriate width were glued to 5 x 5 cm square portions to give five grooves per square of width 0.5, 1.0, 2.0, or 5.0 mm x 1 mm deep. Sample squares were fastened to the undersides of petri dish lids, one sample per jar (non-choice situation).

(d) Effect of eggs present on further oviposition

Eggs were collected on 4.25 cm diameter filter papers by exposing them behind muslin mesh in jars of ovipositing moths for 24 h. Oviposition was prevented on half the area of some discs by covering with polythene film. The number of eggs on each paper was then counted and the most suitable selected for setting up the experiment. Four treatments were included: filter paper discs with eggs over entire surface, discs with eggs on one half of area only, discs with no eggs, and discs with no eggs but covered with muslin mesh. The samples were fastened to the petri dish lids of glass preserving jars with double sided sticky tape. Ten pairs of moths were placed in each container. On assessment, the number of eggs on each sample was counted and additional eggs laid on those samples set up with eggs calculated by difference. The two halves of the samples offered with eggs on one half only, were counted separately.

(e) Orientation of the oviposition surface

To compare the preference for oviposition on vertical (walls), horizontal (floor) and horizontal inverted (ceiling) surfaces, sample discs 5.0 cm in diameter were prepared from filter paper covered with muslin mesh. Three sample discs were placed in each experimental container fastened to the floor, wall and ceiling respectively. Two types of containers were used, 500 g glass preserving jars with glass petri dish lids each with 10 pairs of moths and terylene net cages of 30 cm^3 size each with 20 pairs of moths.

(f) Effect of moisture on oviposition

Plaster of Paris discs 5.0 cm in diameter and approximately 1.0 cm thick were prepared and were allowed to dry out completely over several days. Half of the samples were re-moistened by soaking in water overnight and then drying off the surface water on absorbent paper. Each disc was then faced with filter paper on one surface with muslin mesh stretched tightly over it. Discs were offered in pairs to groups of ten pairs of moths in 500 g glass preserving jars to give the following comparisons: moist versus moist, moist versus dry, and dry versus dry.

(g) Structure of the ovipositor

The ovipositor of freshly killed moths was extruded by gently squeezing the abdomen with forceps. The tip of the abdomen was then removed and prepared for examination by scanning electron microscopy.

RESULTS

(a) Nature of the material backing a standard mesh size

No differences occurred between treatments in the total number of eggs laid per container regardless of whether the backing material was above the mesh (behind it, with respect to the moths) or below it (in front of it, with respect to the moths). There were, however, large differences in the distribution of eggs between different treatments as depicted in Fig. 3.

With the sample discs behind the mesh (with respect to the moths), almost all eggs were laid on the disc in the case of filter paper and this effect was even more marked with paper towelling which had a rough surface. Gloss paper behind the mesh was also well accepted, but waxed paper, polythene and aluminium foil showed a marked deterrent effect for egg laying. The results with sample discs in front of the mesh (with respect to moths) were quite different. In all cases very few eggs were laid on the exposed surface of the samples themselves even with those materials that were very readily accepted when covered with mesh (filter paper and paper towelling). There was a tendency instead for moths to insert their eggs around the margins of the samples, between them and the gauze layer. Most eggs were laid on the gauze itself in these instances.

(b) Smooth compared to hairy surfaces

When smooth fibred terylene mesh was compared with hairy fibred muslin, each backed with filter paper, no marked preference was shown for one or the other and almost all eggs within the containers were laid on sample discs. When compared without backing however, muslin was strongly favoured over terylene both in choice and non-choice

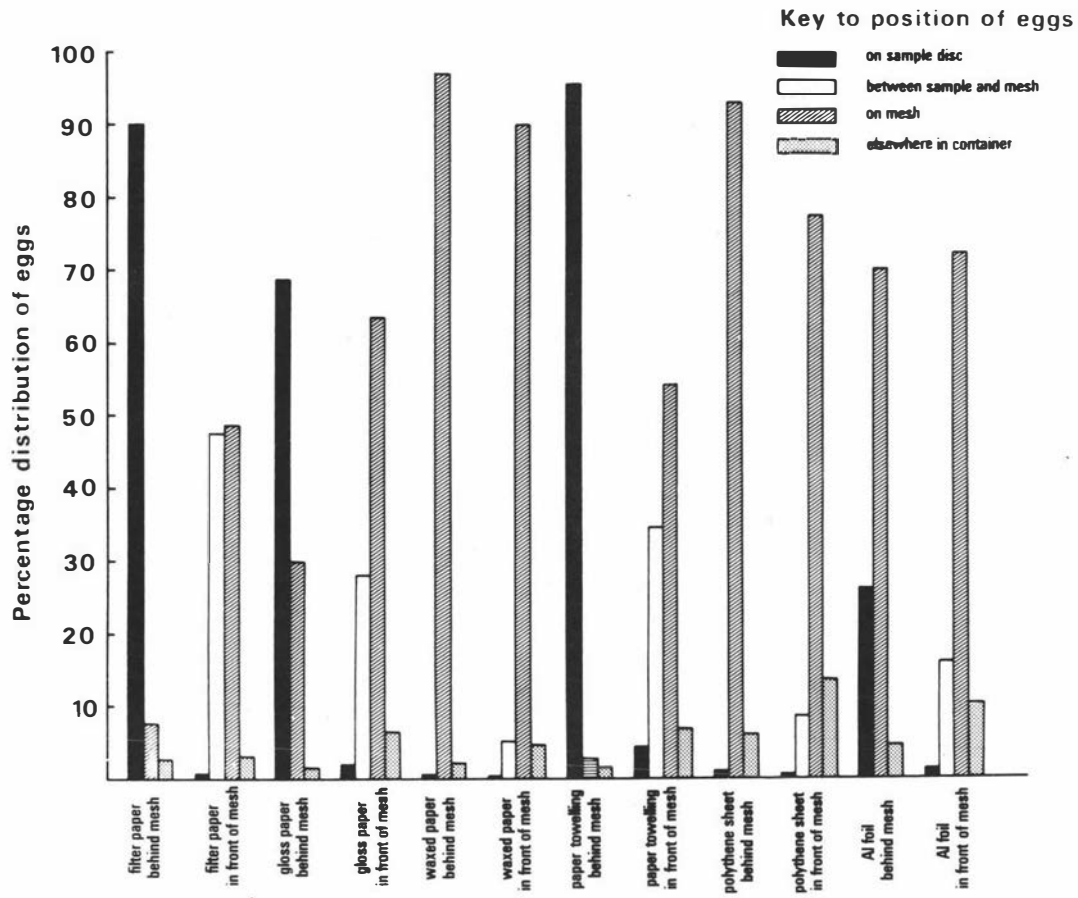


Fig. 3. Distribution of eggs with different materials backing a 0.5 mm^2 terylene mesh.

situations. The total number of eggs was also significantly reduced in treatments which included terylene mesh without backing, and an appreciable percentage of eggs was laid away from the sample discs elsewhere on the walls of the glass containers. Details of results are given in Table 3.

The results of comparisons between discs of felt and of muslin with filter paper backing gave a slight preference in favour of muslin when a choice was offered (significantly different at 5% level, t-test on counts $\sqrt{x+1}$) but no significant difference in a non-choice situation. There were no significant differences between any treatments in the total number of eggs laid including that in which no oviposition site was provided. In the latter case eggs were distributed over the walls, floor and ceiling of the containers.

(c) Dimensions of mesh openings and surface grooves

Over the range of mesh openings (120 to 650 microns) provided by nylon bolting cloth, no significant differences occurred in the total numbers of eggs laid in the containers whether the mesh was backed by filter paper or unbacked. In the case of samples offered with filter paper backing, the smallest (120 microns) and the largest (650 microns) mesh sizes received significantly fewer eggs deposited on the sample surface than most other mesh sizes. There was no clear separation of preference over the range of mesh size 170 to 525 microns but from the proportions of eggs laid elsewhere in the containers, the optimum appeared to be from 170 to 270 microns (Table 4 and Fig. 4(a)).

When samples were offered without filter paper backing, the most notable feature was the high proportion of eggs that were laid elsewhere in the containers in every case except with the muslin mesh standard. No preference for any particular mesh size was apparent amongst the range of nylon bolting cloths. Details are given in Table 4 and Fig. 4(b).

The results of offering moths grooves 1 mm deep and 0.5 to 5.0 mm wide are shown in Table 5 and Fig. 5. The smallest groove width (0.5 mm) was readily accepted and gave results similar to the

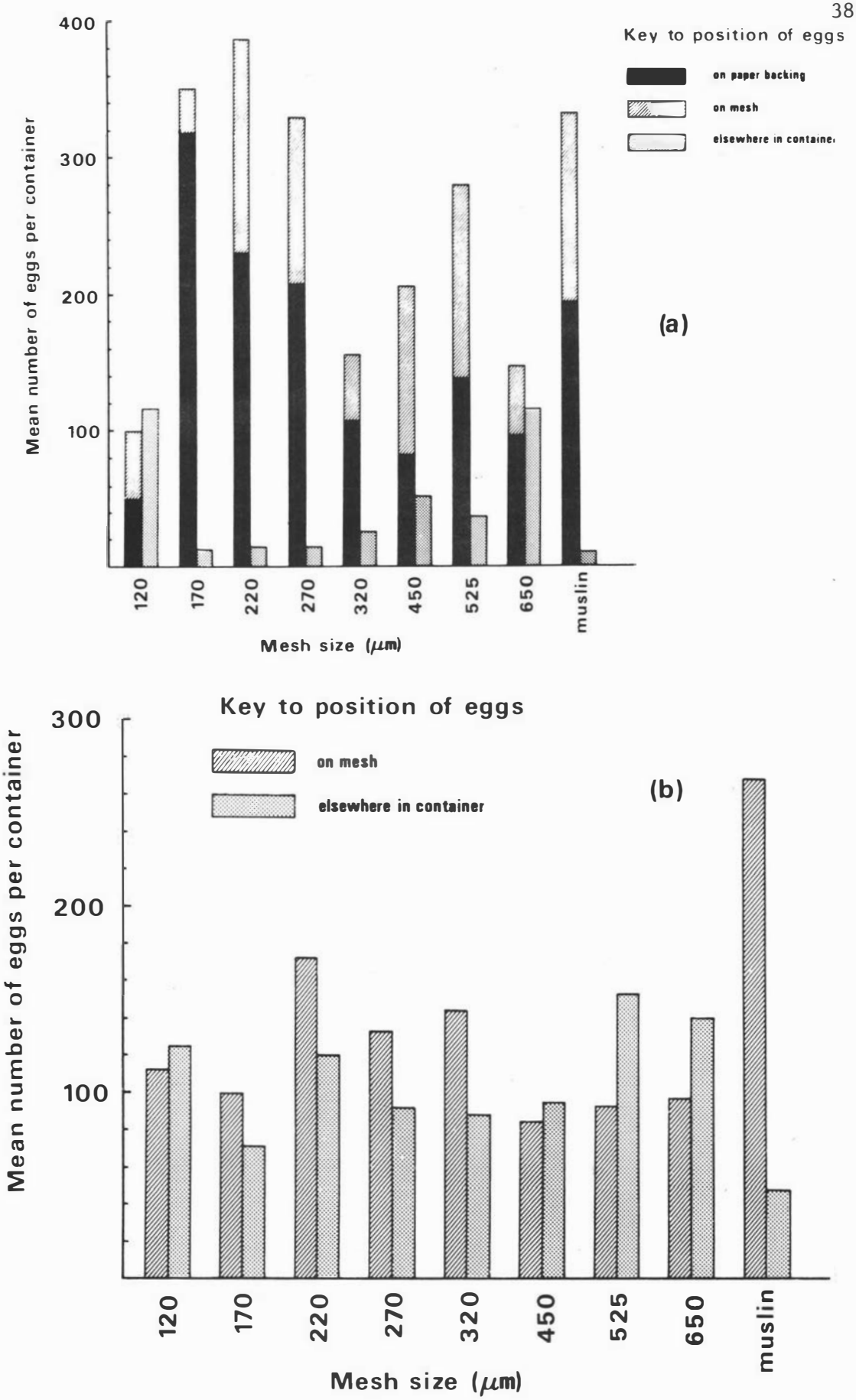


Fig. 4. Distribution of eggs with agraded series of nylon bolting cloths and muslin: (a) with paper backing; (b) without backing.

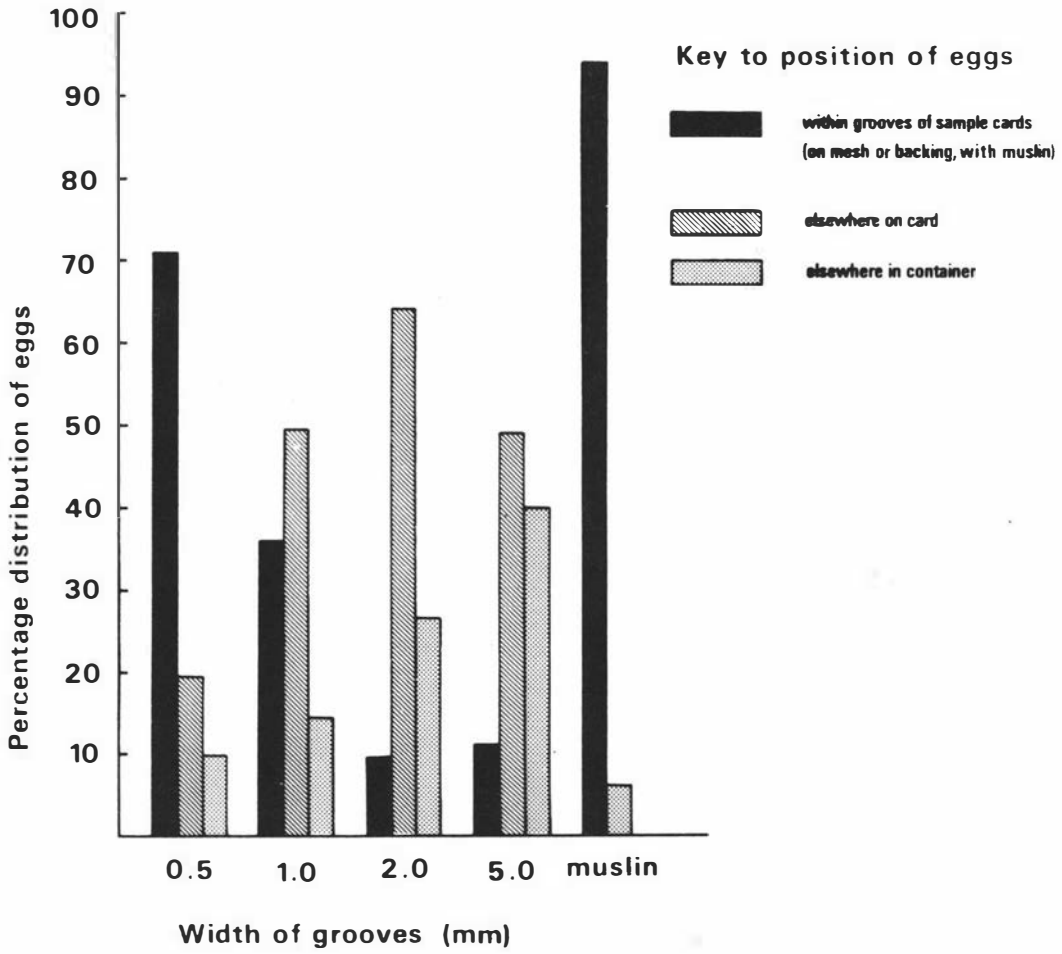


Fig. 5. Distribution of eggs on a card surface with grooves of various widths.

standard (muslin backed with filter paper). About half as many eggs were laid in the grooves when the width was 1 mm, and about one eighth the number for groove widths of 2.0 and 5.0 mm. The total numbers of eggs laid in the containers were not significantly different.

(d) Effect of eggs present on further oviposition

Slightly more eggs were laid on filter papers with eggs at the commencement of the experiment than those without but the difference was not significant (Table 6). In the case of filter papers bearing eggs on one half of their area only, nearly all additional eggs were laid on that side rather than on the blank side. Differences between treatments in the total number of eggs laid in the containers, were not significant.

(e) Orientation of the oviposition surface

In both large (30 cm^3 net cages) and small (500 g glass jars) containers most eggs were laid on samples attached to the roof. Fewer were laid on samples attached to the walls and least on those placed on the floor. All differences were highly significant (Table 7).

(f) Effect of a moist substrate on oviposition

The results of comparing muslin backed with filter paper in dry and moist conditions are given in Table 8. There was a strong preference for the dry substrate both in choice and non-choice situations. Furthermore, in contrast to almost all other experiments, the total number of eggs laid in the containers was significantly reduced when moist substrates were present.

(g) The ovipositor

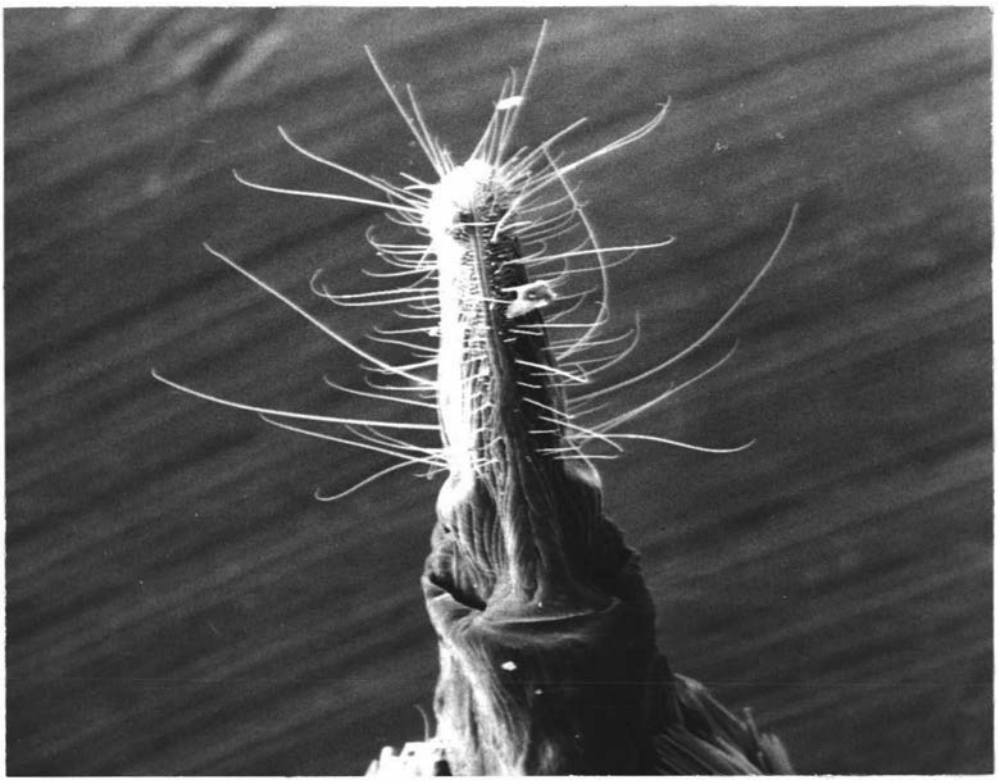
The ovipositor of potato tuber moth is approximately 1.5 x 0.3 mm when fully extended. There are 30-40 prominent, gently tapering hairs on either side ranging in length from about 0.03 to 0.30 mm (Plate 1(a) and (b)). They have a raised ring-like base of attachment (Plate 1(c)) of a flexible socket pattern. No pores or openings are visible along

their length. These hairs are thus typical trichoid sensilla in structure (Dethier 1963, McIver 1975) and are clearly primarily tactile in nature. At the tip of the ovipositor, very numerous much smaller hairs are regularly spaced over much of the area between the large hairs (Plate 1(c) and (d)). These appear to be more rigidly attached at the base. No sensilla are present which could be entirely chemosensory in nature though it is possible that the trichoid sensilla could serve a dual function. The structure of the ovipositor is thus consistent with the requirement of a mechanical stimulus for egg laying, but chemical sensitivity is not necessarily precluded (see part 3 of this chapter).

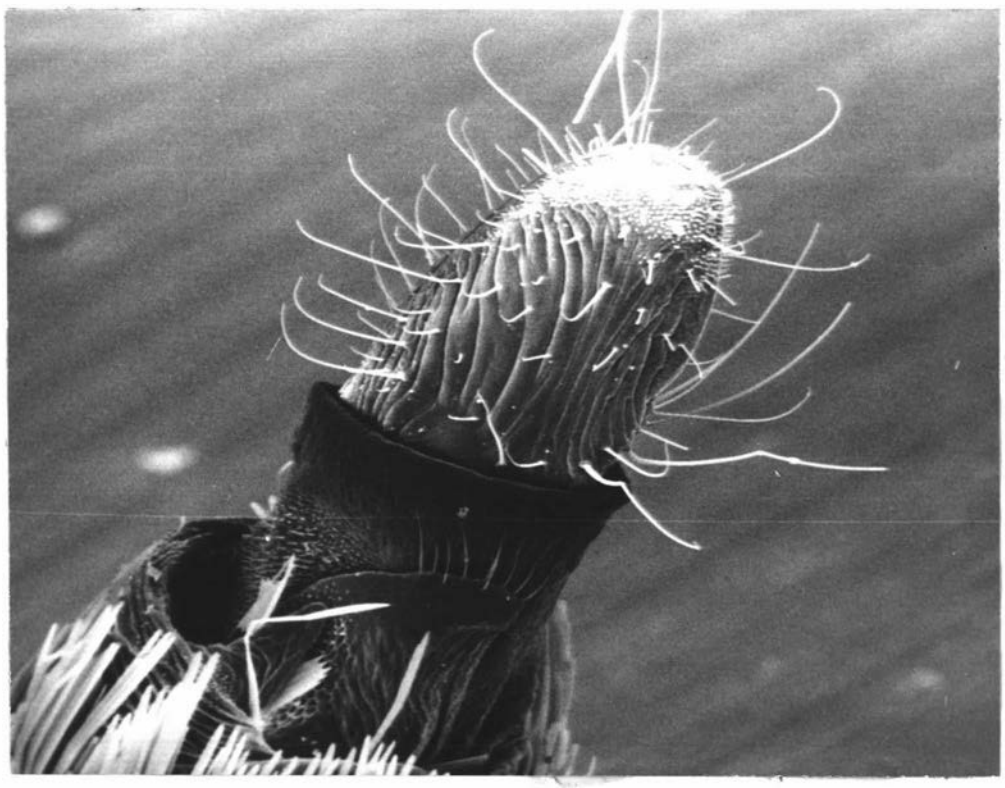
DISCUSSION

In most experiments similar numbers of eggs were laid per female during the 48 h experimental period regardless of the substrates offered suggesting that egg deposition is primarily a function of physiological age. When highly deterrent surfaces for oviposition were presented however, the number of eggs laid was in some instances reduced. This was particularly the case with a moist substrate, and may account in part for the reported depressant effect of irrigation on field infestations of this insect (Foot, 1974) though newly hatched larvae may also be adversely affected by moisture (Mahajan and Mogal 1978). With these exceptions, all experimental effects were on distribution of eggs within the containers rather than on total numbers of eggs laid.

From experiments with various sizes of mesh opening and of surface grooves the preferred dimensions of surface depressions appear to be from about 0.2 to 0.5 mm^2. Sizes much smaller or larger than this were not readily accepted. Traynier (1975) described preferred substrates as having irregularities large enough to accommodate eggs and gave dimensions of the egg as approximately 0.3 to 0.4 mm. The present findings suggest that it would be more accurate to describe preferred depressions as being just large enough to accommodate eggs. When they are much larger they are not well accepted even in the absence of alternative sites.

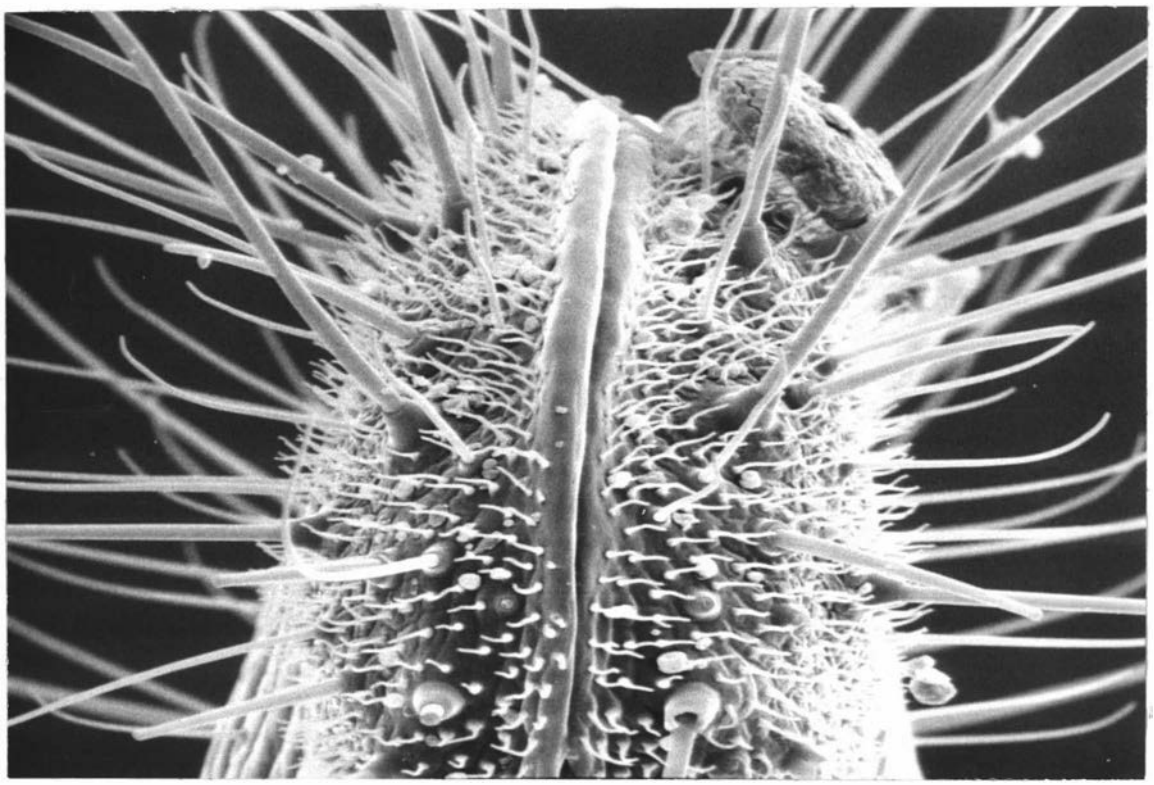


(a)

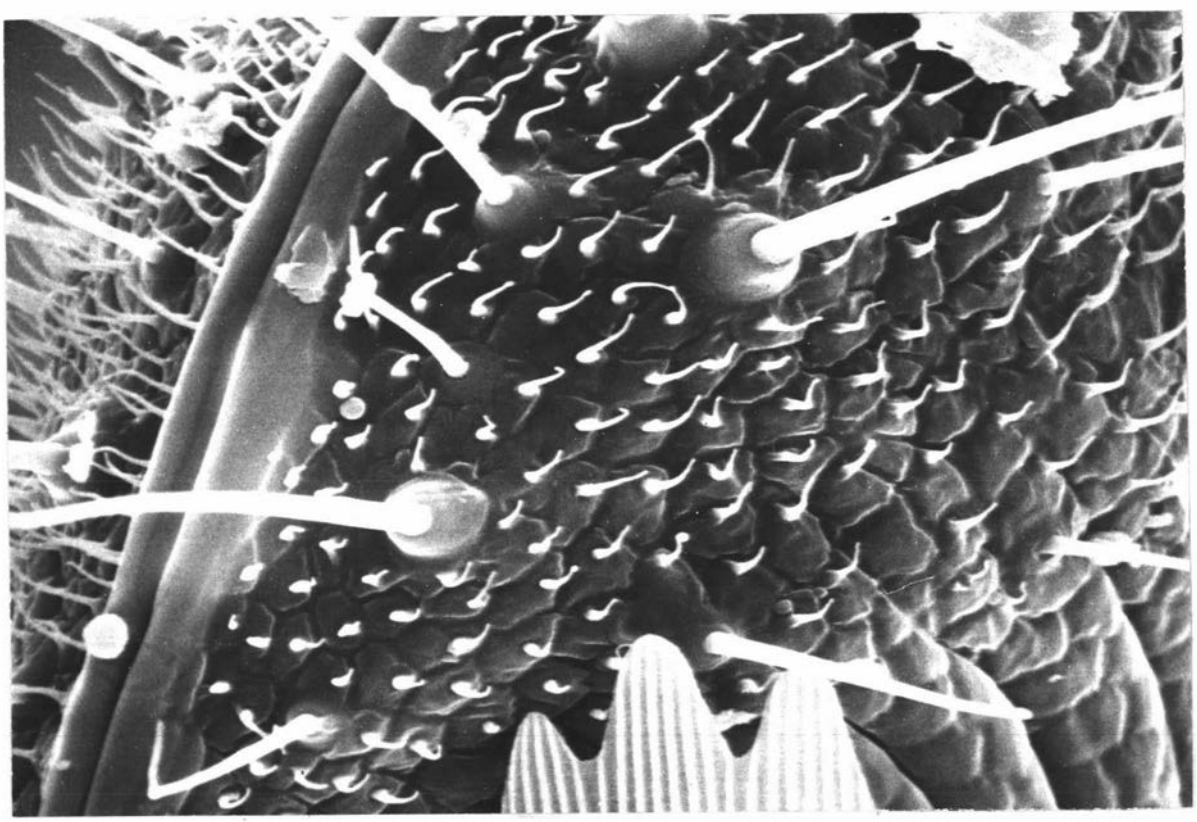


(b)

Plate 1. External structure of the ovipositor of potato tuber moth: (a) entire ovipositor, ventral view (x80); (b) entire ovipositor, lateral view (x95).



(c)



(d)

Plate 1. (c,d) part of the tip of the ovipositor in close up, showing two types of hairs (x570 and x950 respectively).

Table 3. Comparison of smooth fibred mesh (terylene) with hairy fibred mesh (muslin) for oviposition acceptance by potato tuber moth

		Mean number of eggs per sample disc		Mean total number of eggs per container	% of eggs laid on sample discs
With filter paper backing	muslin	364.2	†NS	644.2ϕ a A	95.1
	terylene	248.2			
	muslin	313.9	NS	638.8 a A	94.7
	muslin	292.2			
	terylene	301.4	NS	606.0 a A	90.5
	terylene	246.2			
Without filter paper backing	muslin	272.2	**	396.8 b BC	83.6
	terylene	59.4			
	muslin	218.8	NS	449.4 b AB	87.2
	muslin	173.2			
	terylene	121.0	NS	281.8 c C	66.0
	terylene	65.0			

† Significance of difference between means calculated by t-test on counts transformed $\sqrt{x}$.
NS - not significant;
* - significant at 5% level;
** - significant at 1% level.

ϕ Significant differences and lettering according to Duncan's Multiple Range test applied to counts transformed $\sqrt{x}$.

Capital letters indicate 1% level of significance
and small letters indicate 5% level of significance

Table 4. Comparison of a graded series of nylon bolting cloths and muslin for oviposition acceptance by potato tuber moth

Mesh opening in microns	With backing (filter paper)		Without backing	
	Mean number of eggs per sample disc	Percentage of eggs laid on sample disc	Mean number of eggs per sample disc	Percentage of eggs laid on sample disc
120	98.4 c Cϕ	61.9	112.0 b ABϕ	47.3
170	354.8 a A	96.4	98.6 b AB	58.3
220	386.0 a A	96.2	172.6 ab AB	58.9
270	329.4 a AB	95.5	132.6 ab AB	59.0
320	156.2 bc ABC	85.9	143.8 ab AB	62.1
450	206.8 abc ABC	78.9	83.6 b B	46.9
525	279.2 ab AB	88.1	93.2 b AB	41.7
650	155.0 c BC	57.4	97.4 b AB	44.9
muslin	331.6 a AB	97.1	270.0 a A	85.3

ϕ Significant differences and lettering according to Duncan's Multiple Range Test applied to counts transformed $\sqrt{x}$.

Table 5. Comparison of various widths of grooves on paper card surface for oviposition acceptance by potato tuber moth

Groove width in mm (depth 1 mm)	Mean number of eggs laid within grooves	Number of eggs within grooves as percentage of total
0.5	396.8 a ABϕ	70.9
1.0	194.4 b B	35.9
2.0	45.8 c C	9.3
5.0	48.6 c BC	11.1
Muslin with filter paper backing	525.0 a A	93.9

ϕ Significant differences and lettering according to Duncan's Multiple Range Test applied to counts transformed $\sqrt{x}$.

Table 6. Effect of eggs present on further oviposition by potato tuber moth (filter paper surface)

Condition of filter paper disc at beginning of experiment	Additional eggs laid on samples. Mean per container		Percentage of eggs laid on sample discs
Eggs over whole area (Mean of 131.8 per paper)	75.6 b Bϕ		18.2
Eggs over half area (Mean of 139.8 per paper)	Blank half ** 9.4 Half with eggs 53.8	63.2 b B	21.3
No eggs	41.8 b B		9.9
Muslin with filter paper backing. No eggs	415.0 a A		85.2

ϕ Significant differences and lettering according to Duncan's Multiple Range Test applied to counts transformed $\sqrt{x+1}$.

** Significantly different at the 1% level. t-test on transformed counts.

Table 7. Effect of position of sample discs within experimental containers on oviposition by potato tuber moth

Position of sample disc	500 g glass jars[1] Mean number of eggs per sample disc	30 cm^2 terylene net[2] cages Mean number of eggs per sample disc
Ceiling	449.4 a Aϕ	468.2 a Aϕ
Wall	242.2 b B	214.0 b B
Floor	95.2 c C	19.2 c C

1 10 pairs of moths per container.

2 20 pairs of moths per container.

ϕ Significant differences and lettering according to Duncan's Multiple Range Test applied to counts transformed $\sqrt{x+1}$.

Table 8. Effect of a moist substrate on oviposition by potato tuber moth

Choice of substrates offered	Mean number of eggs per sample disc		Mean total number of eggs per container
dry	329.2	NS	721.6 a Aϕ
dry	378.2		
moist	104.2	NS	242.8 b B
moist	122.6		
dry	505.8	**	552.6 c A
moist	37.2		

** Significantly different at the 1% level.
t-test on counts transformed $\sqrt{x}$.

ϕ Significant differences and lettering according to Duncan's Multiple Range Test applied to counts transformed $\sqrt{x}$.

Although depressions of a suitable size on an otherwise smooth surface are acceptable for oviposition, the fine structure of the surface is also of importance. When very smooth materials (polythene film, aluminium foil) were used to back an otherwise suitable mesh size, they were not accepted, whereas materials with a slightly rough surface (filter paper, paper towelling) were readily accepted. Furthermore, comparisons of a hairy with a smooth fibred mesh and with a densely hairy surface without distinct depressions (felt), confirm the importance of surface texture and the highly stimulative effect of a hairy substrate (with or without depressions) compared to a smooth one. An optimum natural oviposition site should thus be one which combines surface depressions of suitable size with a hairy texture of the surface itself.

The stimulative nature of hairy substrates and the dimensions of acceptable surface depressions may be accounted for by the considerable number of long tactile hairs on the ovipositor. The dimensions of preferred depressions may in fact be associated more with the overall width of the ovipositor plus tactile hairs (0.4 - 0.9 mm) rather than with the dimensions of the egg.

3. THE INFLUENCE OF PLANT TISSUE ON OVIPOSITION BEHAVIOUR

The work described in the previous section confirms that the physical nature of surfaces is important in the choice of oviposition sites by Potato Tuber Moth. Such factors are likely to influence oviposition behaviour with respect to plant surfaces as well as inanimate ones, but are clearly not solely responsible for determining choice of oviposition sites in the field. As pointed out in the Literature Review, Meisner *et al.* (1974b) have shown that oviposition is stimulated by ethanolic extracts of potato peel of which L-glutamic acid appears to be an important component. Traynier's work (1975) indicated that the juices expressed from the leaves of various host plant species tended to stimulate oviposition whilst juices from non-host plants tended to be deterrent. The object of this part of the present study was to extend and amplify these findings as to the role of plant tissue in regulating oviposition behaviour and to examine modes of perception of the factors involved.

MATERIALS AND METHODS

Experimental containers consisted of 500 g wide mouthed glass jars closed by half a glass petri dish. Ten pairs of moths were used per container with five replications of each treatment. Experiments were run for 48 h in darkness at 25°C.

On the basis of the work reported in part 2 of this chapter, a standard blank oviposition sample was adopted consisting of cotton muslin stretched over a 4.25 cm filter paper enclosed in a 5 cm diameter plastic ring. Test samples consisted of similar sized portions of leaf, or other material, with or without muslin overlay, according to treatment, unless otherwise stated.

Samples were presented in pairs to provide a choice to ovipositing moths: one sample consisting of a standard blank and the other of the test material. The samples were fastened by sticky tape in an upright position to opposite sides of the test containers.

Few eggs were laid other than on the sample discs. When the distribution of eggs between samples was being compared, these extra eggs were ignored, but in comparisons of <u>total</u> eggs laid they were included. Egg counts were transformed ($\sqrt{x+1}$) before analysis. Two comparisons and statistical evaluations were made with data from each experiment:

1. Number of eggs laid on each sample (paired comparison). An index of oviposition stimulation/deterrence was calculated from the expression $\frac{A-B}{A+B} \times 100$, where A = number of eggs on plant sample and B = number of eggs on blank sample. The value of the index could thus range from +100 for total stimulation, through 0 for no effect, to -100 for total deterrence. A dependent t-test was conducted on transformed counts ($\sqrt{x+1}$).

2. Total number of eggs laid within each treatment (including any laid on the inner surfaces of the containers as well as on the test samples) subjected to analysis of variance, F-test and calculation of significant differences using Duncan's Multiple Range Test.

Plants used in experiments were grown in a glasshouse in a peat/gravel mixture. Samples were taken from young leaves only and were fresh at the commencement of each experiment. Plant species used and their host plant status for Potato Tuber Moth are listed in Table 9.

The following series of experiments was conducted in which test samples were compared with the standard blank disc:

(a) Intact portions of leaves supported in small vials of water; approximately equal in area to blank sample discs; or in the case of potato peel, small intact tubers.

(b) Leaf discs (or portions of leaf) equal in area to blank sample discs, covered with a layer of cotton muslin.

(c) As (b) but samples crushed by hand pressure with a pestle immediately before setting up and juices allowed to soak into the muslin covering.

(d) As (c) but crushed leaf and muslin dried gently in a stream of warm air for 15-20 minutes before setting up the experiment, so that totally dry surfaces were presented.

(e) As (b) but the surface of leaf discs brushed lightly with a stiff nylon test tube brush before covering with muslin. (Treatment visibly scratched the surface of most leaves but was not sufficient to release plant juices).

(f) As (c) but second untreated layer of muslin backed by perforated filter paper placed approximately 2 mm above the layer contaminated with plant juices.

(g) As (d) but antennae removed from some groups of moths immediately before setting up the experiment.

(h) In view of the stimulative effect consistently found with potato peel on total eggs laid by mated moths (see Tables 10 and 11), an experiment was conducted to determine whether any stimulation of oviposition was produced with virgin moths. Five replications each of ten moths were used as for other experiments.

Table 9. Plant species used in experiments on influence of plant tissue on oviposition behaviour and host plant status for potato tuber moth

Plant species	Host plant status
Potato - *Solanum tuberosum* L. cv. Ilam Hardy	Major host plant.
Egg plant - *Solanum melongena* L. cv. Black Beauty	Host plant (Mendes 1938, Cunningham 1969, Broodryk 1971, Meisner, Ascher and Lavie 1974a).
Tobacco - *Nicotiana tabacum* L. cv. White Burley	Host plant. (Mendes 1938, Cunningham 1969, Broodryk 1971, Meisner, Ascher and Lavie 1974a)
Tomato - *Lycopersicon esculentum* Mill. cv. Moneymaker	Normally acceptable as a host plant but reports not consistent. (Doreste and Nieves 1968, Cunningham 1969, Broodryk 1971, Meisner, Ascher and Lavie 1974a)
Silver beet - *Beta vulgaris* L. cv. Medium Green	Sugar beet has been reported as attacked (Haines 1977) but not generally regarded as a host plant.
Bean - *Phaseolus vulgaris* L. cv. Beanfeast	Non-host plant.
Pea - *Pisum sativum* L. cv. Greenfeast	Non-host plant.
Radish - *Raphanus sativus* L. cv. French Breakfast	Non-host plant.
Ryegrass - *Lolium perenne* L. cv. Manawa	Non-host plant.

RESULTS

The results of experiments (a) and (b) in which plant samples were offered without and with muslin covering each in comparison with a standard blank disc, are given in Table 10. Potato tubers, and leaves of potato and of egg plant (both known host plants) were accepted as well as (but not in preference to) blank muslin discs. All other plant species tested, including the recorded host plants tobacco and tomato, were strongly discriminated against in favour of blank discs. In addition, treatments involving potato tubers and egg plant foliage stimulated significantly greater total egg deposition than the blank control treatment.

When the plant samples were covered with a layer of muslin (Experiment (b)) discrimination against tobacco, tomato and all the non-host plant species was removed (there were no significant differences between the test samples and the blanks). When covered with muslin, potato peel and egg plant foliage were preferred to blank samples and the total number of eggs laid was boosted in the case of potato peel. Although the figures suggest that the acceptance of potato leaf was increased by covering with muslin, the difference did not reach statistical significance.

The effects of expressing plant juices from the samples immediately before setting up the experiment are shown in Table 11 (c). All known non-host plants and tomato were rendered highly deterrent to oviposition by such treatment, though totals of eggs laid were not significantly reduced in any case. Potato and egg plant foliage produced a positive stimulative effect on egg laying whilst potato peel and tobacco foliage were without effect. Total eggs laid were again increased by potato peel and also in this case by potato foliage.

When the experiment was repeated and the expressed plant juices were dried before introducing the moths (Table 11 (d)) the results were essentially the same, except that with ryegrass the deterrent effect now did not reach significance. Total egg deposition was stimulated by potato foliage and peel and by egg plant foliage.

The results of experiment (e) in which leaf samples were brushed with a nylon brush before being covered with muslin, are presented in Table 12 (e). In the case of tomato, silver beet, pea and radish, brushing resulted in significant deterrence of oviposition similar to, but not as great as, that produced by crushing the leaves. An anomalous result occurred with potato in that brushing resulted in a small but significant deterrent (rather than stimulative) effect. Because of this anomaly the test with potato was repeated, but with the same result. No effect was produced by brushing leaves of egg plant or bean.

In experiment (f) leaf samples were freshly crushed but were separated from the muslin/filter paper oviposition surface by about 2 mm. Results are presented in Table 12 (f). Only in the case of silver beet was any significant effect (mildly deterrent) produced.

The results of antennal removal on response of moths to oviposition stimulation (potato) and oviposition deterrence (bean) (Experiment (g)) are given in Table 13. Antennal removal reduced, but did not eliminate, positive discrimination for potato and negative discrimination against bean. It did however result in the loss of stimulation of total eggs laid provided by potato with intact moths.

Exposing virgin moths to potato peel (Experiment (h)) resulted in a mean of 4.8 eggs laid per moth compared to 4.4 eggs per moth without peel. There was thus no significant stimulation of oviposition, neither was there any discrimination between blank discs and those with potato peel.

DISCUSSION

The fact that leaves of all non-host plants tested were rendered acceptable for oviposition when covered with a layer of muslin (Experiments (a) and (b)) suggests that the physical nature of the leaf surface of these plants is unsuitable (highly smooth in the case of pea and beet) or that chemical oviposition deterrent factors, perceived only by contact, are present.

Expressed juices rendered known host plants more acceptable and non-host plants less acceptable, except for tomato which was rendered deterrent and tobacco and potato peel which showed no effect. Other than these anomalies, this confirms the presence of oviposition stimulants in host plants and of oviposition deterrents in non-host plants. How such substances might be detected by ovipositing moths however presents a problem. In some instances, gentle probing of the leaf surface (with the insect's ovipositor) might be sufficient to release them, as brushing of the leaf surface (without producing free sap) resulted in a deterrent effect in the case of tomato, beet, pea and radish but no positive effects for known host plants.

When expressed juices were separated from moths by a short distance (Experiment (f)), no marked stimulative or deterrent effects were produced (other than a slight deterrence in the case of beet), indicating that the factors involved are not volatile. Antennal removal did not eliminate the response of moths to oviposition stimulation from potato (though it did reduce the number of eggs laid) or oviposition deterrence from bean (but response was reduced in both cases), so that the site of perception of these factors must be other than on the antennae.

The following tentative conclusions are put forward as to the nature of plant selection for oviposition:

1. Host plants for the most part, contain oviposition stimulant factors (chemical) which are only detected on contact and by probing of the plant surface (apparently not present in tobacco).

2. Non-host plants possess oviposition deterrent factors of similar location and mode of detection. Physically unsuitable surfaces (i.e. smooth) may also be an additional factor in plant avoidance.

3. Neither the oviposition stimulant or deterrent factors are volatile and can be detected only by contact. They cannot therefore provide olfactory guidance to host plant finding from a distance. If plant odours are involved in host plant location (not examined in this study) they must be distinct from those stimulating or deterring oviposition. The only exception to this may be potato where the peel of tubers was stimulative when covered with muslin (Table 10 (b)).

Besides the effects on location of eggs, some host plants stimulated greater total egg deposition during the experimental period than the control treatment (no plant material). This was most consistent with potato tuber material but also occurred with potato foliage when crushed and to a lesser extent with egg plant. Total egg lay was not reduced by non-host plants. The stimulative effect of potato tuber material on fecundity when moths were exposed over their whole life span was confirmed in other experiments (see Chapter V Part 2). This stimulative effect on total eggs laid was eliminated by antennal removal (Table 13) suggesting that separate factors regulate choice of oviposition site and numbers of eggs laid as postulated for Plodia interpunctella by Deseö (1976).

Table 10. Effect of plant tissue, with and without muslin covering, on oviposition by potato tuber moth

Plant species	(a) Intact plant sample without muslin covering		(b) Intact plant sample with muslin covering	
	Index† of oviposition stimulation/ deterrence	Total no. of eggs relative to control = 100	Index of oviposition stimulation/ deterrence	Total no. of eggs relative to control = 100
Potato	-37.1 NS	158 NS	+28.8 NS	127 NS
Potato (tuber, peel)	-6.7 NS	189 *	+71.7 **	232 *
Egg plant	+21.3 NS	162 *	+32.1 **	113 NS
Tobacco	-88.6 **	146 NS	+15.0 NS	104 NS
Tomato	-72.3 **	76 NS	+11.2 NS	96 NS
Silver beet	-96.9 **	67 NS	-7.0 NS	106 NS
Bean	-79.3 **	99 NS	+10.7 NS	89 NS
Pea	-99.7 **	127 NS	-6.3 NS	80 NS
Radish	-93.9 **	84 NS	-14.5 NS	98 NS
Ryegrass	-94.3 **	104 NS	+40.7 NS	97 NS
Control	-8.8 NS	100	+15.8 NS	100

† Calculated from the expression $\frac{A - B}{A + B} \times 100$ where A = number of eggs on plant sample and B = number of eggs on blank sample.

NS Not significant.

* Significant $p < 0.05$.

** Significant $p < 0.01$.

Table 11. Effect of plant juices, freshly expressed and air dried, on oviposition by potato tuber moth

Plant species	(c) Plant sample with juices freshly expressed		(d) Plant sample with juices expressed and air dried	
	Index† of oviposition stimulation/ deterrence	Total no. of eggs relative to control = 100	Index of oviposition stimulation/ deterrence	Total no. of eggs relative to control = 100
Potato	+49.6 **	339 **	+69.8 **	216 **
Potato (tuber, peel)	-16.0 NS	208 *	+19.6 NS	197 **
Egg plant	+41.9 **	174 NS	+34.3 *	171 *
Tobacco	+7.3 NS	195 NS	+7.9 NS	109 NS
Tomato	-90.8 **	83 NS	-57.0 **	117 NS
Silver beet	-97.9 **	121 NS	-75.2 **	106 NS
Bean	-94.5 **	83 NS	-83.7 **	87 NS
Pea	-90.6 **	135 NS	-35.0 *	109 NS
Radish	-94.1 **	115 NS	-46.7 **	102 NS
Ryegrass	-80.3 *	97 NS	-32.8 NS	125 NS
Control	+17.8 NS	100	-3.4 NS	100

† See footnote to Table 10.

Table 13. Effect of antennal removal on response of potato tuber moths to oviposition stimulant (potato leaf) and oviposition deterrent (bean leaf) factors (Experiment g)

	Sample	Index of oviposition stimulation/deterrence	Total no. of eggs relative to control = 100
Intact moths	Potato	+84.2 **	255 **
	Bean	-50.4 **	88 NS
	Control	+5.1 NS	100
Moths with antennae removed	Potato	+47.2 *	145 NS
	Bean	-36.3 *	83 NS
	Control	-3.8 NS	102 NS

4. EXTRACTION OF OVIPOSITION STIMULANTS AND DETERRENTS

To provide further confirmation that chemical constituents of plants are involved in regulating oviposition, extracts of host and non-host plants were made and evaluated for biological activity.

MATERIALS AND METHODS

Preparation of samples

Three extraction procedures were used utilizing different solvents. They were:

Treatment	Types of plant constituents likely to be removed
(a) Immersion of intact leaves (and tubers in the case of potato) for 10 minutes in 200 ml of petroleum ether (40-60°C BP) with occasional agitation.	Non-polar compounds from surface layers.
(b) As (a) but with chloroform.	Non-polar plus polar compounds from surface layers.
(c) Maceration in 200 ml methanol for 2 minutes in a Waring blender followed by filtration under vacuum through a Buchner funnel to remove solids.	All plant constituents.

Immediately after extraction of the plant material solvents were evaporated almost to dryness in a rotary evaporator under reduced pressure with a water bath temperature of 25°C. Residues were re-dissolved in the same solvent used to make the initial extraction (except in the case of maceration in methanol where 50:50 methanol chloroform was used) and made up to 10 ml in a volumetric flask. Extracts prepared in this way were stored in a refrigerator until used for tests.

All plant species listed in Table 9 were tested and each was subjected to all three extraction procedures. The leaf area of each plant species was measured on a sample of leaves with an electronic leaf area meter and related to fresh weight in each case. Appropriate fresh weights of leaves for each species were then calculated to provide the desired area for extraction. In the case of potato tubers, surface area was computed on the assumption that each tuber was a sphere with a diameter equal to the mean of three measurements in different planes made on the tuber itself. Extractions were performed on fresh plant material except for methanol extraction of potato tubers, which were first peeled and the peel air dried at 25°C before maceration.

The area of test discs used for biological evaluation of extracts (muslin stretched over filter paper, see Part 3 of this Chapter) was 14.2 cm^2. Solvent extract from twice this leaf area (or tuber surface in the case of potato tubers) was applied to the test disc in 0.4 ml of solvent in two separate treatments each of 0.2 ml. Complete extraction of plant samples would thus have presented extracted substances at 2 x their plant concentration on the test discs.

Biological evaluation

The procedure for evaluation of plant extracts was as described for intact plant samples in Part 3 of this Chapter. Test discs were presented in pairs, one blank disc and one treated with extract. There were five replications each of ten pairs of moths. Discs were freshly prepared for each test and were used as soon as the solvent had completely evaporated. Two plant species, each with three methods of extraction, were tested at a time to give a total of six treatments plus an untreated control blank.

The extracts were also used for tests on behaviour of first instar larvae (see Chapter VI, Part 2).

RESULTS

Results were assessed after 48 h by counting the numbers of eggs on each disc and elsewhere in the container as described for similar tests with intact leaf samples in Part 3 of this Chapter. Results are summarized in Table 14.

Extracts prepared by surface washing with petroleum ether or chloroform were colourless or nearly so in all cases, while extracts prepared from leaves by maceration in methanol were deeply pigmented green.

DISCUSSION

For convenience of discussion the results of extractions of plant materials are summarized in Table 15 together with the results obtained with expressed plant juices previously presented in Table 11. It will be seen that total extraction (maceration in methanol) provided active extracts for all plants whether stimulatory or deterrent for oviposition, except in the case of pea. This was strongly deterrent with freshly expressed plant juices but the extract was inactive. Those plant samples that were neutral (inactive) as expressed plant juices (tobacco foliage and potato peel) were also inactive as extracts. The results also confirm the deterrent property of tomato which was previously found in experiments with whole leaf samples and expressed juices.

The position of potato tuber material appears to be anomalous as Meisner *et al.* (1974b) reported strong stimulation of oviposition with ethanolic extracts of potato peel. Results of surface washing with petroleum ether may provide some clue to this apparent anomaly, and also to the inactivity of tobacco with expressed plant juices and total extraction. Petroleum ether washings of these two plant materials gave positive stimulation of oviposition especially in the case of tobacco (see Table 15). On the other hand surface washing with chloroform, which could be expected to extract a wider range of substances than petroleum ether, was inactive in the case of potato peel

and deterrent for tobacco. It seems therefore that for these two plant materials, chemical factors responsible for stimulation of oviposition may be located close to the surface and thus readily removed by surface washing with petroleum ether. At the same time it may be postulated that more deep seated substances acting as oviposition deterrents are released with more vigorous extraction procedures and cancel out the effect of the superficial stimulants. If the chemical nature of oviposition deterrents/stimulants is to be determined it seems essential that extraction procedures suited to each particular plant material be evaluated.

In terms of total eggs laid during the experimental period, total extracts of egg plant and of tobacco and surface extraction of tobacco with pet. ether gave significant positive stimulation. No extracts depressed total eggs laid as was the case with expressed plant juices (see Table 11). The positive effect of total extract of tobacco in this respect is interesting as it had no effect on the distribution of eggs. This provides additional evidence for the suggestion made earlier that separate mechanisms may be involved in the selection of oviposition site and regulation of total eggs laid.

Table 14. Results of extraction of plant material with solvents on oviposition stimulation and deterrence

Plant species	Method of extraction					
	(a) Surface extraction of intact leaves with petroleum ether		(b) Surface extraction of intact leaves with chloroform		(c) Maceration of leaves with methanol	
	Index of oviposition stimulation/ deterrence	TOTAL eggs laid cf. control	Index of oviposition stimulation/ deterrence	TOTAL eggs laid cf. control	Index of oviposition stimulation/ deterrence	TOTAL eggs laid cf. control
Tobacco	+59.6 **	185 *	-50.6 *	69 NS	-24.9 NS	161 *
Pea	-40.0 NS	78 NS	-31.5 NS	192 *	-22.4 NS	65 NS
Control	+16.0 NS	100	-	-	-	-
Egg plant	+25.1 NS	129 NS	-3.1 NS	78 NS	+59.9 **	187 **
Ryegrass	+14.7 NS	86 NS	-13.4 NS	98 NS	-39.2 **	92 NS
Control	+18.3 NS	100	-	-	-	-
Potato	-7.0 NS	96 NS	+20.3 NS	112 NS	+50.5 **	129 NS
Tomato	-17.5 NS	104 NS	-8.3 NS	110 NS	-44.2 *	111 NS
Control	+19.6 NS	100	-	-	-	-
Potato (tuber)	+39.2 *	128 NS	+35.8 NS	103 NS	-2.7 NS	86 NS
Silver beet	-16.8 NS	90 NS	-8.4 NS	89 NS	-49.3 **	78 NS
Control	+5.9 NS	100	-	-	-	-
Bean	-3.9 NS	128 NS	-41.8 NS	67 NS	-66.1 *	74 NS
Radish	-17.7 NS	120 NS	-19.1 NS	63 NS	-45.4 **	85 NS
Control	+1.5 NS	100	-	-	-	-

Table 15. Summary of effects of expressed plant juices on oviposition compared with effects of solvent extracts

Plant species	Effect on oviposition			
	Expressed plant juices	Surface extraction pet. ether	Surface extraction chloroform	Total extraction methanol
Potato (foliage)	++	0	0	++
Potato (tuber)	0	+	0	0
Egg plant	++	0	0	++
Tobacco	0	++	-	0
Tomato	--	0	0	-
Silver beet	--	0	0	--
Bean	--	0	0	-
Pea	--	0	0	0
Radish	-	0	0	--
Ryegrass	-	0	0	-

\+ stimulative

++ strongly stimulative

0 neutral

\- deterrent

-- strongly deterrent

Chapter V

FACTORS AFFECTING FECUNDITY

Although Potato Tuber Moth lays its eggs freely in the absence of plant material, this does not preclude the possibility of host plants having some influence on fecundity. There are several reports of the fecundity of other insects being stimulated by the presence of their host plants though they are not essential for oviposition (Hillyer 1965, Deseö 1969, Hillyer and Thorsteinson 1969). This possibility has been examined for Potato Tuber Moth by exposing adult moths to potato tuber material in various ways throughout their life span.

It was found earlier (see Chapter IV, Part 1) that fecundity of moths provided with sucrose solution was not significantly correlated with pupal weight, at least in the absence of host plant material. A partial explanation of this may be the fact that the number of mature eggs in the ovaries at emergence is insufficient to account for total eggs laid so that further maturation of eggs must take place during adult life. Availability of food to adult moths is thus likely to affect fecundity (as reported by Labeyrie 1957 and Abul-Nasr *et al.* 1971), and to obscure any relationship of fecundity to pupal weight. As a consequence, fecundity may be more closely correlated to pupal weight when moths are starved. These possibilities have been examined as part of the present study.

Anaesthetization with carbon dioxide has been reported to reduce longevity, mating and fecundity of some insects (Whisenant and Brady 1965, White *et al.* 1969, Hooper 1970, Perron *et al.* 1972, Henneberry and Kishaba 1976). As CO_2 anaesthetization has been used to permit handling and sexing of moths in virtually all experiments reported here, an experiment was conducted to determine the effect on fecundity and longevity of Potato Tuber Moth.

1. EFFECT OF ANAESTHETIZATION WITH CARBON DIOXIDE

MATERIALS AND METHODS

Pupae were dissected free from their silken cocoon and either placed singly into small stoppered tubes (in the case of moths to be anaesthetized with CO_2) or sexed and placed in pairs directly into experimental containers for emergence (no CO_2 treatment). Both groups of pupae were held at 25°C until adult emergence.

Experimental containers were wide mouthed, 110 ml glass jars with a hole cut in the side near the base to allow a length of cotton dental roll to be inserted. The mouth of each jar was closed with two layers of cotton muslin held in place with a rubber band. A disc of 4.25 cm filter paper was sandwiched between the layers of muslin.

Pupae were checked daily for emergence and moths from small tubes anaesthetized with CO_2 and transferred in pairs to the experimental containers. Moths from pupae placed directly into the containers, were utilized only when male and female emerged within 48 h of each other. Otherwise they were discarded. 40 pairs for each treatment were initially set up in this way. If any pair failed to produce eggs during the lifespan of the female, additional pairs were set up until a total of 40 egg laying females was obtained.

During the course of the experiment the cotton dental rolls were moistened daily with distilled water and the muslin and filter paper renewed every other day, until death of the female in the container concerned. Lifespan of females was recorded to the nearest day. The experiment was conducted in darkness at 25°C.

RESULTS AND DISCUSSION

Out of 40 pairs of moths subjected to CO_2 anaesthetization, one pair failed to produce eggs compared to two pairs for moths not anaesthetized. The mean fecundity of moths subjected to CO_2 was 144.05 ± S.E. 11.74 and mean lifespan of females 11.6 ± 0.4 days, compared to 137.85 ± 10.35 and mean lifespan of 12.4 ± 0.6 days for those not anaesthetized. There was thus no detectable effect from CO_2 anaesthetization. Compared to other insects for which detrimental effects have been reported, Potato Tuber Moth may be less sensitive or the period of anaesthesia may have been much shorter (about 5 minutes) than that employed by other workers (up to 30 minutes).

2. INFLUENCE OF ADULT FOOD, PUPAL WEIGHT AND HOST PLANT TISSUE ON FECUNDITY

Two types of experiments were undertaken. In experiment (1) moths of varying pupal weight were exposed to portions of cut potato peel and either starved, fed water or fed 5% sucrose solution, and compared to similar groups of moths without exposure to potato peel. In experiments (2) and (3) moths were continually exposed to whole potato tubers and compared to moths without such treatment.

MATERIALS AND METHODS

Experiment (1). Influence of pupal weight, adult food and potato peel on fecundity

Pupae were dissected free from their cocoons and weighed individually to the nearest 0.01 mg. They were then placed separately into small glass tubes, held at 25°C and checked daily until emergence. As moths emerged, they were placed in pairs of each sex into experimental containers; pairs were allocated to treatments in rotation.

Experimental containers were wide mouthed, 110 ml glass jars closed by a double layer of cotton muslin as described for the experiment on effect of CO_2 anaesthetization on fecundity. Water or sugar solution (5% sucrose) was provided on a length of cotton dental roll inserted through the side of the jar. For treatments in which moths were exposed to potato tuber material, slivers of potato peel were placed between the layers of muslin. The filter paper, muslin, and potato peel were renewed every other day until the female moth died. The following treatments were established:

No potato peel	Potato peel
(a) moths not fed	(d) moths not fed
(b) moths fed distilled water	(e) moths fed distilled water
(c) moths fed sucrose solution	(f) moths fed sucrose solution.

40 pairs of moths were set up initially under each treatment. Since a few females in each treatment failed to produce eggs, additional containers were set up until 40 egg producing females were obtained. All calculations were based on these 40 fertile pairs. Containers were kept in darkness at 25°C. Humidity was not controlled. Treatments involving potato peel were kept in a separate temperature cabinet from those without peel.

Experiments (2) and (3). Influence of whole potato tubers on fecundity

In these experiments moths were continually exposed to intact potato tubers throughout their life span, rather than to pieces of potato peel renewed every other day. The experimental containers were 500 g glass preserving jars closed with a glass petri dish. 5% sucrose solution was provided in all treatments in a small glass vial into which cotton dental rolls were inserted.

Treatments provided the following conditions:

(a) No odour of potato tuber, no access to tuber surface (control treatment):
Cotton wool dummy covered with four layers of cotton muslin (in place of potato tuber included in other treatments).

(b) Odour of potato tuber, no access to tuber surface:
Potato tuber covered with four layers of cotton muslin.

(c) Odour of potato tuber, access to tuber surface:
Potato tuber without muslin covering.

(d) Odour of potato tuber, access to tuber surface, additional oviposition sites:
Potato tuber with approximately 25% of surface area covered with bands of cotton muslin.

Moths were placed into containers within 24 h of emergence from the pupa. They were lightly anaesthetized with CO_2 to facilitate sexing and handling. Every 2 days thereafter the potato tuber or cotton wool dummy was replaced by transferring the moths to a clean container. Dead moths were removed at the same time and the process was repeated until all females had died.

Experiment (2)

The first three treatments only, (a), (b) and (c), were included. There were 5 replications each with 5 pairs of moths per container. Dead moths were not retained for dissection.

Experiment (3)

All four treatments were included, and the number of pairs of moths per container was increased to 10. In addition to recording the number of eggs laid, all female moths were retained for dissection. Since some may have been dead for up to 48 h before they were removed, not all were suitable for dissection, but sufficient were obtained in good condition to allow the number of eggs in the ovaries to be counted. Dissection was undertaken as described in Chapter IV.

The time taken for 50% oviposition to occur (ET_{50}) was calculated for each treatment by plotting cumulative percentage eggs laid against time and reading off the value in days at the 50% point.

RESULTS

The results of Experiment (1) in which influence of pupal weight, adult food and potato peel on fecundity were examined, are summarised in Table 16 and Fig.6. Moths provided with water only, laid twice as many eggs as those starved, both in the presence and absence of potato peel. Provision of 5% sucrose solution did not significantly increase fecundity further.

The life span of female moths (females only recorded) was increased by the availability of water, compared to those starved, and further increased by the provision of sucrose solution. These differences occurred whether potato peel was present or not, and all were significant ($p < 0.01$). Starved moths (Fig.6(a) and (d)) laid their eggs more rapidly than moths provided with water or sugar solution (Fig.6(b), (c), (e) and (f)).

The presence of potato peel in this experiment did not increase fecundity or influence life span ($p = 0.05$), nor is there any indication from Fig.6 that it accelerated egg deposition.

Coefficients of linear correlation between fecundity and pupal weight are shown for each treatment in Table 16. There was a strong positive and significant correlation between fecundity and pupal weight in all treatments except for moths fed sugar solution and not exposed to potato peel.

The results of Experiment (2) are summarised in Table 17 and Fig.7. Moths continually exposed to odour of and contact with potato tubers (Treatment (c)) laid approximately 40% more eggs over their life span than moths provided with a cotton wool dummy (Treatment (a)). The same effect was produced with moths exposed to the odour of potato tuber but prevented from coming in contact with it (Treatment (b)). These differences were statistically significant ($P < 0.05$).

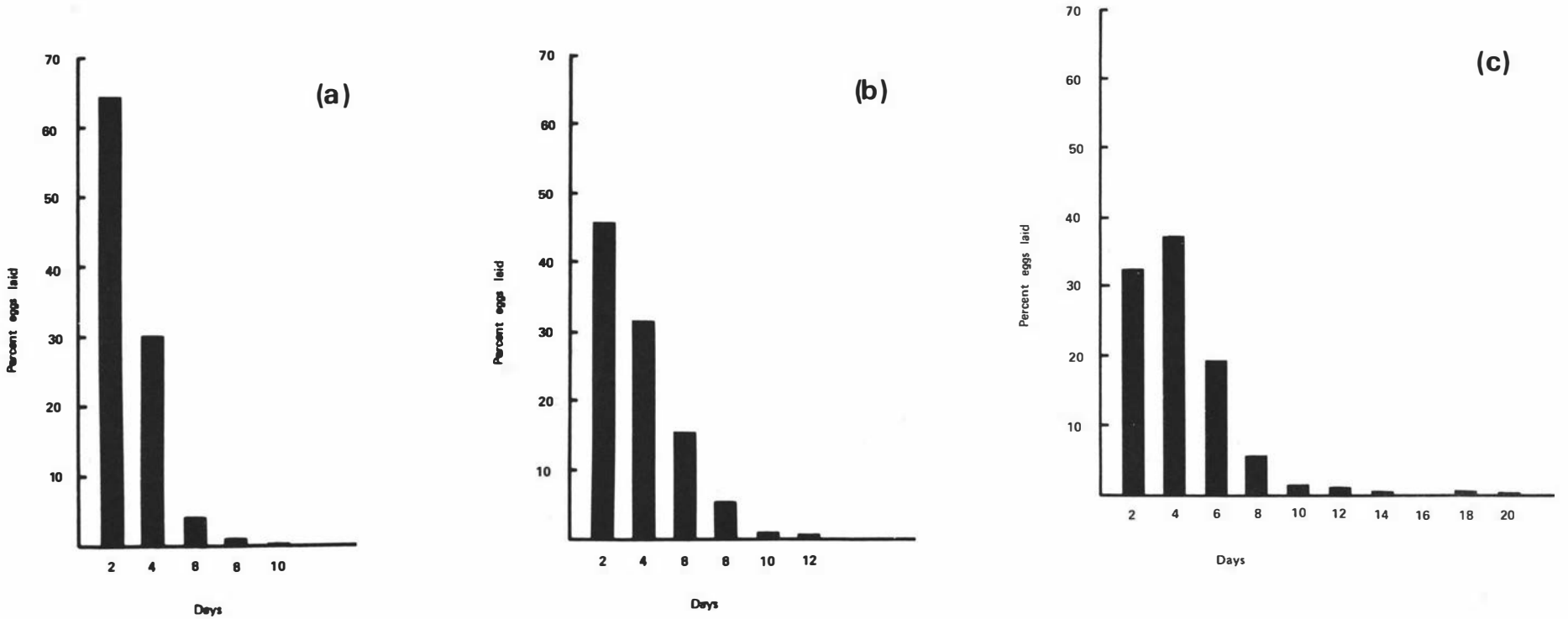


Fig. 6. Patterns of egg laying for Exp. (1):
(a) No potato peel. Moths starved. ET_{50} = 1.6 days.
(b) No potato peel. Moths fed distilled water. ET_{50} = 2.2 days.
(c) No potato peel. Moths fed 5% sucrose solution. ET_{50} = 2.9 days.

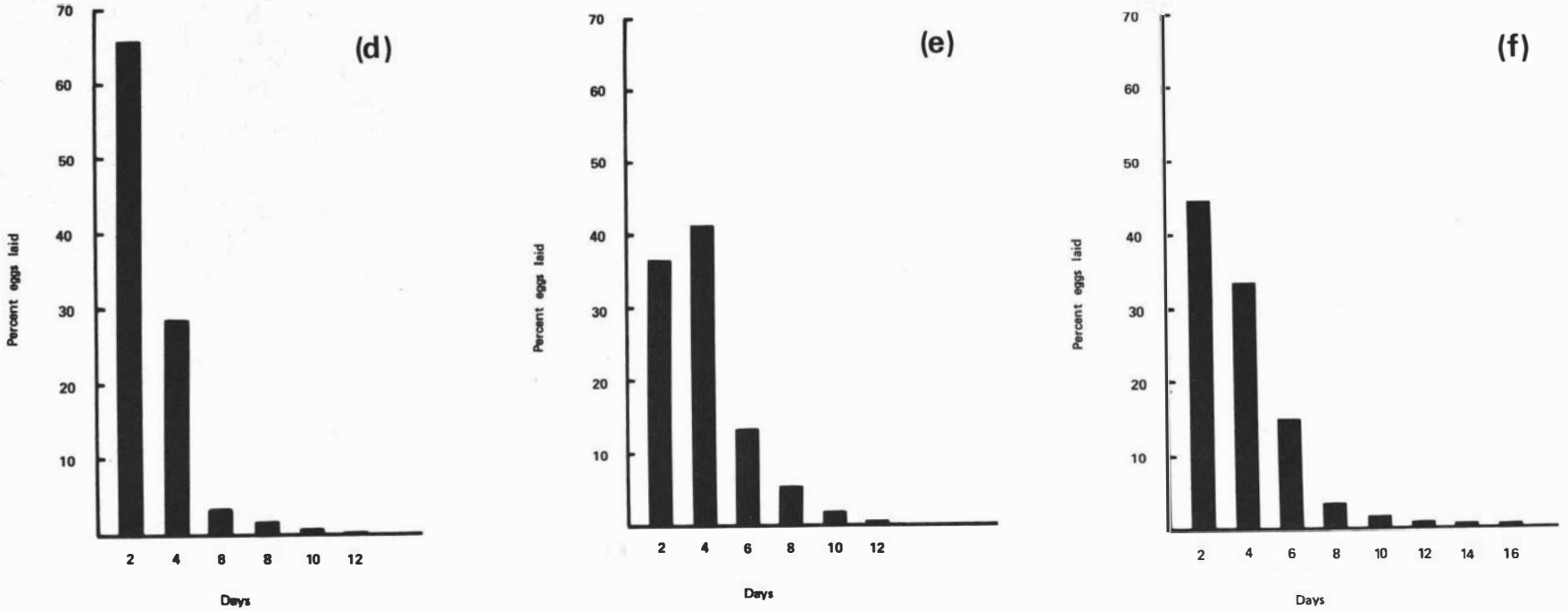


Fig. 6. (d) Potato peel. Moths starved. ET_{50} = 1.5 days.
(e) Potato peel. Moths fed distilled water.
ET_{50} = 2.6 days.
(f) Potato peel. Moths fed 5% sucrose solution.
ET_{50} = 2.3 days.

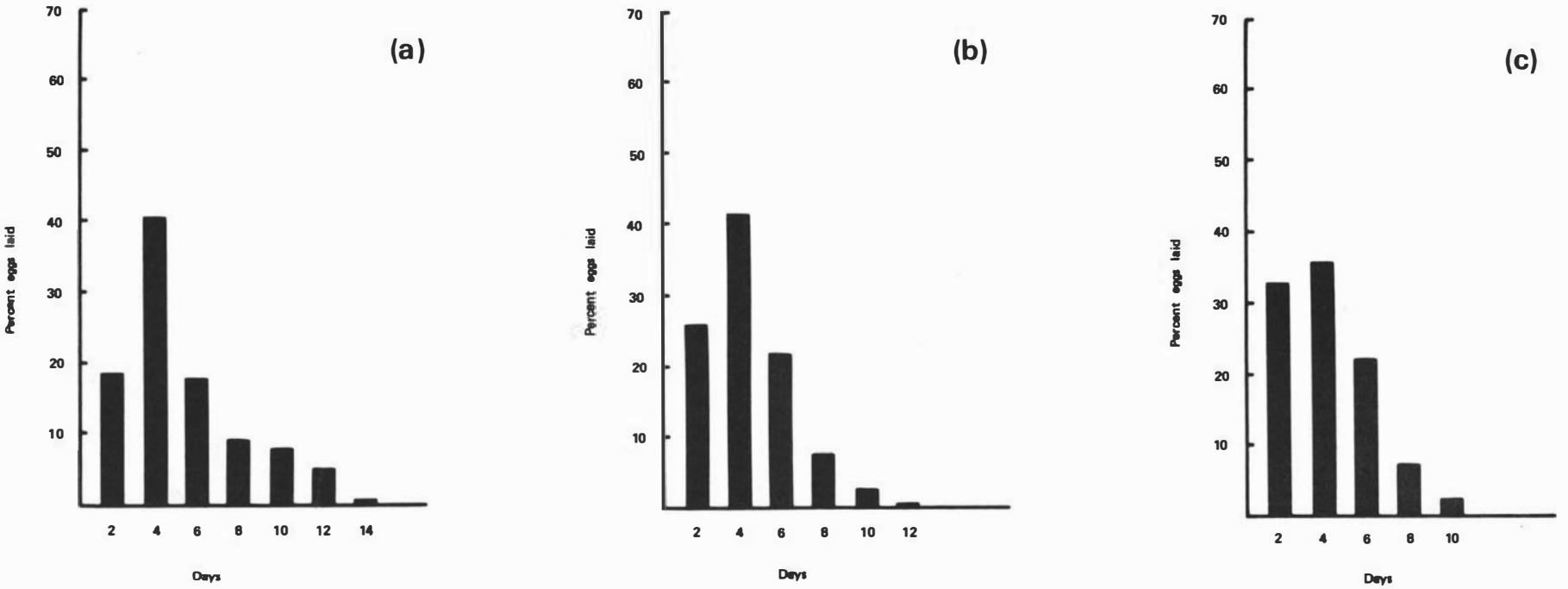


Fig. 7. Patterns of egg laying for Exp. (2).
(a) No access to potato tuber. No odour.
ET_{50} = 3.4 days.
(b) No access to potato tuber. Odour. ET_{50} = 3.1 days.
(c) Access to potato tuber. Odour. ET_{50} = 3.0 days.

Time to 50% oviposition (ET_{50}) was not significantly reduced by exposure to odour of or contact with potato tubers. Life span was similar for all groups of moths.

The results of Experiment (3), in which the number of moths was doubled compared to Experiment (2), are summarised in Table 18 and Fig.8. Treatment (d), which exposed moths to the odour of potato tubers, allowed access to their surface and provided additional oviposition sites, resulted in twice as many eggs compared to a cotton wool dummy (Treatment (a)). Access to bare tubers, and odour of tubers without access, gave intermediate effects (Treatments (c) and (b) respectively). The significance of differences between treatments is indicated in Table 18. In addition, exposure to odour of potato tubers, and contact with them (Treatments (c) and (d)) resulted in significantly accelerated deposition of eggs ($P < 0.05$) compared to no odour and no access (Treatment (a)) (ET_{50}s of 3.7 and 3.4 days cf. 5.7 days).

Dissection of female moths at death showed that those exposed to a cotton wool dummy had about three times as many developed eggs in the ovaries (mean 25.9) as those exposed to potato tubers in the other three treatments (means 7.3 - 9.3). Similarly, the proportion at death of females with less than 8 mature eggs (1 per ovariole) was only 40% for the cotton wool dummy treatment, compared to 62 - 73% for the other treatments.

DISCUSSION

Although a few females out of the initial 40 pairs set up under each treatment in Experiment (1) failed to lay eggs (maximum 4), it is clear that mating is not dependent on the presence of host plant material. Whether such infertility was due to failure to mate or to male or female sterility was not determined.

As the complement of fully developed eggs in the ovaries at eclosion from the pupa was previously found to be 68.7 ± S.E. 4.1 (see Chapter IV Part 1), most eggs laid by starved moths in the present experiment (83.8 ± 3.8) were produced without much post-eclosion egg

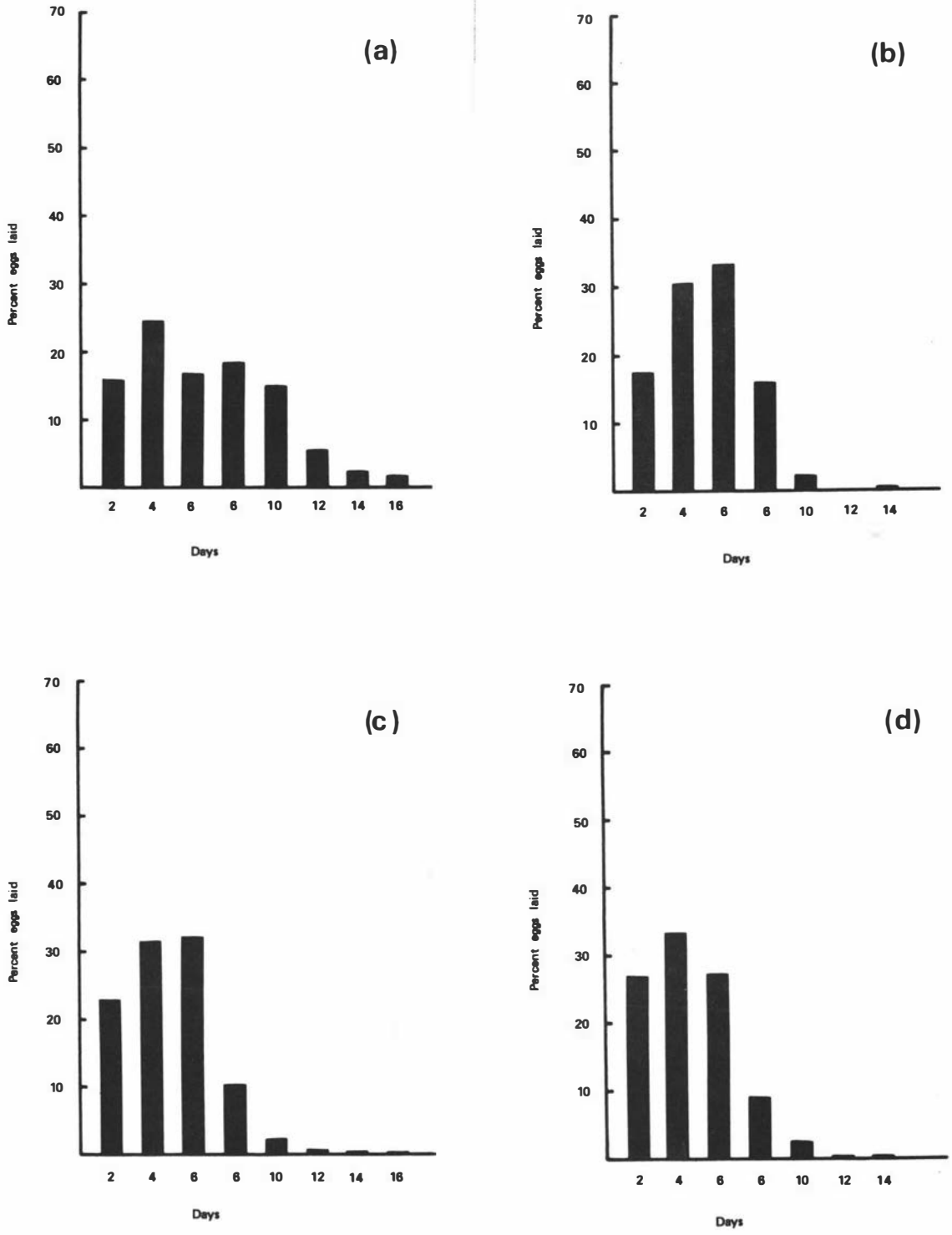


Fig. 8. Patterns of egg laying for Exp. (3):
(a) No access to potato tuber. No odour. ET_{50} = 5.7 days.
(b) No access to potato tuber. Odour. ET_{50} = 4.2 days.
(c) Access to potato tuber. Odour. ET_{50} = 3.4 days.
(d) Access to potato tuber. Odour. Plus additional oviposition sites. ET_{50} = 3.7 days.

egg development taking place. The provision of water almost doubled fecundity and Labeyrie (1957) reported a similar effect. However, in the present experiment, provision of 5% sucrose solution rather than water alone did not significantly increase fecundity further. This differs from Labeyrie's (1957) finding that honey solution caused a substantial increase in egg production compared to water alone. It may be concluded that access to water allows mobilisation of food reserves not available to starved moths, but that maximum fecundity requires additional nutrients provided by honey but not by sucrose alone.

In starved moths and those allowed access to water only, fecundity was positively correlated with pupal weight, but as reported in Chapter IV, moths fed sugar solution showed no such correlation in the absence of potato tuber material. However, when potato peel was present there was a positive correlation between fecundity and pupal weight. The reason for this is not apparent, since fecundity was not increased by this treatment in the present experiment.

Although pieces of potato peel did not increase fecundity in Experiment (1), the results of Experiments (2) and (3) show that exposure of moths to whole potato tubers did have a significant positive effect on fecundity. This difference in response could be due to a quantitative effect brought about by the greater bulk and continued presence of tuber material, or to a qualitative effect of biochemical changes in cut portions of peel. The stimulative effect of potato tubers appears to be primarily one of odour but may be additionally enhanced by contact.

It is concluded that although potato tuber moth will lay eggs freely in the absence of host plant material, maximum fecundity is achieved only in the presence of host plant tissue, when suitably textured oviposition substrates are available, and when moths have access to water.

Table 16. Influence of adult food and potato peel on fecundity and lifespan and relationship of fecundity to pupal weight

	Treatment	Number of infertile pairs/40	Mean total eggs laid ± S.E. (n = 40)	Significance of difference	Coefficient of linear correlation total eggs laid against pupal weight	Mean life span (females only) in days ± S.E.	Significance of difference
No potato peel				P < 0.01			P < 0.01
	Not fed	3	77.12 ± 5.02	B	0.423 **	9.4 ± 0.5	C
	Fed water	4	154.32 ± 11.26	A	0.501 **	11.1 ± 0.4	B
	Fed 5% sucrose	2	162.45 ± 10.70	A	0.040 NS	17.9 ± 0.9	A
Potato peel	Not fed	3	90.50 ± 5.51	B	0.334 *	10.0 ± 0.4	C
	Fed water	4	156.57 ± 10.75	A	0.472 **	11.6 ± 0.3	B
	Fed 5% sucrose	2	174.50 ± 11.17	A	0.559 **	15.9 ± 0.9	A

Values sharing the same letter do not differ significantly.

NS Not significant.

* Significant P < 0.05

** Significant P < 0.01

Mean pupal weight for entire experiment (n = 240) - 11.74 mg ± S.E. 0.12 (range 5.92 - 16.85).

Table 17. Influence of whole potato tubers on fecundity. Results of Experiment (2)

	Treatment	Mean total eggs laid per ♀ (n = 25)	Mean life span of females ± S.E.
(a)	No access No odour (cotton wool dummy)	75.12	9.6 ± 0.7
(b)	No access Odour of potato tuber	107.96 *	10.4 ± 0.4
(c)	Access (bare tuber) Odour	107.80 *	8.7† ± 0.6

* Significantly greater than treatment (a) ($P < 0.05$)

† Significantly less than treatment (b) ($P < 0.05$)

Table 18. Influence of whole potato tubers on fecundity. Results of Experiment (3).

Treatment	Mean total eggs laid per ♀ (n = 50)	Significance of differences* P<0.05	p<0.01	Mean number of eggs in ovaries at death	Mean total egg production†	Percentage of moths with < 8 eggs (1 per ovariole) at death	Mean life span (females only) in days ± S.E.	Significance of differences* p < 0.01
(a) No access No odour (Cotton wool dummy)	73.20	c	C	25.9 n=35	99.1	40.0	12.6 ± 0.5	A
(b) No access Odour of potato tuber	121.58	b	AB	7.3 n=40	128.9	65.8	10.5 ± 0.4	B
(c) Access Odour (Bare tuber)	104.28	b	B	7.5 n=37	111.8	62.5	10.6 ± 0.3	B
(d) Access Odour plus additional oviposition sites	141.84	a	A	9.3 n=40	149.3	73.0	10.0 ± 0.4	B

* Values sharing the same letter do not differ significantly.

† Total of eggs laid plus eggs in ovaries at death.

Chapter VI

STUDIES ON LARVAL BEHAVIOUR WITH RESPECT TO PLANT TISSUE

Eggs of Potato Tuber Moth appear normally to be laid under field conditions directly on host plants suitable for the larvae, though Traynier (1975) reported that a high proportion may be laid in soil adjacent to host plants rather than on the plants themselves. The ability of newly hatched first instar larvae to locate host plants and to distinguish between suitable and non-suitable plants may not therefore be strongly developed. There is no previous published information on this aspect. Yamamoto (1974) has produced evidence that newly hatched larvae of Tobacco Hornworm are somewhat naive with respect to food plants and will accept a wider range of species than older larvae. Yamamoto suggests that preference is largely induced according to the plant species on which the larva first fed.

If first instar larvae have to locate host plants, the distance that they can move, and their ability to survive without feeding under various conditions are also of relevance. These features have therefore been studied in preliminary experiments together with orientational response to light and moisture.

1. PRELIMINARY EXPERIMENTS

MATERIALS AND METHODS

Newly hatched (< 4 h old) first instar larvae that had not fed or had contact with plant material were used for all experiments. Individual larvae were used once only, then discarded. Experiments, unless otherwise stated, were conducted at room temperature, which ranged 20-25^{o}C, and at ambient humidity, in diffuse daylight.

Response to light

Five 5.0 cm petri dish bases were placed on a window bench out of direct sunlight. Ten first instar larvae were placed into the centre of each dish which was then closed with half of a larger petri dish. The edges of the smaller dishes had been ground to ensure a tight fit and prevent larvae escaping. After 30 minutes the number of larvae in each half of each dish was counted; either towards the window or away from it.

Response to moisture

Pieces of filter paper 2.0 x 1.0 cm were placed vertically on opposite sides of 5.0 cm petri dishes. One piece of paper in each case was moistened with a drop of distilled water. The dishes were so arranged that a line connecting the two pieces of filter paper was at right angles to light from the window. Ten larvae were placed in the centre of each dish which was then closed with half of a larger dish. The position of the larvae was assessed after 15 minutes as, on or behind the filter paper, or elsewhere.

Rate of movement

Groups of 5 first instar larvae were placed in the centre of a large sheet of white card. The distance that each travelled after 5 minutes was measured. Data for 20 larvae ~~was~~ were recorded.

Survival of 1st instar larvae at different relative humidities and temperatures

Sulphuric acid solutions were prepared to provide relative humidities of 20, 40, 50 and 80 per cent (Solomon 1951) and placed in 500 g wide mouthed jars. Larvae were confined in 5 x 1.5 cm glass tubes with perforated stoppers covered with fine organdie. Ten larvae were placed in each tube, the tubes supported above the sulphuric acid solution and the containers sealed. Each humidity treatment was run at 15, 20 and 25^{o}C. The experiment was conducted

in darkness except for daily assessment. The number of larvae live and dead in each tube was counted every 24 h until all the larvae had died. Cumulative percentage mortality was calculated for each temperature and humidity and plotted against time.

RESULTS AND DISCUSSION

Response to light

The results of this experiment are given in Table 19. In every replicate more larvae moved towards the light than away from it. Also the total figures of 38 towards and 12 away from the light are outside the 95% confidence limits of binomial distribution for 50% effect (32:18) and are thus unlikely to be due to chance. It may be concluded that 1st instar larvae showed a positive phototactic response under the experimental conditions.

Response to moisture

No larvae out of a total of 50 tested were located on the moist filter paper at the end of the test period compared to 4 on the dry samples. Details are given in Table 20. First instar larvae therefore showed no response to moisture under the experimental conditions. Moisture content of plant samples is thus unlikely to complicate behavioural responses with respect to them (see second part of this chapter).

Rate of movement

The mean distance moved by 20 larvae was 17.0 ± S.E. 1.7 cm in the test period of 5 minutes, with a range of 5.5 - 28.3 cms. Over a period of 24-48 h, which is the likely survival time without feeding (see next section) larvae could therefore travel several metres though they are unlikely to move all of the time.

Survival of 1st instar larvae at different relative humidites and temperatures

Results of this experiment are presented in the form of mortality curves in Fig. 9. The curves are steep in all cases (less so for 15°C) so that once larvae started to die under one set of conditions the remainder in that group rapidly died also. At 20° and 25° larvae were continually active so the cause of death may have been depletion of energy stores and thus differences in humidity made little difference to the pattern of mortality. At 15° however, larvae were inactive (they had to be warmed to 20-25° before assessments could be made) and at this temperature mortality increased with decreasing humidity. In this case dehydration may have been the major mortality factor.

2. BEHAVIOUR OF 1st INSTAR LARVAE IN THE PRESENCE OF PLANT MATERIAL

Experiments were conducted to determine the ability of newly hatched 1st instar larvae to locate plant tissue when released in close proximity to it and to distinguish between host and non-host plants.

MATERIALS AND METHODS

Newly hatched 1st instar larvae were used for all experiments as described in the previous section. All experiments were conducted in diffuse daylight at 20-25°C.

(a) Response of 1st instar larvae to portions of plant tissue and to solvent extracts of plant tissue

5.0 cm petri dishes were set up with a 2.0 x 1.0 cm piece of plant leaf or other tissue vertically on one side and a similar sized piece of moist filter paper on the opposite side. Similar tests were run with solvent extracts of plant tissue (see Chapter IV, section 4) from some plant species, applied to pieces of filter paper.

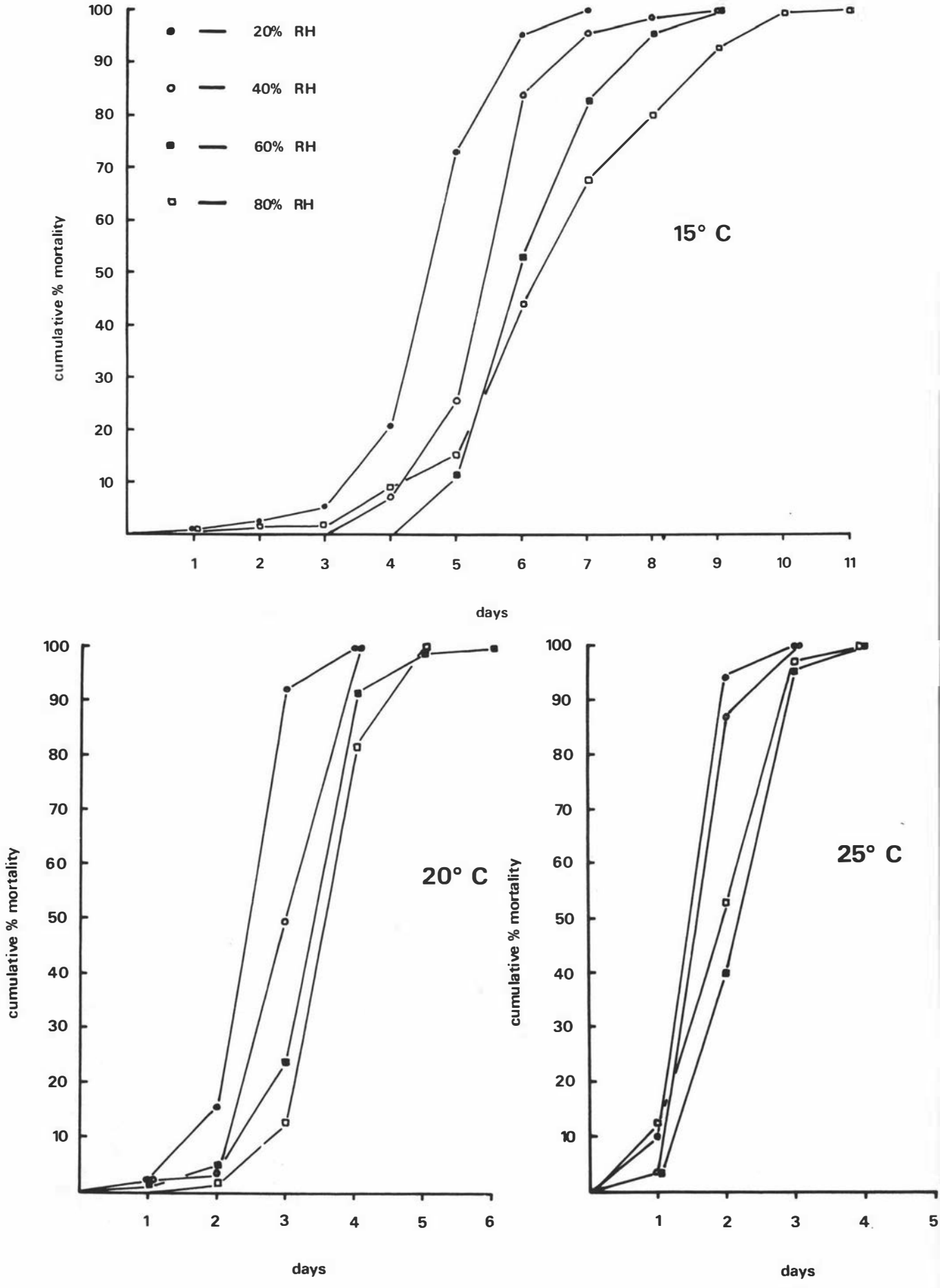


Fig. 9. Mortality of starved lst instar larvae at various temperatures and humidities.

The solvent was allowed to evaporate completely from the samples before tests were set up. Blank samples were treated with the appropriate solvent.

To determine whether a visual component was of importance in larvae locating plant samples, tests were run with several plants in which the samples were placed vertically against the outside of the dish, rather than in a corresponding position inside. Such tests were also conducted with solvent extracts of these plants.

The dishes were arranged with respect to window light as described for tests on response to moisture. Ten first instar larvae were introduced into the centre of each dish which was then closed with half of a larger petri dish. The position of the larvae was counted after 5, 10, 15 and 30 minutes as - on plant sample, on filter paper, or elsewhere.

In the case of samples outside the dish, larvae were counted as "on" the sample if they were located adjacent to it inside the dish. Each test was repeated ten times.

(b) Tests to determine direction of initial movement of larvae

Three plant species that showed strong positive (potato, egg plant and tobacco) and two that showed strong negative effects (bean and radish) in test (a) were evaluated to determine the direction of initial movement of individual larvae when released at measured distances from test samples. The test arena was a 5.0 cm petri dish set up as described in (a) above.

The dishes were placed on paper on which concentric rings at 1 cm spacing had been drawn centred on the position of the test sample. Individual larvae were tested by releasing them at a set distance (1, 2, or 3 cm) from the test sample, closing the dish immediately, then observing whether the larva moved towards or away from the sample during its first 1 cm of movement. Its position after 5 minutes was also recorded. Fifty larvae were tested at each of the three distances for each plant species.

(c) Olfactometer tests

A simple Y-tube olfactometer was constructed from glass tubing of I.D. 0.6 cm as shown in Fig. 10. Air movement through the apparatus was provided by means of a 5 L aspirator. Flow rate was adjusted to give an air speed of approximately 4 cm/sec through the stem of the Y-tube. Preliminary experimentation showed that if the Y-tube was orientated with the arms towards the window, larvae moved phototactically from the stem into the extremities of the arms. In initial tests counts of the position of larvae were made every 10 minutes over one hour. Forty minutes was chosen as a suitable time to run a test.

Batches of 10 larvae were used for each test. If less than 6 larvae responded, i.e. failed to move out of the stem of the Y-tube, the results were discarded. Tests were continued with each plant species until a minimum of 50 responding larvae had been recorded.

RESULTS

The results of tests to determine the response of first instar larvae to portions of plant material when samples were presented inside the dish are given in Table 21 and results of similar tests with solvent extracts of some plants in Table 22. The results of tests with samples of plant material and of solvent extracts presented outside the dish are given in Table 23.

Results of tests to determine initial direction of movement of larvae with respect to potato, tobacco, egg plant, bean and radish leaves are summarized in Table 24, and of olfactometer tests in Table 25.

DISCUSSION

In tests with portions of plant material placed inside 5.0 cm petri dishes, most larvae located samples of known "good" host plants (potato, egg plant, tobacco - see Table 9) after 15 minutes.

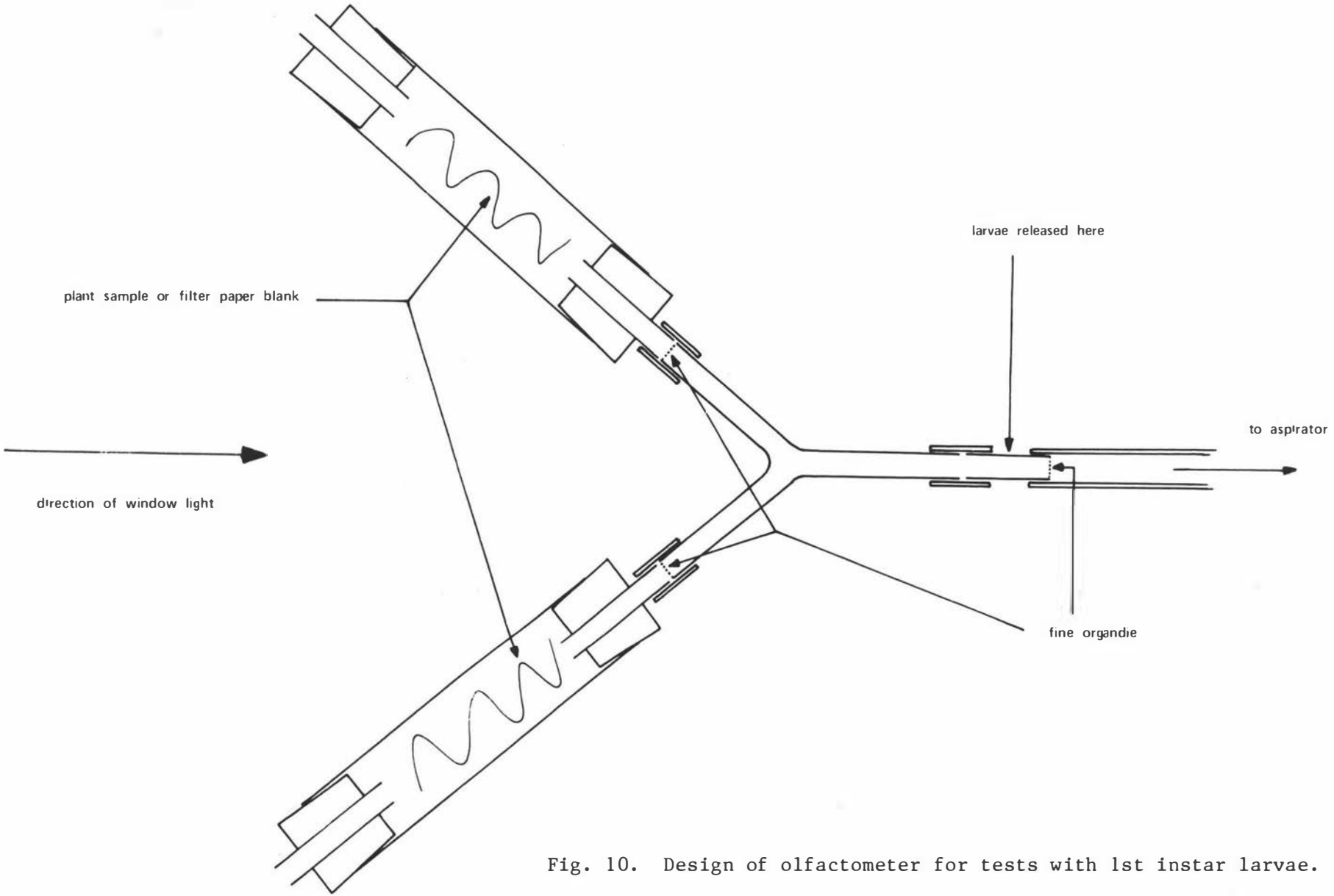


Fig. 10. Design of olfactometer for tests with 1st instar larvae.

The numbers increased only slightly more after 30 minutes. With potato, similar results were obtained with leaf, peel and stem surface samples. Tobacco gave highest effect with 100 per cent of the larvae on the samples after 15 minutes. Larvae showed only moderate interest in tomato, with little over 50 per cent on the samples after 30 minutes. Most known non-host plants were clearly of no interest, though in all cases more larvae were recorded on plant samples than on the blanks (moist filter paper).

In some cases (e.g. beet and ryegrass) the numbers of larvae on the samples progressively decreased from 5 to 30 minutes. Two exceptions to non-positive results for known non-host plants were pea and ryegrass where appreciable percentages of larvae were recorded on the samples.

When similar tests were run with leaf samples placed outside the dish, positive results were still obtained with the two host plants tested (egg plant and tobacco) but at a lower level compared to samples inside the dish. The two non-host plants tested (bean and radish), also gave positive results outside the dish which in this case were greater than when samples of the same plants were tested inside the dish. These results suggest that there is a visual component in larval location of plant material and that the non-host plants bean and radish may possess chemically repellent properties which are rendered inoperative when samples are placed outside the dish.

Solvent extraction of leaves of egg plant and of tobacco by surface washing with petroleum ether or chloroform was not effective in extracting the factors responsible for aggregation of larvae except for chloroform treatment of tobacco which was slightly active. Maceration and extraction with methanol produced active extracts in all cases including bean and radish. Repellent properties of whole leaf of the latter two plants may thus have been lost in the extraction and sample concentration procedures.

Solvent extracts were normally tested on dry filter paper after the solvent had evaporated. Moistening of the paper so treated slightly increased the effectiveness of the tobacco leaf sample, the only one evaluated in this way.

Solvent extracts showed slight activity when applied to filter paper samples placed outside the dishes, but in all cases the effect was considerably less than for corresponding whole leaf samples. There thus appears to be some spectral property of whole leaf which is not adequately reproduced when the leaf pigments are extracted (apparently completely, as the residue was almost colourless in each case) and deposited onto filter paper.

The results of the above tests gave no indication whether larvae which congregated on plant samples were attracted from a distance, or whether location occurred by chance following random movement though there is some suggestion that they may be repelled by non-host plants. Test (b), which recorded direction of initial movement following release at set distances and (c) olfactometer tests, were designed to provide information on this point. There was slight evidence in some cases (potato peel, tobacco) that more larvae moved towards host plant samples from closer distances than wider ones but in only two instances (potato stem and tobacco foliage each at 1 cm) did results exceed the limits of probability expected by chance. Similarly, there was no evidence of movement away from the two non-host plants tested (bean and radish) when larvae were released at 1 cm distance.

Olfactometer tests also gave no evidence of attraction to host plants but a slight degree of repellency was exhibited by the three non-host plants tested, though only when the leaves were crushed in the case of bean and radish. Beet gave an anomalous result in that intact leaf was somewhat repellent but showed no effect when crushed. Strongly repellent samples would presumably have rendered olfactometer tests inoperative if they prevented larval movement from the stem of the Y into the arms.

There is no substantial evidence from this evaluation to indicate that first instar larvae are attracted to host plant tissue. Location appears to be primarily by random movement, which is vigorous immediately after hatching, and chance location, though repellency by non-host plants could be an additional factor. In addition, acceptable plants must possess some arrestant factor which unacceptable

plants do not, so that larvae remain after contact with them but continue movement after encounter with unacceptable species.

3. FEEDING ACCEPTANCE OF PLANT SPECIES

The tests described in Part 2 of this chapter provided information only on larval movement with respect to host and non-host plant tissue. They did not determine whether feeding took place. For this purpose a test of longer duration (48 h) was required. The main question to be answered was whether newly hatched first instar larvae inherit the ability to discriminate between plant species or whether they are naive in this respect.

MATERIALS AND METHODS

Various methods of confining first instar larvae with portions of plant leaf were tried, e.g. discs of leaf in glass vials, but were discarded as unsatisfactory, either because the plant material dried out too rapidly or because of excessive condensation in which larvae tended to drown. The following technique was finally adopted.

One per cent agar was poured to a depth of 3-4 mm in plastic petri-dishes. When set, four discs per dish were removed from this with an 18 mm cork borer. Similar sized discs or portions of leaf material were placed into the holes so formed. Five first instar larvae were placed onto each portion of leaf which was then capped with a slightly larger celluloid ring covered with fine organdie to prevent the larvae escaping. The entire dish was then closed with the lid which was perforated with four small holes to provide additional ventilation. The dishes were held in darkness for 48 h at 25°C. Plant samples prepared in this way retained turgidity and generally did not discolour.

Assessments were made at 2, 24 and 48 h. At each of these intervals, the number of larvae feeding (tunnelling within the leaf and showing feeding movements) was recorded by examination of the unopened dish through the base using sub-stage illumination with a stereo zoom microscope. In addition, at 48 h, when the test was concluded, the number of larvae dead on each leaf disc was counted and an eye estimate made of the percentage leaf area consumed. Tests were conducted with all of the plant species evaluated for behavioural response of larvae and also with a number of other Solanaceous and non-Solanaceous plants. 50 larvae were tested with each species.

RESULTS AND DISCUSSION

The results of feeding tests with first instar larvae are given in Table 26. On "good" host plants (potato, tobacco, egg plant) larvae started feeding rapidly (most within 2 h and > 90% by 24 h). The odd result that fewer were feeding on these species after 48 h, was because some larvae had started to moult to second instar by this time and had become quiescent. Of the other Solanaceous plants tested, tomato and nightshade were poorly accepted, Schizanthus very poorly and Petunia not at all. Salpiglossis (not previously recorded as a host plant) was well accepted.

Among the plant families Convolvulaceae and Scrophulariaceae, which are classified by Rendle (1925) and Manning (1965) as those closest to the Solanaceae, one genus of Convolulaceae (Ipomea) was moderately well accepted, but the other genera tested hardly at all. With the more distantly related plants from a variety of families, all were virtually rejected with the exception of pea on which 20 out of 50 larvae fed.

The amount of leaf material eaten after 48 h was in proportion to the number of larvae feeding and reached 15-20% for the most favourable plants. A small amount of leaf material was consumed in almost every case, though feeding did not continue, as though larvae

had to take test bites to determine whether the plant was acceptable or not.

On favourable plant species, nil or negligible mortality of larvae occurred during the test period but with increasing unacceptability of plant species, mortality increased. The degree of mortality on unacceptable species was comparable to that obtained under starvation conditions (see Part (1) of this Chapter) so lack of food was probably the main mortality factor rather than toxicity.

It is clear from these results that first instar larvae hatch with the inherited ability to distinguish between host and non-host plants, though the partial acceptance of pea is an anomaly. The results of feeding acceptance (Table 26) correlate well with the results of the plant location tests given in Table 21, including the anomalous performance of pea as a non-host plant.

Table 19. Response of 1st instar larvae to light

	Position after 30 minutes	
Replication	Window side	Room side
1	7	3
2	8	2
3	6	4
4	9	1
5	8	2
TOTAL	38	12

Table 20. Response of 1st instar larvae to moisture

	Position after 15 minutes		
Replication	Dry sample	Moist sample	Elsewhere
1	1	0	9
2	1	0	9
3	1	0	9
4	0	0	10
5	1	0	9
TOTAL	4	0	46

Table 21. Response of 1st instar larvae to portions of plant tissue - samples inside dish

Plant material	Elapsed time (minutes)	Number of larvae in each position (100 larvae tested) Sample	Blank	Elsewhere
Potato (leaf)	5	56	0	44
	10	69	0	31
	15	80	0	20
	30	86	0	14
Potato (peel)	5	65	1	34
	10	78	0	22
	15	84	0	16
	30	90	0	10
Potato (stem surface)	5	64	3	33
	10	80	1	19
	15	87	1	12
	30	90	1	9
Egg plant	5	68	2	30
	10	83	1	16
	15	87	0	13
	30	94	0	6
Tobacco	5	97	0	3
	10	98	0	2
	15	100	0	0
	30	100	0	0
Tomato	5	54	2	44
	10	59	1	40
	15	57	1	42
	30	55	0	45

continued/...

Table 21 (continued)

Plant material	Elapsed time (minutes)	Number of larvae in each position (100 larvae tested)		
		Sample	Blank	Elsewhere
Beet	5	33	1	66
	10	28	0	72
	15	22	0	78
	30	19	2	79
Bean	5	13	0	87
	10	6	0	94
	15	7	2	91
	30	6	1	93
Pea	5	54	2	44
	10	56	1	43
	15	63	0	37
	30	43	0	57
Radish	5	4	0	96
	10	10	0	90
	15	5	1	94
	30	5	0	95
Ryegrass	5	40	3	57
	10	35	1	64
	15	35	2	63
	30	27	1	72

Table 22. Response of 1st instar larvae to solvent extracts* of plant tissue applied to filter paper - samples inside dish

Sample	Elapsed time (minutes)	Number of larvae in each position (100 larvae tested) Sample	Blank	Elsewhere
Egg plant	5	1	3	96
surface extract	10	2	7	91
pet. ether	15	4	9	87
	30	4	4	92
Egg plant	5	4	9	87
surface extract	10	6	9	85
chloroform	15	12	9	79
	30	6	14	80
Egg plant	5	26	4	70
total extract	10	28	2	70
methanol	15	30	4	66
	30	26	4	72
Tobacco	5	4	9	87
surface extract	10	8	9	83
pet. ether	15	2	13	85
	30	4	6	90
Tobacco	5	20	11	69
surface extract	10	22	8	70
chloroform	15	24	9	67
	30	29	6	65
Tobacco	5	42	1	57
total extract	10	48	2	50
methanol	15	43	0	57
	30	43	2	55

continued/...

* For details of preparation of extracts see Chapter IV, Section 4.

Table 22 (continued)

Sample	Elapsed time (minutes)	Number of larvae in each position (100 larvae tested)		
		Sample	Blank	Elsewhere
Tobacco	5	42	0	58
total extract	10	50	1	49
methanol (sample	15	54	0	46
moistened with water)	30	62	0	38
Bean	5	30	5	65
total extract	10	16	1	83
methanol	15	19	5	76
	30	16	2	82
Radish	5	19	2	79
total extract	10	24	3	73
methanol	15	25	5	70
	30	23	4	73

Table 23. Response of 1st instar larvae to portions of plant tissue and to solvent extracts (methanol) applied to filter paper - samples outside dish

Sample	Elapsed time (minutes)	Number of larvae in each position (100 larvae tested)		
		Sample	Blank	Elsewhere
Egg plant leaf	5	33	1	66
	10	35	3	62
	15	35	2	63
	30	33	2	65
Egg plant leaf	5	5	4	91
methanol extract	10	5	2	93
	15	12	1	87
	30	7	3	90
Tobacco leaf	5	37	4	59
	10	29	1	70
	15	27	3	70
	30	25	0	75
Tobacco leaf	5	18	4	78
methanol extract	10	19	1	80
	15	21	2	77
	30	15	2	83
Bean leaf	5	20	1	79
	10	23	0	77
	15	21	3	76
	30	12	1	87
Bean leaf	5	8	0	92
methanol extract	10	15	1	84
	15	12	2	86
	30	10	1	89

continued/...

Table 23 (continued)

Sample	Elapsed time (minutes)	Number of larvae in each position (100 larvae tested)		
		Sample	Blank	Elsewhere
Radish leaf	5	18	4	78
	10	36	1	63
	15	34	1	65
	30	31	0	69
Radish leaf methanol extract	5	7	3	90
	10	9	2	89
	15	15	0	85
	30	11	1	88

Table 24. Results of tests to determine direction of initial movement of larvae with respect to plant tissue - samples inside dish

	Distance of release from plant sample	Direction of initial movement with respect to plant sample		Number of larvae in each position after 5 minutes. (50 larvae tested)		
	cm	Towards	Away from	Sample	Blank	Elsewhere
Potato	1	26	24	33	0	17
(leaf)	2	16	34	17	4	29
	3	22	28	22	5	23
Potato	1	29	21	26	0	24
(peel)	2	23	27	13	0	37
	3	17	33	12	0	38
Potato	1	38	12	34	0	16
(stem)	2	24	26	32	0	18
	3	28	22	33	0	17
Egg plant	1	28	22	39	3	8
	2	19	31	30	2	18
	3	20	30	27	4	19
Tobacco	1	37	13	47	0	3
	2	31	19	34	5	11
	3	22	28	40	0	10
Bean	1*	27	23	11	1	38
Radish	1*	26	24	13	1	36

95% confidence limits for 50% effect on sample size 50=32:18 (binomial distribution)

* Only distance tested.

Table 25. Results of olfactometer tests with first instar larvae

	Number of larvae in each arm after 40 minutes (percentages in brackets)	
	Sample	Blank
Potato (leaf) - intact	29 (47)	33 (53)
- crushed	23 (40)	35 (60)
Potato (peel)	30 (59)	21 (41)
Tobacco - intact	32 (50)	32 (50)
- crushed	24 (45)	29 (55)
Beet - intact	*13 (25)	39 (75)
- crushed	26 (52)	24 (48)
Bean - intact	29 (46)	34 (54)
- crushed	*18 (30)	42 (70)
Radish - intact	28 (52)	26 (48)
- crushed	*16 (28)	41 (72)
Control (filter paper v. filter paper)	51 (55)	42 (45)
95% confidence limits for 50% effect on sample size 50 (binomial distribution)	(36)	(64)
size 100	(40)	(60)

* Outside 95% confidence limits.

Table 26. Acceptance for feeding of various plant species by newly hatched first instar larvae

Plant species	Number of larvae feeding/50			Number of larvae dead/50 at 48 h	Mean % leaf consumed at 48 h
	2 h	24 h	48 h		
Solanaceae					
Solanum tuberosum (potato)	44	50	41	0	19
S. melongena (egg plant)	43	47	39	0	19
Nicotiana tabacum (tobacco)	31	45	43	2	14
Lycopersicon esculentum (tomato)	6	17	22	14	5
Solanum nigrum complex (Nightshade)	5	17	12	16	< 5
Petunia sp.	0	0	3	22	< 5
Salpiglossis sp.	23	41	43	0	6
Schizanthus sp.	4	5	3	24	< 5
Convolvulaceae					
Convolvulus sp.	2	11	4	14	< 5
Ipomea sp.	26	33	13	9	< 5
Scrophulariaceae					
Antirrhimum sp.	0	1	2	6	< 5
Nemesia sp.	1	1	3	10	< 5
Linaria sp.	0	3	6	13	< 5
Other					
Beta vulgaris (beet)	0	0	2	39	< 5
Pisum sativum (pea)	5	20	19	13	5
Phaseolus vulgaris (bean)	0	0	2	38	< 5
Raphanus sativus (radish)	2	5	9	24	< 5
Lolium perenne (ryegrass)	0	1	0	29	< 5
Malus sp. (apple)	0	0	0	21	0

Chapter VII

THE RELATIVE SUSCEPTIBILITY OF POTATO CULTIVARS TO POTATO TUBER MOTH

That differences exist between cultivated varieties of potatoes as to degree of infestation by tuber moth under field conditions has been recognised for some time (Bald and Helson, 1944; Helson 1949; Abdel-Salam *et al.*, 1972; Bedi 1974), though only a few authors appear to have set out specifically to make inter-varietal comparisons (Foot 1976; Guglielmett 1978). Laboratory screening for resistance has been described only very recently (Anon. 1979). Differences between cultivars in degree of field infestation have usually been attributed to differences in the growth habit of the plant (Bald and Helson 1944) including the depth at which tubers are formed in the soil (Langford 1933). Undoubtedly such factors are important as Langford (1933) found that percentage tuber infestation for the same cultivar was reduced from 46.2% for 2 in. planting depth to 4.8% for 4 in. planting depth. Differences in depth of tuber formation between cultivars could therefore contribute towards different levels of tuber infestation under field conditions.

The possibility exists however that more fundamental differences may occur between cultivars such as oviposition preference, ability of larvae to establish, larval development and adult fecundity. There appear to be no reports of such investigations in the literature. The object of this aspect of the present study was to examine a selection of potato cultivars grown in New Zealand

(a) to confirm that differences in degree of tuber moth infestation occur under field conditions;

and (b) to determine whether differences in oviposition preference, larval establishment and development, and adult fecundity could be detected in the laboratory.

MATERIALS AND METHODS

Seed tubers of named cultivars (and some coded breeding lines) were obtained from Crop Research Division, Department of Scientific and Industrial Research. Two trials to evaluate differences in the degree of infestation under normal growing conditions were conducted; one under glass in 1976/77 and the other in the field in 1977/78.

1. Glasshouse trial 1976/77

Ten named cultivars (Ilam Hardy, Whitu, Rua, Katahdin, Pentland Dell, Wha, Red King Edward, Tahi, Sebago and Toru) were included plus nine coded breeding lines. The glasshouse used was 6.1 x 6.1 m with an earth floor. Tubers were planted at a depth of 10-12 cm with 26 cm spacing between plants and 80 cm between rows. The layout was a randomized block design with six replications and single plant plots. Planting took place on 5 October 1976. The plants were ridged up and hoed by hand during the trial. Watering was by hand hose twice weekly.

60 pairs of laboratory reared moths 24-48 h old were released into the glasshouse on 26 November and a further 40 pairs on 2 December.

As no signs of foliage mining were detected up to 22 December, a further 60 pairs of moths were introduced on that date. The tops were cut off at ground level and removed on 22 February 1977 and the tubers dug by hand on 8 March. Tubers from each plant were placed into individual bags and held in a cool store at 5-7^{o}C until assessment a week later.

Method of assessment

Tubers from each plant were sorted into the following categories according to the degree of larval tunnelling visible from external examination:

Category	Definition	Weighting factor
Clean	No visible signs of infestation	0
Slight	One or two mines such that damage could be removed readily on peeling	x 1
Moderate	More than two mines present and up to one third of the tuber surface showing damage	x 2
Severe	More than one third of the tuber surface showing damage	x 3

Tubers with any green colouration were set aside whether damaged or undamaged so that the percentage of tubers with greening for each cultivar could be calculated.

From the numbers of tubers within each damage category a damage index was derived by the following formula:

$$\frac{\text{No. in slight category} \times 1 + \text{No. in moderate category} \times 2 + \text{No. in severe category} \times 3}{\text{Total no. of tubers}} \times 10$$

The maximum possible damage index value is thus 30 if all tubers fall into the severe category. Such values were calculated for each replicate (single plant) of each cultivar and the figures subjected to analysis of variance. The coefficient of linear correlation between damage index values and percentage greening of tubers was calculated for each cultivar.

2. Field trial 1977/78

Twelve named cultivars (Ilam Hardy, Whitu, Rua, Katahdin, Wha, Red King Edward, Tahi, Sebago, Pentland Dell, Toru, Ono and Rima) were included plus nine coded breeding lines. The trial was laid down on an area of Massey farm land which had not grown potatoes for

at least the preceding five years. The soil type was Tokomaru Silt Loam (yellow grey earth group) with a slight northerly aspect. A randomized block layout was used with five replications. Each plot consisted of two rows each of five plants of the same cultivar. All plots were separated by two buffer rows of one cultivar (Ilam Hardy) and the whole trial was similarly surrounded. Planting depth was approximately 10-12 cm with 30 cm plant spacing within the rows and a row width of 76 cm. A gap of 122 cm was left between plots along the length of the rows. Planting was undertaken by hand on 8 November 1977.

400 pairs of laboratory reared moths 24-48 h old were released into the trial area between 1 and 4 January 1978 by walking along plot rows with an open container. Releases were made in the late afternoon. In addition, over the same dates, approximately 400 pupae were distributed onto the ground surface along the length of the guard rows within the trial area.

The plants were earthed up by tractor equipment once in an early stage of growth. Weed control was by hand hoeing. No irrigation was provided.

The plots were harvested by hand digging on 4 April 1978. Tubers from the ten plants of each cultivar comprising each plot were bulked and placed in paper sacks in a cool store at 5-7^{o}C until assessment. This was undertaken over the three days 9-11 May 1978 in the same manner as described for the earlier glasshouse trial except that no record was kept of the percentage of tubers showing greening. All tubers of less than 2.0 cm diameter were discounted.

3. Laboratory evaluations

Three types of comparative biological evaluation were undertaken using the 12 named cultivars included in field trials. Coded breeding lines were not examined in the laboratory.

(a) Oviposition preference tests with tubers and foliage;

(b) Percentage larval survival, rate of larval development and pupal weight according to cultivar;

and (c) Fecundity according to cultivar on which the larvae were raised.

In addition

(d) Tests were undertaken to measure the resistance to skin puncture with tubers of the twelve named cultivars.

(a) Oviposition preference

Tests were conducted in 30 cm^3 terylene net cages over 48 h in darkness at 25°C with 20 pairs of moths 24-48 h old. Each cage contained one tuber, or portion of foliage, of the test cultivar and one of the standard that was used for comparison in all tests (Ilam Hardy). Five per cent sugar solution was provided in a small glass vial into which short lengths of cotton dental roll were inserted. Each test was replicated five times.

Because of the importance of surface texture in choice of oviposition site (see Chapter IV Part 2) two series of tests were run with potato tubers. In one series, washed and dried tubers were placed on the floor of the cage about 20 cm apart. In the second series tubers were similarly prepared and positioned but were covered with four layers of cotton muslin so that each cultivar presented an identical surface in terms of texture.

Each cultivar was also evaluated for numbers of eggs laid under a non-choice situation by placing a single tuber within a 500 ml glass jar containing 10 pairs of moths and closed with half a glass petri dish. Tests were similarly run for 48 h at 25°C in darkness. At the end of the test period eggs on the surface of potato tubers, muslin covering, or potato foliage were counted with the aid of a stereo-microscope. Very few eggs were laid elsewhere, either on the wall of the terylene net cages or on the inner surfaces of the glass jars and were ignored. Counts were subjected to square root transformation before statistical analysis.

(b) Larval survival, rate of development and pupal weight

Two experiments were conducted. Experiment 1, set up in 1978, consisted of five replications of each cultivar. As differences in percentage pupation between cultivars did not reach significance a second experiment (Experiment 2), was conducted in 1979 with ten replications of each cultivar.

Experiment 1 (1978)

Approximately 100 g weight of potato tuber (single tuber or two smaller ones) was placed on top of crumpled tissue paper in the bottom of a wide mouthed 500 g glass jar. 30 newly hatched (< 12 h old) first instar larvae were placed onto the tuber surface. The jar was closed with half a glass petri dish for 5 days until the larvae had established. The glass lid was then replaced with terylene net to provide free air circulation and thus minimize mould growth. Five jars were prepared with tubers of each cultivar. Jars were held at 25°C in darkness with humidity regulated at 40-50% RH. Pupae formed were removed on the 12th day and thence every other day until none were recovered over a 4 day period.

Tubers were retained for a further 5 days after the last pupa was recovered as it was found that one or two adult moths emerged in each jar from pupae evidently formed within the tuber and not previously recorded. These adults were added to the total of pupae recovered in calculating final percentage pupation (Tables 29 and 30). 100 pupae of mixed sexes were weighed individually from each cultivar.

A second series of tubers was prepared in which the skin was perforated immediately before seeding with larvae, by rolling them over a board with spikes at approximately 1 cm^2 spacing. The remainder of the experimental procedure was the same as for intact tubers.

Experiment 2 (1979)

Tubers of each variety were selected within the size range 60-100 g. The number of eyes on each tuber was recorded, and the tubers set up in 500 g glass jars as described for Experiment 1. Twenty 1st instar larvae were seeded onto each tuber and there were 10 replications of each cultivar. The remainder of the procedure was as for Experiment 1 except that removal of pupae was commenced on the 10th rather than the 12th day. Fifty female pupae from each cultivar were separated and weighed individually.

As with Experiment 1, a second series of tubers was set up in which the skin was perforated before larvae were introduced.

(c) Fecundity

Pupae from Experiment 1 were held at 25°C until emergence of the adults. Moths within 24 h of emergence were placed in 110 ml wide mouthed jars as described for the experiment on effect of CO_2 anaesthetization on fecundity (Chapter V Part 1). Groups of 5 pairs of moths were placed into each jar, provided with distilled water and eggs collected every other day until death of all females in the container concerned. There were eight replications of each cultivar to give a total of 40 pairs of moths per cultivar.

(d) Skin puncture tests

An Ottawa Texture Meter coupled to a chart recorder was used to determine the pressure required to penetrate the skin of potato tubers using a small (7 mm diameter) Magnus-Taylor probe. The instrument was adjusted so that full deflection of the pen was equal to a pressure of 20 kg. The chart speed was 10 cm/minute. Potato tubers were cut in half and each hemisphere of the tuber presented with the intact surface uppermost. The probe was directed to flat areas of the tuber surface as far as possible. Twenty recordings were made for each cultivar involving a minimum of five different tubers. Tests were conducted in July (1979) after tubers had been in cool store at 5-7°C for 12 weeks.

Pressure at the point of skin rupture (indicated by a sharp peak on the recordings) was read off from the chart for each test.

RESULTS

1. Glasshouse trial 1976/77

Very little foliage mining was detected during the course of this trial. No foliage mines were found up to 22 December (11 weeks from planting and 4 weeks from first introduction of adult moths) and even by 22 February mines were confined to the lower parts of the plants. Large numbers of moths were present in the glasshouse on the latter date however, indicating that at least one generation had successfully completed development since introductions were made.

Mean damage indices for tubers at harvest ranged from 4.2 for Whitu to 14.9 for Ilam Hardy but no differences between cultivars were statistically significant due to high within-cultivar variation. The coefficient of linear correlation between percentage tubers with green colouration and tuber damage index values was low ($r = 0.02$) and non-significant.

2. Field trial 1977/78

No foliage mining was observed at any stage during this trial. Results of assessment of tuber infestation are summarized in Table 27. Data for coded breeding lines have not been included as no laboratory work was undertaken with them. Damage indices covered a similar range to that recorded from the glasshouse trial (5.92 - 14.53). Statistical anslysis in this case showed that many between cultivar differences were significant. Details are presented in Table 27.

3. Laboratory evaluations

(a) Oviposition preference

The results of oviposition preference tests are presented in Table 28. Egg counts have been converted in each case relative to the standard cultivar Ilam Hardy = 100. When bare tubers were offered distinct discrimination was shown against Rua and to a lesser extent against Ono, Red King Edward and Wha. When tubers of these cultivars were covered with muslin however, no differences in preference compared to Ilam Hardy occurred. Instead, three cultivars (Pentland Dell, Whitu and Sebago) were preferred to Ilam Hardy though not when tested as bare tubers. In non-choice tests, no difference occurred between any cultivar and Ilam Hardy whether tubers were wrapped in muslin or not wrapped.

With foliage comparisons, only Pentland Dell was significantly different (lower) than Ilam Hardy.

(b) Larval survival, rate of development and pupal weight

The results of Experiment 1 with intact and pricked tubers are given in Table 29. Although percentage pupation ranged from 42% (Rua) to 72% (Sebago) for intact tubers, differences were not statistically significant due to high within cultivar variation. Pricking of tubers resulted in higher percentage pupation with all cultivars, the difference reaching significance for five cultivars. The results of Experiment 2 with intact and pricked tubers are given in Table 30.

Weights of pupae of mixed sexes (from Experiment 1) are given in Table 31 and weights of female pupae (from Experiment 2) in Table 32. Some differences between pupal weights according to cultivar on which the larvae fed were significant as indicated in the tables.

(c) Fecundity

Data for fecundity according to the cultivar on which the larvae were raised are given in Table 33. The highest mean fecundity (Ono) exceeded the lowest (Rua) by nearly 50% and was highly significant ($P < 0.01$). Some intermediate differences were significant at a lower level of probability.

(d) Skin puncture tests

The results of skin puncture tests are given in Table 34.

DISCUSSION

Field trials

The field trial conducted in 1977/78 produced significant differences between potato cultivars with respect to degree of tuber infestation. The results were consistent with the findings of Bedi (1974) and Foot (1976). Ilam Hardy recorded the highest level of tuber infestation and Rua the lowest. A curious feature of this trial was that no foliage mining by Potato Tuber Moth larvae was recorded.

The glasshouse trial conducted the previous season (1976/77), gave a similar range of tuber infestation between cultivars from lowest to highest compared to the outdoor trial, but differences between cultivars were not statistically significant. This was possibly associated with the single plant plots used and the likely effect of the glasshouse enclosure on the distribution of moths.

Laboratory evaluations

(a) Oviposition preference

In oviposition preference tests with bare tubers of the named potato cultivars, the standard cultivar (Ilam Hardy) was preferred compared to Wha, Red King Edward, Ono and Rua, but these preferences disappeared when tubers of the same cultivars were covered in muslin. This suggests that surface texture of tubers is important in determining oviposition preference as might be expected from investigations of the physical nature of oviposition substrates reported in Chapter IV Part 2.

With muslin covered tubers, which presented a uniform substrate for oviposition, three cultivars (Sebago, Pentland Dell and Whitu) were strongly preferred to Ilam Hardy suggesting that odour differences were involved. Odour may also have played a part in preferences between bare tubers but would have been complicated by differences in surface texture.

The fact that no differences occurred between cultivars under non-choice conditions, whether tubers were covered with muslin or not, suggests that under normal growing conditions with sizeable areas of single cultivars, preference differences might not be important. This possibility is also supported by the fact that in comparisons of foliage, no preferences were detected except in the case of Pentland Dell v. Ilam Hardy where the latter was preferred.

(b) Larval survival, rate of development and pupal weight

In the first experiment of five replications conducted to compare percentage pupation between cultivars following the introduction of a known number of first instar larvae onto tubers, differences between cultivars were not significant though pupation ranged from 42% for Rua to 72% for Sebago, indicating a high degree of within cultivar variation. Increasing replication to ten and more stringent selection of tubers in the second experiment, produced significant differences between many cultivars.

Pricking the surface of tubers by rolling them over a spiked board, before infesting with 1st instar larvae, resulted in increased pupation for all cultivars compared with intact tubers. This difference was more marked (and was statistically significant) for some cultivars compared to others.

In both experiments pupae were removed every other day with a view to determining whether differences occurred in rates of development between cultivars. When plotted as cumulative percentage pupation curves, however, the results were extremely variable, due perhaps to the relatively small numbers concerned, and precluded further analysis.

Pupal weights

When pupae of mixed sexes were weighed from each cultivar, differences between some cultivars were significant. Separating and weighing female pupae resulted in higher mean weights but variability was not reduced (S.E. ± 2.02% of the mean for female pupae compared to S.E. ± 1.71% of the mean for pupae of mixed sexes). In detecting possible differences between cultivars in terms of pupal weight there is thus little to be gained from sexing of pupae.

(c) Fecundity

Significant differences in fecundity were found according to the cultivar on which larvae were raised, the highest (Ono) exceeding the lowest (Rua) by about 50 per cent. As these fecundity measurements were made in the absence of host plant material they were probably not maximum values (see Chapter V Part 2) but should have been valid on a relative basis between cultivars.

Fecundity by cultivar was not correlated with pupal weight ($r = -0.23$ NS for female pupae v. fecundity). In fact for pupae of mixed sexes, the highest pupal weight (Rua) gave the lowest fecundity and the lowest pupal weight (Whitu) the second highest fecundity. It seems therefore that nutritional factors, other than those

affecting mere body weight, may differ between cultivars and result in differences in fecundity of the ensuing adults.

(d) Skin puncture tests

The fact that pricking the skin of tubers improved the percentage production of pupae from known numbers of larvae, compared to intact tubers with all cultivars, suggests that the peel of the tuber may act as a barrier to first instar establishment. Thus one might expect some degree of negative correlation between the resistance of the skin to puncture and percentage pupation. Although a negative value was found it did not reach significance (regression of percentage pupation totals for Experiment 1 plus Experiment 2 with intact tubers, on skin rupture pressure, $r = -0.40$ NS). Neither is there any consistent relationship between resistance to skin puncture and those cultivars which benefited most by skin puncture with respect to pupae produced, e.g. Toru, Ono, Red King Edward (see Tables 29 and 30).

With intact tubers, first instar larvae almost invariably enter through the eyes, so that resistance to puncture of the general skin surface may not be particularly relevant. Instead, the number of eyes per tuber could perhaps be associated with ease of larval establishment. Differences were found between cultivars in the number of eyes per tuber (see Table 35) but again there was no correlation with success of larval establishment as measured by percentage pupation. (Regression of percentage pupation for intact tubers on number of eyes per tuber, $r = 0.07$ NS).

The reasons for differences between cultivars in percentage pupation have not therefore been resolved in this study. The possibility remains that the form of the eyes and the nature of the skin in their immediate vicinity may be the important factors.

Differences in percentage pupation may not of course reflect accurately success of establishment of first instar larvae as mortality after establishment may also occur. This however, seems unlikely to be a significant factor, as the larva is well protected

within the tuber and provided with ample food once established, at least with the low levels of infestation employed in these experiments.

Correlation of laboratory evaluations with levels of infestation recorded in the field

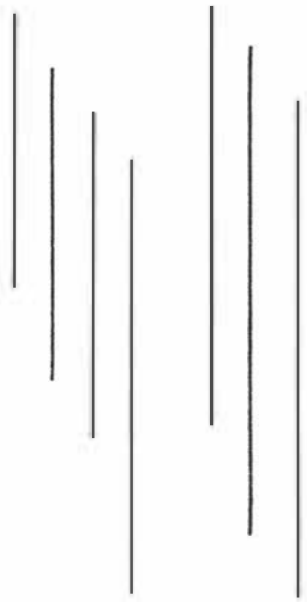
If differences between cultivars in terms of oviposition preference, percentage pupation and fecundity as determined in laboratory comparisons also operate under field conditions, they could account in part at least for differences in degree of infestation in the field.

In Table 36 relative rankings of cultivars are given in the first three columns for oviposition preference (bare tubers), percentage pupation (based on means of Experiment 1 and Experiment 2 with intact tubers), and fecundity. Highest values are ranked 1 and lowest 12 in each case. The fourth column lists the sums of the rank values from the first three columns and in column five the sum values are converted to an overall rank. Where two cultivars tied with the same rank value in column four (as occurred in three instances) they have been given the same rank in column five but the following rank value was omitted in each case so that the lowest rank was still 12. Finally, in column six, cultivars are ranked according to the degree of tuber infestation recorded in the 1977/78 field trial.

It will be seen that the correspondence between the two final sets of rank values is for the most part extremely close. It corresponds exactly for four out of the twelve cultivars, and for another four there is a discrepancy of only one rank point. The maximum divergence is 5 points (Sebago). It is suggested therefore that for most of the cultivars examined, differences which occur in degree of infestation under field conditions are due primarily to intrinsic differences between them rather than to such factors as depth of tuber formation or other features of growth habit.

Table 27. Results of field trial to compare potato cultivars for degree of infestation by potato tuber moth, 1977/78

Cultivar	Mean tuber damage index	Significance of differences*	
		5%	1%
Ilam Hardy	14.08		
Katahdin	13.25		
Ono	11.96		
Toru	10.48		
Pentland Dell	10.35		
Whitu	10.24		
Tahi	9.16		
Sebago	9.08		
Rima	8.32		
Red King Edward	7.74		
Wha	6.93		
Rua	5.92		



* Values underscored by the same line are not significantly different. Duncan's Multiple Range Test.

Table 28. Results of oviposition preference tests with tubers and foliage of named potato cultivars

Cultivar	Tubers not wrapped	Tubers wrapped in 4 layers of cotton muslin	Foliage
Ilam Hardy (standard of comparison)	100	100	100
Toru	126 NS	92 NS	122 NS
Sebago	110 NS	178 **	66 NS
Pentland Dell	97 NS	235 **	67 **
Katahdin	88 NS	83 NS	71 NS
Rima	71 NS	65 NS	199 NS
Wha	67 *	102 NS	115 NS
Whitu	62 NS	232 **	92 NS
Tahi	61 NS	100 NS	80 NS
Red King Edward	56 **	156 NS	99 NS
Ono	51 *	96 NS	112 NS
Rua	28 **	78 NS	128 NS

** Significantly different from Ilam Hardy $P < 0.01$.

* Significantly different from Ilam Hardy $P < 0.05$.

NS Not significantly different from Ilam Hardy.

Table 29. Percentage pupation following introduction of first instar larvae onto intact and pricked tubers of named potato cultivars (Experiment 1, 1978)

Cultivar	Percentage pupation[1]		Significance of difference. Pricked v. intact
	Intact[2]	Pricked[2]	
Sebago	72.0	76.0	NS
Pentland Dell	70.7	86.0	NS
Katahdin	70.0	75.3	NS
Wha	68.0	82.7	NS
Red King Edward	64.7	85.3	**
Whitu	61.3	80.7	**
Rima	60.0	67.3	NS
Tahi	59.3	68.0	NS
Ono	58.7	89.3	**
Ilam Hardy	56.7	75.3	NS
Toru	54.7	81.3	**
Rua	42.0	69.3	*

[1] Based on total pupae recovered compared to number of 1st instar larvae introduced.

[2] Differences between cultivars not statistically significant due to high within cultivar variation.

** Pricked significantly higher than intact tubers $P < 0.01$.

* Pricked significantly higher than intact tubers $P < 0.05$.

NS Pricked not significantly higher than intact.

Table 30. Percentage pupation following introduction of first instar larvae onto intact and pricked tubers of named potato cultivars (Experiment 2, 1979)

Intact				Pricked			
Cultivar	Percentage pupation	Significance of differences[1]		Cultivar	Percentage pupation	Significance of differences[1]	
		5%	1%			5%	1%
Sebago	62.5			Katahdin	88.5 **		
Toru	58.5			Pentland Dell	86.5 **		
Red King Edward	56.0			Ono	84.5 **		
Katahdin	56.0			Wha	83.0 NS		
Pentland Dell	53.0			Sebago	79.5 NS		
Tahi	50.0			Rima	78.0 **		
Ono	43.0			Whitu	77.5 **		
Ilam Hardy	41.5			Tahi	77.0 *		
Rua	40.0			Rua	76.5 **		
Whitu	38.5			Toru	75.0 *		
Wha	35.5			Red King Edward	72.5 NS		
Rima	32.5			Ilam Hardy	67.5 **		

[1] Values underscored by the same line are not significantly different. Duncan's Multiple Range Test.

** Pricked significantly higher than intact tubers $P < 0.01$.

* Pricked significantly higher than intact tubers $P < 0.05$.

NS Pricked not significantly higher than intact.

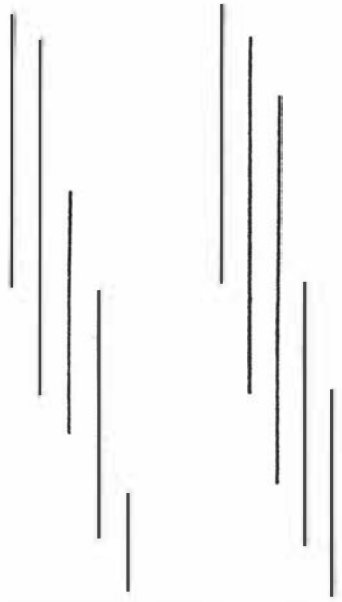
Table 31. Mean weights of pupae of mixed sexes according to potato cultivar on which the larvae fed (Experiment 1)

Cultivar	Mean pupal weight mg	Significance of differences* 5%	1%
Rua	11.22		
Katahdin	11.06		
Ilam Hardy	10.96		
Tahi	10.80		
Wha	10.65		
Sebago	10.57		
Ono	10.52		
Pentland Dell	10.50		
Rima	10.43		
Red King Edward	10.41		
Toru	10.41		
Whitu	10.19		

* Values underscored by the same line are not significantly different. Duncan's Multiple Range Test.

Table 32. Mean weights of female pupae according to the potato cultivar on which the larvae fed (Experiment 2)

Cultivar	Mean pupal weight mg	Significance of differences*	
		5%	1%
Sebago	12.70		
Ilam Hardy	12.24		
Toru	12.19		
Katahdin	12.16		
Rua	12.08		
Tahi	11.94		
Ono	11.68		
Wha	11.53		
Rima	11.21		
Red King Edward	11.71		
Pentland Dell	10.93		
Whitu	10.39		



* Values underscored by the same line are not significantly different. Duncan's Multiple Range Test.

Table 33. Fecundity of potato tuber moth according to the cultivar on which the larvae fed (Experiment 1)

Cultivar	Mean fecundity (total eggs laid per female)[1]	Significance of differences*	
		5%	1%
Ono	160.5		
Whitu	155.8		
Ilam Hardy	149.7		
Toru	142.3		
Tahi	137.6		
Rima	130.1		
Wha	129.1		
Katahdin	128.1		
Red King Edward	126.6		
Pentland Dell	125.9		
Sebago	123.3		
Rua	110.6		

* Values underscored by the same line are not significantly different. Duncan's Multiple Range Test.

[1] Adults fed distilled water; muslin oviposition substrate; no plant material present.

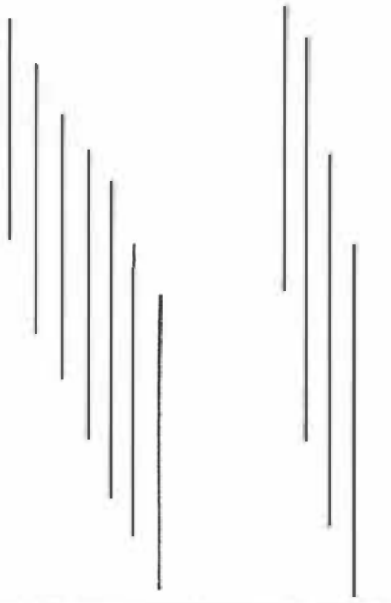
Table 34. The results of skin puncture tests with tubers of named potato cultivars

Cultivar	Mean pressure in kg at point of skin rupture	Significance of differences* 5%	1%
Whitu	13.39		
Rima	13.35		
Ono	13.21		
Wha	12.50		
Tahi	12.24		
Toru	11.44		
Red King Edward	11.35		
Pentland Dell	11.29		
Sebago	11.06		
Rua	10.86		
Katahdin	10.75		
Ilam Hardy	10.58		

* Values underscored by the same line are not significantly different. Duncan's Multiple Range Test.

Table 35. The number of eyes per tuber according to cultivar

Cultivar	Mean number of eyes per tuber	Significance of differences*	
		5%	1%
Sebago	12.3		
Rima	11.6		
Ilam Hardy	11.3		
Toru	10.8		
Whitu	10.5		
Tahi	10.1		
Rua	9.8		
Ono	9.6		
Katahdin	9.3		
Pentland Dell	8.8		
Red King Edward	8.5		
Wha	8.0		



* Values underscored by the same line are not significantly different. Duncan's Multiple Range Test.

Table 36. Ranking of potato cultivars on the basis of various laboratory evaluations and relationship to field infestation (for full explanation see text)

Cultivar	Oviposition preference (bare tubers) Rank*	Percentage pupation[1] Rank*	Fecundity Rank*	Sum of ranking values	Overall rank	Field infestation[2] Rank*
Ilam Hardy	1	10	3	14	2	1
Toru	2	5	4	11	1	4
Sebago	3	1	11	15	3	8
Pentland Dell	4	3	10	17	5	5
Katahdin	5	2	8	15	3	2
Rima	6	11	6	23	10	9
Wha	7	8	7	22	9	11
Whitu	8	9	2	19	6	6
Tahi	9	6	6	20	8	7
Red King Edward	10	4	9	23	10	10
Ono	11	7	1	19	6	3
Rua	12	12	12	36	12	12

* 1 = highest value; 12 = lowest value.

1 Means of Experiment 1 and Experiment 2, based on number of pupae recovered following introduction of first instar larvae onto intact tubers.

2 Based on mean tuber damage index 1977/78 field trial.

Chapter VIII

GENERAL DISCUSSION AND CONCLUSIONS

The oligophagous habit of Potato Tuber Moth has been well established by previous workers (Picard 1913a, Attia and Mattar 1939, Cunningham 1969), its host range being effectively restricted to certain genera within the plant family Solanaceae, including the economically important plants potato, tobacco, tomato and egg plant. In a holometabolous insect, such as tuber moth, in which the adult is winged and mobile whilst young larvae are capable of only limited movement, it seems logical that plant selection should be undertaken primarily by the ovipositing adult for the ensuing larvae. Tuber moth however mates and lays eggs freely in the absence of plant material of any kind as some aspects of the present study have confirmed. On non-plant surfaces, choice of oviposition site is influenced by surface conformation and texture. Physically optimum surfaces contain depressions just large enough to accommodate eggs and should preferably be hairy. Mechano-receptors on the ovipositor itself probably largely account for these effects. In addition, egg laying is strongly deterred by the presence of moisture.

It seems likely from these findings that the physical nature of plant surfaces also is important in choice of oviposition site, and this is supported by the observation that eggs on potato tubers are almost invariably laid in depressions and angles around the eyes. Also, smooth plant surfaces including the leaves of non-host plants such as pea and beet which are normally avoided for egg laying, become acceptable when covered with a layer of muslin. Physical factors alone cannot however be solely responsible for selection of oviposition sites by this insect in nature, otherwise eggs would be laid in many situations unsuitable for larval development, such as non-food plants for the larvae and non-plant surfaces of appropriate physical nature. Such behaviour is a biologically feasible strategy

for a polyphagous insect with high fecundity, e.g. Wiseana spp., but not for an oligophagous insect such as tuber moth with limited egg production. Other properties of plants must therefore guide choice of oviposition site and the most likely a priori choice is chemical.

The present study has shown clearly that selection of plants for oviposition is guided by stimulative substances in host plants and by deterrent substances in non-host plants. Such substances are unlikely to be involved in attraction (or repellence) from a distance however, as they do not seem to be volatile and require contact by the insect for detection. Quite how they are detected in the intact leaf is unclear, as for the most part they are released only when the plant tissue is crushed. There is the possibility however that probing of the plant surface by the insect with its ovipositor might be sufficient for detection as mild abrasion of the leaf surface without the release of plant juices did induce a response in some cases. No evidence has been produced from the present study to indicate whether single chemical entities are predominantly involved or whether the insects respond to the total chemical sensory input from the plant. It may be concluded that the most favoured natural oviposition sites will be those that combine optimum physical properties with maximum chemical stimulation. The non-volatility of these oviposition stimulants and deterrents does not preclude the possibility that orientational responses of flying adults to plant odours could take place involving other chemicals. This was not investigated in the present study.

It is interesting to note that tomato performed like known non-host plants as regards oviposition behaviour rather than like prime known host plants. The same was also true to a considerable extent with regard to behaviour of first instar larvae (see later discussion). Potato Tuber Moth is not regarded as a significant pest of tomatoes in New Zealand though it is recorded as such in some other countries. A related species (Scrobipalpa plaesiosema (Turner)) does occur sporadically as a pest of tomatoes in New Zealand (Ferro 1976). It seems likely therefore that the genetic strain of Phthorimaea operculella present in New Zealand is not well adapted to this plant.

A more subtle interaction of insect and host-plant has been revealed by the discovery that fecundity is significantly boosted by the presence of potato tubers. Furthermore, the effect seems to be primarily one of odour so that the mechanism may be quite distinct from that governing choice of oviposition site. Similar effects probably also occur with other prime host plants as the number of eggs laid in short term oviposition experiments was frequently significantly increased by their presence. The influence of host plants in this way appears to account in part for the fact that there is not a simple relationship for this species between fecundity and body weight.

Although plant selection under field conditions is probably determined primarily by oviposition behaviour of the adult, newly hatched first instar larvae without prior exposure to plant material discriminate strongly between plant species. This discriminatory ability is thus innate rather than induced. Acceptability of plant species for feeding by first instar larvae is closely related to acceptability for oviposition by the adult. One exception to this however is pea which was moderately well accepted by larvae for feeding but was deterrent for egg laying. Salpiglossis (Solanaceae) and Ipomea (Convolvulaceae) were also quite well accepted by larvae. These plants were not tested for oviposition acceptance. Sugar beet has been recorded as a host plant for Potato Tuber Moth in Europe (Haines 1977) but silver beet in the present studies was neither accepted for oviposition nor for feeding by larvae.

Although first instar larvae have well developed discriminatory ability their capacity for host plant location is poor. Their movement for the most part is non-directional with respect to plant material even when placed in close proximity. There are however arrestant properties possessed by host plants which induce larvae to remain on them once contact has been made. Non-host plants (which are not repellent) on the other hand do not possess such properties so that if larvae encounter them their movement is not arrested. Such behaviour is obviously consistent with the normal site of egg laying being directly on plants which are suitable for larval feeding.

The main findings with respect to this part of the thesis (refer to points 1 through 6 of Table 1) are summarized in Table 37. Some contribution has been made to all questions with the exception of 1. - host plant location by the adult - which was not examined. Points 7 through 9 of Table 1 are more pertinent to discussion of the relative susceptibility of potato cultivars which follows.

Table 37. Effects of plant material on behaviour of adults and first instar larvae of potato tuber moth

Developmental stage	Behavioural step	Plant influence
1. Mature virgin adult (♂ and ♀)		Attraction and/or arrestance by host plant, repellence by non-host plant. Not examined.
2. Mature virgin adult (♂ and ♀)	copulation	Presence of host plant not required.
3. Mature female	oviposition	Stimulated by contact with host plants. Deterred by contact with non-host plants.
4. Mature female	fecundity	Stimulated by presence of host plant.
5. Newly hatched 1st instar larva	plant location	Movement arrested but not attracted by host plants. Movement not arrested, not repelled by non-host plants.
6. 1st instar larva	plant recognition and feeding	Ability to discriminate inherited.

In laboratory comparisons distinct differences were found between potato cultivars with respect to oviposition preference (tubers), success of larval establishment and development, and fecundity. Such differences largely accounted for the differences in relative susceptibility of cultivars found under field conditions.

Oviposition preferences between tubers of different potato cultivars are probably due to both chemical and physical factors as preference changed depending whether tubers were covered in a layer of muslin or not. Non-preference was not sufficiently marked to produce any differences between cultivars in non-choice tests.

The differences recorded between cultivars in terms of percentage pupae recovered relative to numbers of first instar larvae introduced could be due both to success of larval establishment and to suitability of the cultivar for growth and development. That the skin of potato tubers does present a physical barrier to larval penetration is indicated by the fact that pricking the skin improved percentage pupation for all cultivars. The relationship is however obviously not a simple one as no correlation was found between physical resistance of tuber skin to rupture and percentage pupal recovery. Differential larval mortality after penetration could also of course complicate the picture.

Differences in fecundity according to the cultivar on which the larvae fed were not primarily a matter of pupal size so that nutritional factors of particular relevance to egg production must also be involved.

Although none of the potato cultivars examined is resistant to Potato Tuber Moth in a practical sense, differences between cultivars were sufficient to suggest that a search for more resistant material amongst tuber forming Solanum species would be worth while.

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APPENDIX: Publications resulting from work undertaken towards this thesis (as at December 1979).

FENEMORE, P.G. 1977: Oviposition of potato tuber moth, Phthorimaea operculella Zell. (Lepidoptera: Gelechiidae); fecundity in relation to mated state, age and pupal weight. N.Z. Journal of Zoology. 4: 187-191.

FENEMORE, P.G. 1978: Oviposition of potato tuber moth, Phthorimaea operculella Zell. (Lepidoptera: Gelechiidae); the physical nature of the oviposition substrate. Ibid. 5: 591-599.

FENEMORE, P.G. 1979: Oviposition of potato tuber moth, Phthorimaea operculella Zell. (Lepidoptera: Gelechiidae); the influence of adult food, pupal weight, and host-plant tissue on fecundity. Ibid. 6: 389-395.

FENEMORE, P.G. (in press): The relative susceptibility of potato cultivars to potato tuber moth, Phthorimaea operculella Zell. (Lepidoptera: Gelechiidae). N.Z. Journal of Agricultural Research.