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EFFECTS OF SOME ALKALOIDS ON THE DARK-SIDED CUTWORM EUXOA MESSORIA (LEPIDOPTERA : NOCTUIDAE).

By

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The littlest bugs have the biggest names.
It is thus also, sometimes, with men.

W. J. Holland

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ABSTRACT

The dark-sided cutworm, Euxoa messoria (Harr.) was reared under laboratory conditions on 8 artificial diets, a meridic diet containing various concentrations of one of the alkaloids, veratrine, berberine, nicotine, or atropine, and on two varieties of Nicotiana tabacum, Lonibow and Delhi-34. Observations of the development times, larval and pupal weights, survival, and number and widths of head capsules were recorded. Feeding preference studies were carried out to look at possible food choice mechanisms used by the larvae.

Larvae showed quantitative requirements for ascorbic acid and cholesterol. Soybean protein was unsuitable as the sole protein source but it did supplement casein. Wheat germ provided an unknown nutritional quality to the diet which improved developmental characteristics.

Chronic exposure to alkaloid diets demonstrated that survival and developmental characteristics are variously affected by the source and concentration of alkaloid. Larvae demonstrated a tolerance to levels of 0.01 %, 0.03 %, and 0.1 %, berberine; 0.01 %, and 0.03 % nicotine; and 0.01 %, 0.03 % and 0.1 % atropine. Atropine at all levels tested enhanced survival and larval size. Detrimental effects on growth, development rates, survival and/or number of instars were observed in larvae fed dietary levels of 0.3 % and 1.0 % berberine; 0.1 %, 0.3 %, and 1.0 % nicotine; 0.3 % and 1.0 % atropine; and 0.01 %, 0.03 %,

0.1 %, and 0.3 %, and 1.0 % veratrine, indicating that this insect is susceptible to these compounds at these levels. Larvae were most sensitive to the detrimental (or antibiosis) effects of the alkaloids berberine and nicotine in the early stages of development. There was a degree of plasticity observed in the duration of the prepupal period which allowed the development rates of individuals fed various levels of an alkaloid to become synchronized, thus ensuring that the adults emerged at roughly the same time.

The developmental characteristics of larvae fed two varieties of N. tabacum, Lonibow and Delhi-34, indicated that Delhi-34 shows some resistance to the larvae by decreasing survival, larval and pupal sizes, and increasing the development times.

E. messoria demonstrates a definite preference for some food sources over others, and responds to both nutritive and secondary plant compounds in making a choice. Sucrose, nicotine, and atropine are phagostimulants to the larvae while berberine (at 0.03 %, 0.1 %, 0.3 %, and 1.0 %) and veratrine (at all levels tested) are feeding deterrents. The threshold level for the antifeedant effect of berberine appears to be 0.01 %. Response to the alkaloids seems to be dependant upon the presence of nutrient compounds. Sucrose mixed with atropine had a synergistic effect on the feeding response. Larvae show a preference for some varieties and species of Nicotiana, and strongly preferred Atropa belladona over tobacco. Both the

antennae and maxillary palps are involved in host selection. Responses by maxillectomized larvae suggest that sucrose receptors are located on the maxillary palps and in the buccal cavity, and that the receptors responsible for the synergistic effect of sucrose and atropine are also on the maxillary palps. The presence of the maxillary palps appears to be essential for feeding to occur.

Larval preference for a food source does not guarantee the choice of a diet which is suitable for normal growth and development.

RESUME

Le ver-gris moissonneur, Euxoa messoria (Harr.) a été élevé en laboratoire sur huit diètes artificielles, sur une diète méridique contenant différentes concentrations d'un des alkaloides suivants: vératrine, berbéerine, nicotine, et atropine, et sur deux variétés de Nicotiana tabacum, Lonibow et Delhi-34. On a mesuré le temps requis pour le développement, le poids des larves et des chrysalides et les nombres et les dimensions des capsules céphaliques. Afin d' etablir comment fonctionne le mecanisme utilisé par les larves pour choisir leur nourriture on a procédé à des expériences de préférence alimentaire. Une diète artificielle de type méridique a été développée pour remplacer une diète oligidique à base de haricots.

Les larves on démontré des besoins quantitatifs pour l'acide ascorbique et le cholestérol. Les protéines de soya ne sont pas adéquates comme source exclusive de protéines, mais peuvent servir de supplément à la caséine. Le germe de blé fournit une qualité nutritionelle non définie à la diète, ce qui améliore les caractéristiques de la croissance.

Une exposition chronique à des diètes alkaloides révèle que la survivance et le développement sont affectés par l'origine et la concentration de l'alka-

loide. les larves ont montré une tolérance à des niveaux de 0,01%, 0,03% et 0,1% berbérine, 0,01%, 0,03% de nicotine, 0,01%, 0;03%, 0,1% atropine. A toutes les doses utilisées l'atropine a stimulé la survivance et la dimension des larves. Des effets nocifs sur la croissance, le taux de développement, la survivance et/ou le nombre de stades ont été observés chez les larves nourries à des doses alimentaires de 0,3% et 1,0% berbérine, 0,1%, 0,3% et 1,0% de nicotine, 0,3% et 1,0% atropine et 0,01%, 0,03%, 0,1%, 0,3% et 1,0% veratrine, indiquant que l'insecte est susceptible à ses composés aux doses mentionnées. Les larves sont davantage sensibles aux effets nuisibles (ou antibiose) des alkaloides dans les premiéres phases de leur développement. Il y a un certain degré de plasticité en ce qui a trait à la durée de la période pré-chrysalide ce qui permet au taux de développement des individus nourris à différentes doses d'un alkaloide d'être synchronisé, ce qui assure une émergence presque simultanée des adultes.

Les caractéristiques de croissance des larves nourries aux deux variétés de N. tabacum, Lonibow et Delhi-34, indiquent que Delhi-34 possède une certaine résistance à l'insecte puisqu'il diminue sa survie, la dimension des larves et des chrysalides, et agumente

la durée requise pour le développement larvaire (i.e. effets antibiotiques).

E. messoria démontre une préférence marquée pour certains aliments et réagit aux composés nutritifs et secondaires des plantes en faisant un choix. Le sucrose, la nicotine et l'atropine sont des phagostimulants pour la larve alors que la berbérine (à 0,03%, 0,1%, 0,3%, 1,0%) et la vératrine (à toutes les doses) sont des phagorépresseurs. Le seuil pour les effects antiappétants de la berbérine se situe a 0,01%. La réaction aux alkaloides semble dépendre de la présence de composés nutritifs. Le sucrose mélangé à l'atropine a un effet synergiste sur la réponse trophique. Les larves ont une préférence pour certaines variétés et espéces de Nicotiana. et préfèrent Atropa belladona au tabac. Les palpes antennaires et maxillaires sont impliqués dans la sélection de l'hôte. L'ablation des palpes maxillaires inhibe l'alimentaion. Les réactions de larves maxillectomisées suggérent que les récepteurs du sucrose sont localisés sur les palpes maxillaires et dans la cavité buccale, at que les récepteurs associés aux effets synergistes du sucrose et de l'atropine sont aussi sur les palpes maxillaires.

La préférence des larves pour une source de nourriture ne garantit pas le choix d'une diète qui soit adéquate pour une croissance et développement normaux.

I. INTRODUCTION

The dark-sided cutworm, Euxoa messoria (Harr.) is a member of the order Lepidoptera, family Noctuidae. It is a species native to North America with a distribution ranging from the eastern to the western coasts, and from the southern areas of the North West Territories to southern California (Hardwick, 1970; Beirne, 1971).

a) Life Cycle and Host Plants.

E. messoria has four distinct development stages: egg; larva; pupa; and moth. Like other species of Euxoa it has one generation a year (Cook, 1927). During the late summer to early fall females oviposit in the ground, showing a preference for cultivated sandy soils (Harris and Svec, 1968). Development in the egg proceeds until the larva is fully formed and at this stage it overwinters (Hinks and Byers, 1976). Larval emergence ranges from the end of January to late March (Harris and Svec, 1968; Cheng, 1971; Specht, 1974). The newly emerged larvae commence feeding on almost any available plant (Harris and Svec, 1968). Mature larvae stop feeding in July (Harris and Svec, 1968; Specht, 1974) entering a period of aestivation in the prepupal stage (Hinks and Byers, 1976). The larvae pupate during August and the adults emerge in late summer to early fall (Gibson, 1915; Harris and Svec, 1968; Hardwick, 1970; Specht, 1974).

E. messoria will feed on a wide variety of plants. Information on the host plants of this insect have been obtained from agricultural reports of crop plant damage caused by the larvae. Little is known about the food plants of this insect which are of no economic importance. Larvae have been reported feeding on field and garden crops (including peas, beans, potato, tomato, cucumber, melon, sweet pepper, asparagus, alfalfa, corn, barley, oats, rye, strawberries, blueberries, hops and tobacco), fruit trees, forest trees, ferns, shrubs, flowers, and herbs (Beirne, 1971; Tietz, 1972).

In Canada, damage to crops by the larvae of E. messoria has been economically significant in British Columbia, Ontario, Nova Scotia, and occasionally in the Prairie provinces (Beirne, 1971). The larvae cause severe damage to transplants of various crop plants and have been observed to adopt a climbing habit, causing damage to fruit trees (Crumb, 1929; Walkden, 1950; Hardwick, 1970; Beirne, 1971; Cheng, 1971; Specht, 1974).

Prior to 1942, E. messoria was considered a minor pest. Increased tobacco production influenced the abundance of this insect (Beirne, 1971), which appears to be well adapted to Nicotiana species and the environment of cultivated fields (Specht, 1974). Larvae of E. messoria are the dominant injurious species in most tobacco fields (Cheng, 1971; Specht, 1974). The larvae feed first on rye until it is ploughed under in late April, then move to the transplanted tobacco seedlings (Beirne, 1971). They mainly damage the young plants by severing the stem (Akehurst, 1968).

Until 1948, poisoned baits were used to control E. messoria, subsequently synthetic chemicals have been used (such as D.D.T., aldrin, heptachlor, endrin, and leptophos). By 1961, the species had developed a tolerance to cyclodiene pesticides and it became an important pest (Beirne, 1971). Parasites of E. messoria have been collected in British Columbia; these include 12 species of Hymenoptera and 6 species of Diptera (Can. Insect Pest Review 1962). The use of these as agents of control are not clear (Beirne, 1971).

In order to attain more effective methods of control for phytophagous insects, such as E. messoria, a thorough understanding of the interactions which occur between an insect and the plants it encounters, is necessary. The importance of such information has only recently been appreciated by agriculturalists. Knowledge of the mechanisms involved in insect-host plant relationships can provide valuable tools for use in pest management programs.

b) Insect - Plant Relationships

Phytophagous food habits have been adopted by roughly 50% of the insect taxa with seed-bearing plants serving as the major food source for 70% of this group (Brues, 1946; Southwood, 1973). Observation of the feeding patterns of phytophagous insects shows that they discriminate between plants within their geographical range, choosing only a specific group of plants as food (Thorsteinsen, 1960; Soo Hoo and Fraenkel, 1966; Beck and Reese, 1976). Discrimination between

plants by phytophagous insects is based on the physical and chemical characteristics of the plants (Lipke and Fraenkel, 1956; Yeo, 1973; Futuyma, 1976). Through the recognition of specific plant stimuli an insect is able to maintain itself within a certain host (food) - plant range (Wiklund, 1974).

Depending on the number of plants in an insect's dietary range, insects may be categorized as being monophagous, oligophagous or polyphagous. Monophagous insects are feeding specialists adapted to a very narrow niche and are confined to a single plant species. An example of a monophagous moth is the Chondrilla crown moth, Oporopsamma wertheimsteini (Rebel) which, under natural conditions, feeds exclusively on Chondrilla juncia (Hasan and Wapshere, 1977). The monophagous habit is the least common of the three (Schoonhoven, 1972). Oligophagous insects are also specialists which will accept a small number of taxonomically related plants. Examples of insects with this feeding habit are the tobacco hornworm, Manduca sexta L., which feeds exclusively on one family of plants, the Solanaceae, and the swallow tail butterfly, Papilio machaon L. which feeds on umbelliferous plants (Wiklund, 1973; Yamamoto, 1974). Polyphagous insects are referred to as feeding generalists. These insects will eat a wide variety of taxonomically unrelated plants. An example of an insect with this type of food habit is Prodenia eridania (Cramer) (Soo Hoo and Fraenkel, 1966). It has been observed that insects may show a change in feeding specificity with feeding experience (Wiklund, 1973; Yamamoto, 1974; Hanson, 1976).

Yamamoto (1974) demonstrated that newly hatched larvae of the tobacco hornworm are polyphagous but become oligophagous after a period of induction to solanaceous plants, their normal hosts.

With the evolution of specialized feeding, insects required specialized sensory systems to discriminate between host and nonhost - plants (Schoonhoven, 1972 b). Perception of physical characters, such as vertical silhouettes and colour, are useful in locating plants but are not discriminative enough for food recognition (Schoonhoven, 1972 a). Chemical perception is the most important sensory modality in host selection (Jermy, 1971; Zwolfer and Harris, 1971; Schoonhoven, 1972; Bernay and Chapman, 1975). Insects detect plant chemicals with olfactory and contact chemoreceptors (Thorsteinson,1960; Schoonhoven, 1968). Olfactory receptors are usually located on the antennae but they may also occur on the maxillary and labial palps (Schoonhoven, 1968). Contact or gustatory chemoreceptors are located on the maxillae, labium and the tarsi. Some insect groups have additional specialized areas, as in lepidopterous larvae, which have receptors in the epipharynx and hypopharynx (Packard, 1903; Imms, 1957; Schoonhoven, 1968).

The importance of sensory receptors in host recognition has been demonstrated with ablation, electrophysiological, and behavioral experiments. Removal of sensory organs may increase the host-plant range of an insect to include normally rejected plants (Waldbauer and Fraenkel, 1961) or it may

result in a loss of response to chemical stimuli (Deseo, 1976), Electrophysiological experiments with chemical stimulants have indicated that insects are responsive to a wide variety of plant chemicals (Dethier and Kuch, 1971; Dethier, 1973, 1976; Schoonhoven, 1976; Boer et al, 1977). Behavioral studies to assay the effects of chemicals, plant extracts or plants on host selection have been used to demonstrate the importance of olfaction and gustation in food choice. Olfactometers, artificial substrates such as pith, filter paper, agar, styropor, cork, Poropak-Q, leaf discs, or vacuum infiltrated lettuce, have been used to present chemicals to an insect in choice or no-choice situations (Harris and Mohyudden, 1965; Meisner and Ascher, 1968; Meisner et al, 1974; Smith et al, 1976; Vernon et al 1977). By evaluating the insect's response through observation, weight loss of test substrate, area loss, or frass production, the activity of a test substance can be assessed (Dadd, 1960; Heron, 1965; Akesan et al, 1967; Meisner et al, 1972; Ascher and Meisner, 1973).

Natural products with no nutritive value, often referred to as secondary plant substances, and nutritive substances are the chemicals involved in host selection (Lipke and Fraenkel, 1956; Beck, 1965; Jermy, 1971; Zwolfer and Harris, 1971; Meisner et al, 1974). Secondary plant chemicals are considered to be the most important factor involved in insect-plant relationships (Vershaffelt, 1911; Dethier, 1954, 1970; Fraenkel, 1959; Soo Hoo and Fraenkel, 1966; Wiklund, 1973).

c) Secondary Plant Compounds

Secondary plant substances are synthesized by most plants. These chemicals include glucosides, saponins, tannins, alkaloids, quinones, flavonoids, essential oils, and non-protein amino acids. Specific compounds may only occur in certain families, genera, species or even subspecies. Many of these chemicals have distinct flavours and odours which they impart to the plant and become one of its major chemical characteristics. In general, secondary plant chemicals produced by a genus or series of related genera are structurally similar (Pellêtier, 1970). In some plants they are stored in the roots, seeds, bark, trichome secretions, and vacuoles of leaves (Thurston et al, 1966; Parr and Thurston, 1968). The following factors all influence their site of accumulation and concentration: age of the plant; culturing methods; season; geographic location; time of day; and selective herbivore pressure (Smith 1942; Jeffery, 1959; Dolinger et al, 1973; Robinson, 1974; Mothes, 1976; Ellis et al, 1977.)

Secondary plant chemicals may serve as: (1) a reservoir of precursors for protein synthesis; (2) stimulants to growth, metabolism, or reproduction; (3) detoxification agents to possibly harmful metabolites; and (4) metabolic waste products which accumulate due to the absence of appropriate excretory mechanisms (Pelletier, 1970). However, it is generally felt that secondary plant chemicals are not related to the basic metabolic activities of plants, but instead, are

produced by plants for protection against herbivores and pathogens (Fraendel, 1959; Jermy, 1966; Ehrlich and Raven, 1967; Feeny, 1973, 1976; Mothes, 1976; Rhoades and Cates; 1976).

The evolution of secondary chemicals in plants has been connected to selection pressure on plants by herbivores and pathogens. The influence of these chemicals on insect-plant interactions is attributed to insects co-evolving with their host's chemistry (Fraenkel, 1959, 1969; Jermy, 1966; Ehrlich and Raven, 1967; Ehrlich, 1970; Feeny, 1973). The close associations which result from this co-evolution are demonstrated in insects which characteristically feed on taxonomically and chemically related plants. Many of these insects show distinct sensitivities towards their hosts' chemicals. Examples of this are seen with cruciferous-eating insects, where compounds common to their food plants, such as sinigrin, allyl-isothyocyanates and mustard oil glucosides, are instrumental in host recognition and acceptance (David and Gardiner, 1966; Nair and McEwen, 1976; Tanton, 1977).

d) Insect Responses to Plant Chemicals

Plant chemicals direct insect-host interactions through influencing both behavioral and physiological processes of the insect (Hsiao, 1969). Behavioral responses of an insect are either positive or negative towards plant chemicals (Dethier, 1947). Food choice may be determined by the ovipositing female, or the larvae, or both (Thorsteinson, 1960;

Wiklund, 1974). The process of selection consists of a series of strictly positive or negative reactions which may involve orientation movements (either towards or away), locomotory movements (either towards or away), test biting, and feeding or oviposition (Dethier, 1960; Matsumoto, 1962; Saxena, 1969). A plant will be accepted as a host only if the insect responds in a positive way through all the steps involved in the selection process (Matsumoto, 1962; Hsiao, 1969; Saxena, 1969). Depending on the type of response an insect shows towards a plant chemical that compound may be classified as an arrestant, an attractant, a stimulant, a repellent, or a deterrent (Dethier et al, 1960).

The relative importance of nutrient and secondary plant chemicals in host selection varies from one insect species to another (Bernays and Chapman, 1977). Nutrients, such as sugars, amino acids, steroids, lipids, and vitamins generally act as feeding stimulants (Thorsteinson, 1958, 1960; Vanderzant, 1967; Ma, 1969; Dadd, 1973; Meisner et al, 1974). The chemosensory systems of insects have been found to be sensitive to nutrients such as sugars, inositol, amino acids, and salts (Schoonhoven, 1972; Weiczorek, 1976). Secondary plant chemicals influence feeding by acting as attractants, arrestants and stimulants to guide an insect towards a host plant and, as repellents and deterrents to guide insects away from non-host plants (Bernays and Chapman, 1977). Host-specific (or token) stimuli are required by some insects to locate their hosts (Fraenkel, 1959; Keller and Davich, 1965; David and Gardiner, 1966; Hsiao, 1969;

Dethier, 1970 Pliske, 1975; Nair and McEwen, 1976; Smith et al, 1976; Bernays and Chapman 1977). Sensory receptors specific to secondary plant chemicals of an insect's host plant (s) have been found (Schoonhoven, 1967; Wieczorek, 1976, Ma, 1977). However, the influence of deterrent and repellent secondary plant chemicals are also important in host selection (Dadd, 1960; Jermy, 1966, 1969; Harley and Thorsteinson, 1968).

From the observations of both the positive and negative effects of secondary plant chemicals on host selection, it appears that insects have adopted a two-way chemoreceptor mechanism of host selection (Jermy, 1966). Feeding specialists (the mono-and oligophagous insects) with narrow food plant ranges show a very high sensitivity to repellent and/or deterrent compounds and are more likely to use host specific chemicals as sign stimuli in host selection. In contrast, feeding generalists (the polyphagous insects) show a low sensitivity to repellent and deterrent compounds and do not depend on sign stimuli for host recognition (Thorsteinson, 1958; Dadd, 1960; Jermy, 1966, 1969; Hsiao and Fraenkel, 1968; Bernay and Chapman, 1975, 1977; Ma and Kubo, 1977). However, in both types of feeders, it appears that the presence of repellent or deterrent compounds are largely responsible for guiding on insect's food choice.

Insect behavior towards a plant is invariably influenced by more than one chemical (Dethier, 1947; Nair and McEwen, 1976) and it is the total chemical complex of the plant which is important in the selection process (Schoonhoven, 1968). In

some instances, feeding on plants may be regulated by the ratio of phagostimulant and deterrent compounds (SooHoo and Fraenkel, 1966; Maxwell, 1969; Bernays and Chapman, 1977). Bernay and Chapman (1977) found that the feeding response of Locusta migratoria L. to a mixture of sucrose (a phagostimulant) and tomatin (a phagodeterrent) was affected by the ratio of the two compounds.

Besides influencing the behavior of an insect, ingested plant chemicals also affect an insect physiologically. This is confirmed by the observations that growth, survival, and reproduction of an insect vary with the host plant (Pant et al, 1961; Pandy and Srivastava 1967; Pant and Dang 1969; SooHoo and Fraenkel, 1969; Wiklund 1973; Chew, 1977). Nutrient imbalances and deficiencies may slow growth, affect survival, and reduce fertility and fecundity (Painter, 1958; Cibula et al, 1967) but they do not account for the great differences observed in insects reared on different hosts (Beck and Reese, 1976). The major part of the observed differences have been attributed to the array of secondary plant chemicals peculiar to each host plant (Beck and Reese, 1976). Negative effects (collectively called antibiosis (Painter, 1958)) on an insect's developmental characteristics by secondary plant chemicals have been found to affect such things as growth, pupation, adult emergence, survival and utilization of food (Barney and Rock, 1975; Dahlman and Rosenthal, 1975, 1976; Reese and Beck 1976 a,b; Rhoades and Cates 1976; Meisner et al, 1977, 1978; Sivapalan and Schivarandarajah, 1977).

In order to successfully co-evolve with their food plants, insects have to adapt their physiological processes to cope with the chemistry of their hosts (Cibula et al, 1967). Adaptation to a particular plant involves tolerance to the chemistry of secondary products (Schoonhoven and Derksen-Koppers 1976). Tolerance may be achieved by a variety of mechanisms; by excreting and egesting secondary compounds to prevent a possible build up of harmful concentrations in the haemolymph (Self et al, 1964 a & b; Maddrell and Gardiner, 1976; Rafaeli-Bernstein and Mordue, 1978); insensitivity of the insects tissues to ingested compounds (Vaughan and Jungrees 1977); metabolizing compounds to non-toxic forms (Self et al, 1964 a & b); or development of permeability barriers around sensitive tissues, such as the nervous system (Yang and Guthrie, 1969).

As a result of the large number of food plants used, feeding generalists contact a wide variety of secondary plant compounds whereas feeding specialists are restricted to a few closely related secondary plant chemicals, which are characteristic of their food plants. To cope with the wide variety of secondary plant chemicals, feeding generalists can synthesize a large number of detoxification enzymes (Slansky, 1976).

Some phytophagous insects have adopted the strategy of sequestering certain secondary plant compounds from their host plants for their own use (Riechstein et al, 1968; Rothschild et al, 1972; Schoonhoven, 1972 a; Rothschild et al,

1973; Bernays et al,1977). The stored compounds may have a role in the defense of an insect by rendering it unpalatable (Rothschild and Aplin, 1971; Duffey and Scudder, 1972; Rothschild et al, 1973; Brower and Moffat, 1974; Isman et al, 1977), to repel predators (Common and Bellas, 1977), or they may be used in the production of sex pheromones (Edgar et al, 1971; Culvenor and Edgar 1972; Pliske, 1975).

Insects and plants have been evolving together for the past 200,000 million years (Southwood, 1973). New host-plant relationships are continuing to develop, thus the process is still in motion. In considering interactions between phytophagous insects and plants, secondary plant chemicals and their influence on a given insect is an aspect of insect-host relationships which should be well understood. Information gained from these studies have been applied to areas such as weed control, development of crops resistant to insect injury, and in treatment of crops to reduce damage. The host-specific reaction of insects can be used as a means of biological control of weeds (Harris and Zwolfer, 1968; Zwolfer and Harris, 1971; Peshken and Harris, 1975; Waphshere and Kirk, 1977). However, before an insect can be released for such a purpose, extensive research must first be done to ensure that the insect will not establish itself on plants of economic significance.

Plant resistance to insect injury involves the modalities of antixenosis (or non-preference), antibiosis, and tolerance to insect infestation (Painter, 1958, Kogan and

Ortman, 1978). Antixenosis (nonpreference) and antibiosis are the most valuable forms of plant resistance (Beck, 1965). Non-preference can be expressed by the insect during any of the stages of host selection. A negative response by an insect to a plants chemistry would make the plant unsuitable for the insect, and thus the plant is protected from injury by that insect (Hsiao, 1969). Plant resistance by antixenosis mechanisms has been demonstrated as being the modality of resistance in musk melon, Cucumis melo L. to the melon aphid Aphis gossypii (Glover) (Kennedy et al, 1978) and in Scot's pine, Pinus sylvestris (Smelyants, 1977).

Antibiosis effects, causing premature death, smaller size, and reduced fecundity also aid in plant resistance. Often these effects of the secondary plant chemicals are dependent upon their concentration in plant tissues (Gupta and Thorsteinson, 1960; Prasad and Bhottochang, 1975; Reese and Beck, 1976 a,b; Meisner et al, 1977 a,b, 1978). Developmental characteristics of an insect are affected by the variety of a host plant and can be attributed to variations in the quantities of secondary plant compounds produced (Dahlman and Rosenthal, 1975, 1976; Agarwal and Krishnananda, 1976; Meisner et al, 1977 a,b). An example of this concentration effect is in the relationship of the European corn borer, Ostrinia nubilalis Hbn with corn. Resistance or susceptability of inbred corn strains is, in part, dependent on the concentration of the chemical 2,4 - dihydroxy - 7 - methoxy - 1, 4 (2H)-benzoxazin-3 one, commonly referred to

as DIMBOA. Strains which characteristically maintain high concentrations of this compound are resistant to borer attack, while those which do not, are susceptible (Klun, 1969). Antibiosis as a mechanism of varietal resistance has generally been well documented (Shad et al, 1975; Tingy et al, 1975; Putnam, 1977).

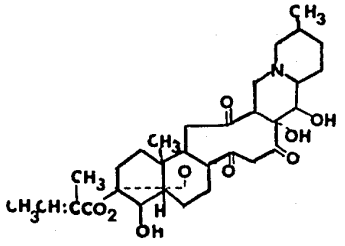
In considering the defensive role of secondary plant chemicals, it could be possible to use these substances in a similar manner as insecticides for crop protection (Jermy, 1971; Chapman, 1974; Hassid et al, 1976). The knowledge of the mechanisms involved in a pest's association with its host plants can be used to find chemical agents which are very specific and would likely not result in the development of resistant strains of insects (Jermy, 1971).

In light of the above implications of insect reactions to plant chemicals and in reviewing the research which has been done in this area, there are apparent gaps in our knowledge of insect-host relationships. Past investigations have dealt primarily with short term effects of an insect's contact with secondary plant chemicals, generally with restricted exposure to one instar or part of an instar. The long term influences of secondary chemicals on an insect are less well understood (Reese and Beck, 1976). For purposes of such studies, polyphagous insects are of interest since their diverse feeding habits brings them into contact with many secondary plant compounds which may have varying influences on growth and development. The dark-sided cutworm, E. messoria

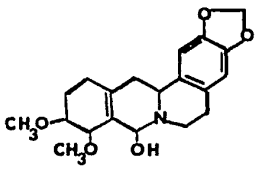
is an example of a polyphagous feeder. Agricultural reports of the food plants of this insect include examples from 15 families and 25 different genera. The mechanisms of food choice and the influence of different plants ingested on the biology of this insect are not well understood.

Of the secondary plant compounds which have been tested for behavioral and physiological activity on phytophagous insects, alkaloids are among the most consistently deterrent (Bernays and Chapman, 1977). Alkaloids are basic, nitrogen-containing, heterocyclic rings which are biosynthetically related to amino acids (Swan 1967; Robinson, 1974). Levin (1976) estimated that roughly 20% of the perennial and 33% of annual plants in North America contain alkaloids. Generally, plants synthesize more than one alkaloid (Mothes, 1960) and different strains of a species may have different alkaloid concentrations (Manske, 1950). Alkaloids are primarily produced in the roots, but synthesis may occur in other organs as well (Mothes, 1960). Production begins at germination and is commonly associated with new tissues (James, 1960; Mothes, 1960).

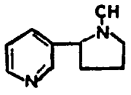
The alkaloids used in the currently-reported experiments were berberine, atropine, veratrine and nicotine (Figure 1). Berberine is a widely distributed alkaloid, occurring in the following families: Berberidaceae; Anonaceae; Menespermaceae; Ranunculaceae; and Rutaceae (Manske and Asheford, 1954). The concentration of berberine in plant tissues of Mahonia



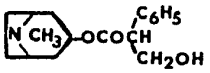
VERATRINE



BERBERINE



NICOTINE



ATROPINE

Figure 1. Structural formulae of the alkaloids veratrine, berberine, nicotine, and atropine.

species were found to range from 2.48% in the roots to none in new leaves (Greathouse and Walkins, 1938). Schoonhoven and Dersken-Koppers (1976) found that berberine reduced survival and was a feeding deterrent to the green peach aphid. Myzus persicae Sulz.

Veratrine, also described as cevadine, has a narrow distribution and has been isolated from Veratrum and related genera (Prelog and Jerger, 1953). In experiments with Melanoplus bivittatus Say Harley and Thorsteinson (1967) found that veratrine had no effect on the growth and feeding behavior of this insect.

Atropine, which is obtained from the deadly nightshade, Atropa belladona, is restricted to solanaceous plants. The racemic form, L-hyascyamine, is the most commonly occurring alkaloid in the Solanaceae family (Holmes, 1950). L-hyascyamine readily changes to atropine in the presence of water, but in most intact plants, atropine is present only in small quantities (Holmes, 1950). Atropine has been found to act as a strong phagodeterrent to M. persicae (Schoonhoven and Derksen-Koppers, 1976).

Nicotine is also a solanaceous alkaloid, and is the principal alkaloid of Nicotiana species. In studies by Jeffery (1959) on 29 species of Nicotiana, the nicotine content was found to range from 0.01% - 7.00% (dry weight basis).

e) Artificial Diets

Artificial diets, which are diets other than an insect's

natural food (Vanderzant, 1974), are commonly used to rear phytophagous insects (House, 1967; Dadd, 1973; Vanderzant, 1974). To be an effective substitute for the natural food, an artificial diet must provide all the nutritional requirements in the correct balance and the food must be freely ingested (Friend, 1958; Dougherty, 1959).

The qualitative dietary needs of all insects are similar (Fraenkel, 1959; Dadd, 1973). The basic nutritional requirements include most or all of the following: carbohydrate, protein (including the 10 amino acids essential to the rat, arginine, histidine, leucine, lysine, methionine, phenylalanine, threonine, tryptophane and valine), sterols, lipogenic factors (choline, inositol), polyunsaturated fatty acids, fat soluble vitamins (α tocopherol, carotene), minerals including potassium, phosphate, magnesium, calcium, sodium, chloride, and trace supplies of iron, zinc, manganese, and copper), B vitamins (including thiamine, riboflavin, nicotinamide, pyridoxine, pantothenic acid, folic acid, biotin and B12), ascorbic acid, and water (Ouye and Vanderzant, 1964; Dadd, 1973; Vanderzant, 1974; Hodgson et al, 1977; Navon, 1977; Singh, 1977).

The proper feeding stimulants must also be supplied if the diet is to promote good growth and development (Dougherty, 1959; House, 1965; Vanderzant, 1969). Feeding stimulants include chemical and physical characters. Chemical stimulants are often provided by the nutrients in the diet but some insects may require the addition of specific secondary plant chemicals (Friend, 1958; Thorsteinson, 1958; Loshiavo, 1965;

David and Gardiner, 1966 a,b; Vanderzant, 1967, Wardojo, 1967). The physical properties of the diet, such as texture, hardness, and shape also affect the insect's acceptance of it (Vanderzant and Davich, 1961; Wardojo, 1967; Vanderzant, 1969). These characteristics are provided by non-nutritive substances which also act as a carrier for the nutrients. Texture (and roughage which aids in the passage of food through the digestive tract) is provided by substances such as cellulose, clay, sawdust, corncob grits, filter-paper, and polyethylene beads. The hardness of the diet is provided by gelling agents, such as agar or sodium alginate (Vanderzant, 1969; Brewer and Martin, 1976).

Artificial diets are easily contaminated by bacteria and fungi. To prevent this, antimicrobial compounds, such as aureomycin, ethanol, formalin, methyl-p-hydroxybenzoate, sorbic acid, and streptomycin, are added (Singh and House, 1970).

Nutrients are supplied through natural and refined chemical substances. Depending on the amounts of defined or undefined chemical substances used, diets may be classified into three general types:

1. Holidic diets which consist of chemically defined ingredients in their simplest form (Dougherty, 1959) and may be presented as a formula listing the specific nutrient requirements of an insect (Singh, 1977, Vanderzant, 1974). Preparation of diets for insects with biting and chewing mouth-parts requires the addition of large molecular substances,

such as agar and cellulose to give the diet the correct physical characteristics. With the addition of these partially defined ingredients, the definition for holidic diets does not apply. Vanderzant (1966) proposed that these diets be referred to as defined diets. Holidic (defined) diets are useful in nutritional studies (Vanderzant, 1974) but they are inadequate for continuous rearing (Beck et al, 1968).

2. Meridic diets are composed primarily of refined nutrient materials combined with one or more natural fractions (Dougherty,1959; Vanderzant, 1966). The use of wheat germ in meridic diets is widespread and is often required for normal growth (Chippendale and Beck, 1964; McMorran, 1965; Vanderzant, 1967; Beck et al, 1968).

3. Oligidic diets are largely composed of unrefined products such as beans. These diets are the most widely used because they are the least expensive to prepare and are usefull for mass rearing (Vanderzant, 1974).

An artificial diet, supplied with the correct balance of nutrients and feeding stimulants should provide optimal growth and fecundity for an indefinite number of generations (Dougherty, 1959). Nutritional inadequacies may not become evident until several generations have been reared on a given diet. Nutrients which are passed on in the eggs may be required in such minute amounts that several generations are necessary to deplete the store of the nutrient (Vanderzant, 1964; Leonard, 1970).

Factors such as uniform development, numbers of adults

produced, adult deformities and viability of eggs should also be considered in evaluating the suitability of a diet (Vanderzant, 1964; Dupnik and Kam 1970 Brewer, 1976).

Suboptimal growth, changes in response to host plants, or reduced vigor, fertility, and fecundity of an insect species reared on an artificial diet may be attributed to nutrient deficiencies, but behavoural and genetic changes from inbreeding may also be responsible (Dupnik and Kamm 1970; Boller, 1972; Hinks and Byers, 1976).

f) Growth of sclerotized parts.

Sclerotized parts of the insect (such as the head capsules) do not change in area during an instar, but only increase in size at ecdysis (Dyar, 1890; Gaines and Campbell, 1935). Dyar, (1890) proposed that the sclerotized parts grow in a geometrical fashion, increasing at each moult by a constant ratio for a given species. Although this rule holds true for some species, it does not hold true for all (Wigglesworth, 1972).

g) Objectives

The objectives of this study of E. messoria were: 1) to develop a meridic diet suitable for rearing the larvae; 2) to study the developmental characteristics of E. messoria when reared on alkaloid diets and on two varieties of N. tabacum, Lonibow and Delhi-34; 3) to observe larval feeding preferences for various diets, plants and chemicals and 4) to examine the role of the antennae and maxillary palps in host selection.

II. MATERIALS AND METHODS

a) Experimental Animals and Rearing Methods

Eggs were obtained from the Biosystematics Research Institute, Agriculture Canada, Ottawa. The eggs had been exposed to 21°C., for approximately 30 days, followed by 2°C for 10 days, and were placed in storage at -4°C for at least two months to break diapause (Hinks and Byers, 1976). The eggs were then brought out to room temperature and placed in clean 2.5 cm clear polystyrene vials which contained a thin slice of artificial diet interleaved with strips of filter paper. Eclosion usually occurred within 24-48 hours.

Larvae were reared under a 16h photoperiod and were usually maintained at 27°C throughout the development period. All larvae were reared individually.

Within 24 hours of hatching, first instar larvae were transferred to 1.5ml clear polystyrene beakers. A small portion of diet was placed in the bottom of each beaker. To control condensation, 1 x 2.5 cm. strips of filter paper were used to line the sides of the beakers. These containers were sealed with snap-on plastic lids, and for ease of handling, placed in wooden blocks (Plate IA). When larvae reached the third instar, they were transferred to 4.5 x 2.3 x 2 cm. clear polystyrene boxes (Plate IB).

Larvae were transferred to clean containers and provided with fresh food every two days. During the first to the third instars, larvae were handled with fine brushes. In the

remaining instars, larvae were large enough to be handled with blunt forceps. The surface areas on which the larvae were handled and all equipment used were frequently rinsed with a disinfectant solution of 5% acetic acid and 70% ethyl alcohol (Hinks and Byers, 1976).

When larvae were in the prepupal stage, they were transferred to clean boxes containing a layer of moist peat moss. (Plate IIA). The commencement of the prepupal period was considered to be the point of larval maturity and was determined by weighing daily the ultimate instar until a definite decline in weight was observed (Hinks and Byers, 1976). During the prepupal stage the peat moss was periodically misted in order to maintain the humidity.

Pupae were maintained in the same manner as described for the prepupae (Plate IIB). The sex of each individual was determined during this stage. Several days before the estimated emergence of the adults, boxes of pupae, with the lids removed, were placed in 8.3 x .7.6 x 4.1cm. clear polysterene boxes to provide ample space for the moths to emerge properly. Emergence of the adult marked the end of the observational period.

b) Diets

Larvae were reared on artificial diets containing various concentrations of four alkaloids and on two varieties of Nicotiana tabacum.

An oligidic bean diet has been successfully used to rear

E. messoria, (Hinks and Byers, 1976). The nutritional adequacy of 7 meridic test diets (Table 1) were tested to find one which could best replace the bean diet. The 7 diets were modified from the artificial diets used to rear the army cutworm, E. auxiliaris (Grote) (Sutter and Miller, 1972) and the pale western cutworm, Agrotis orthogonia Mor. (Kasting and McGinnis, 1967). The meridic diets (Table 1) were prepared as follows:

The agar solution (A) was heated in a double boiler until the mixture reached 90°C. Ingredients of B were placed in a blender, and mixed on low for 1 minute. The agar solution was added, and blended for 1 minute on low. The ingredients of C were added and mixed for 1 minute. The diet was then dispensed into containers. When the agar had solidified, the containers were covered, placed in plastic bags, and refrigerated at 3°C. The diets were prepared once a week.

The test diet which best supported larval growth was chosen for use in the alkaloid rearing experiments. Although a fertility and fecundity study was not done, adults collected from the pupae which had been reared on meridic diet VI, were crossed and the eggs were collected. The progeny of this cross were used in the nicotine diet and Nicotiana tabacum rearings.

Table I: Composition (in grams) of Meridic Test Diets fed to Euxoa messoria.

Ingredients	I	II	III	IV	V	VI	VII
A							
Agar	1.4	1.4	1.4	1.4	1.4	1.4	1.4
Water	87.0	87.0	87.0	87.0	87.0	87.0	87.0
B							
Wheat germ oil	0.7	0.7	0.7	0.7	0.7	0.7	0.7
Wheat germ						2.8	
Casein	3.2	3.2	3.2	3.2	3.2	3.2	
Soybean Protein			3.2		3.2	3.2	3.2
Sucrose	3.2	3.2	3.2	3.2	3.2	3.2	3.2
Salt Mixture W	0.9	0.9	0.9	0.9	0.9	0.9	0.9
Cholesterol	0.006	0.006	0.006	0.06	0.06	0.06	0.006
Vitamine mixture*	1.0	1.0	1.0	1.0	1.0	1.0	1.0
Ascorbic acid		0.13	0.13	0.13	0.13	0.13	0.13
C							
Sorbic acid	0.06	0.06	0.06	0.06	0.06	0.06	0.06
Methylparaben	0.1	0.1	0.1	0.1	0.1	0.1	0.1
10% KOH	1.0	1.0	1.0	1.0	1.0	1.0	1.0
Formalin	0.2	o.2	0.2	0.2	0.2	0.2	0.2

*Vanderzant vitamin mixture

The alkaloids, nicotine, atropine, veratrine and berberine were added to the artificial diet before it had solidified. Appropriate amounts of each alkaloid were added to a portion of diet to attain the concentrations of 0.01%, 0.03%, 0.10%, 0.30% and 1.00% by weight. Atropine, veratrine and berberine, which were provided in a powdered form, were first mixed with a small portion of distilled water to dissolve the chemicals before being mixed into the diet. The water-alkaloid mixture allowed a more even distribution of the alkaloid within the diet.

First instar larvae were introduced to the alkaloid diets within 24 hours of hatching and were reared as described previously.

Two varieties of Nicotiana tabacum, Delhi-34 and Lonibow, were grown from seed in a pesticide free growth chamber. These varieties were chosen on the basis of the differences in alkaloid content. The total alkaloid content of samples of Delhi-34 and Lonibow, taken in 1976-1977, measured 2.50% and 0.23% respectively (White, 1976, 1977).

The seedlings were grown to a height of approximately 15 cm (root crown-bud) before leaves were removed for feeding to the first instar larvae. The mid rib of the leaf was removed and the remaining leaf was cut into strips of approximately equal size to be fed to the larvae. The rearing procedures previously described were followed with the exceptions

that fresh food was provided daily and that fourth instar larvae were transferred to clear polystyrene petri dishes. (Plate IIC). The latter was necessary due to the wet conditions which resulted when fresh leaves were used. The loosely fitting lids of the petri dish aided in keeping the larvae dry.

Growth performance on the different food sources (test diets, alkaloid diets, and tobacco plants) were evaluated by the following measurements ; weight (weekly, maximum larval and pupal); duration (in days) of each instar; total number of days to larval maturity, pupation and adult emergence. The head capsules were also collected and measured. Each test-treatment was run with a control with 30 first instar larvae being introduced to each diet.

c) Feeding Behaviour

To examine the possible phagostimulatory activity of some chemicals and plants, and the role of selected sensory structures, a feeding arena was devised using a large glass dessicator (25 cm dia.) (Plate IIIA). Test materials were presented on millipore discs (25 mm dia.). The millipore discs provided an inert medium (composed of esters of cellulose) of a uniform thickness and the feeding activity of the test materials are easily assessed by measuring the area loss. The discs were supported by stainless steel pins and placed along the perimeter of the arena (Plate IIIB). The discs were

raised approximately 0.5 cm. off the surface, however, the larvae would often climb over the discs, pushing them onto the surface of the arena. Test materials (Table 2) were applied by squashing the material onto the discs (diets and plant materials) or by soaking the discs in test solutions. An equal number of discs from each treatment were placed in the arena. The discs were arranged in a constant order (ex. abc, abc, etc) and in the majority of experiments a total of 18 discs were presented to the larvae. The humidity of the arena was maintained by placing a moistened piece of filter paper on the surface, under the test discs. This was necessary to prevent a disc from drying and thus causing a change in the concentration of test materials. The surface and sides of the arena were thoroughly cleaned after each feeding trial.

Ultimate instar larvae were selected for use approximately 24 hours after ecdysis. To investigate the role of the antennae, and maxillary palps in feeding, larvae were anesthetized with CO_2 and the antennae, maxillary palps or both were removed (Plate IV,V) with the aid of a dissecting microscope and fine edged forceps. The larvae were allowed to recover for 24 hours prior to experimentation. All the larvae used (intact or operated) were deprived of food for 24 hours before use.

Five larvae were introduced into each arena, and were left there for 24 hours. At the end of this period, the larvae were discarded, and the remnants of the test discs were collected and pasted onto sheets of paper. The area loss was measured by the use of a 25 mm diameter clear plastic disc, which had been marked off into 50 squares. The approximate amount consumed was measured by placing the clear disc over the remnants of the test discs and counting the number of squares in the area consumed.

Table 2. Test materials used in feeding preference experiments with Euxoa messoria.

I Diets
1. Veratrine
2. Berberine
3. Nicotine
4. Atropine

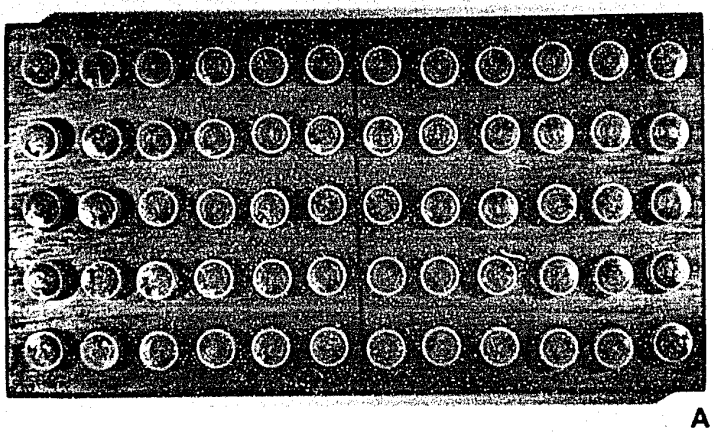
II Solutions
1. Veratrine
2. Berberine
3. Nicotine
4. Atropine
5. 3.2% Sucrose
6. 3.2% Sucrose - Atropine

III Bilateral Antennectomy
1. Veratrine diet

IV Bilateral Maxillectomy
1. Veratrine diet
2. 3.2% Sucrose
3. 3.2% Sucrose - 0.01% Veratrine; 0.01% Berberine; 0.01% Nicotine; 0.03% Atropine

V Bilateral Antennectomy and Maxillectomy
1. Veratrine diet

VI Plants
1. Nicotiana tabacum var. Lonibow, Delhi-34, Burley 21; N. alta, White bidder
2. Atropa belladona; N. tabacum var. Lonibow, Delhi-34, Burley 21
3. Garden plants: Tomato, Lycopersicum esculentum
Ageratum, Ageratum sp.
Delphinium Delphinium grandiflora L var.
Salvia, Salvia splendens (ler-Gawl) var.
Marigold, Tagetes erecta L.



A

B

Plate I. A.- Wooden carrier for 1.5 ml rearing containers.

B.- Polystyrene box used to rear larvae from the third to the ultimate instar.

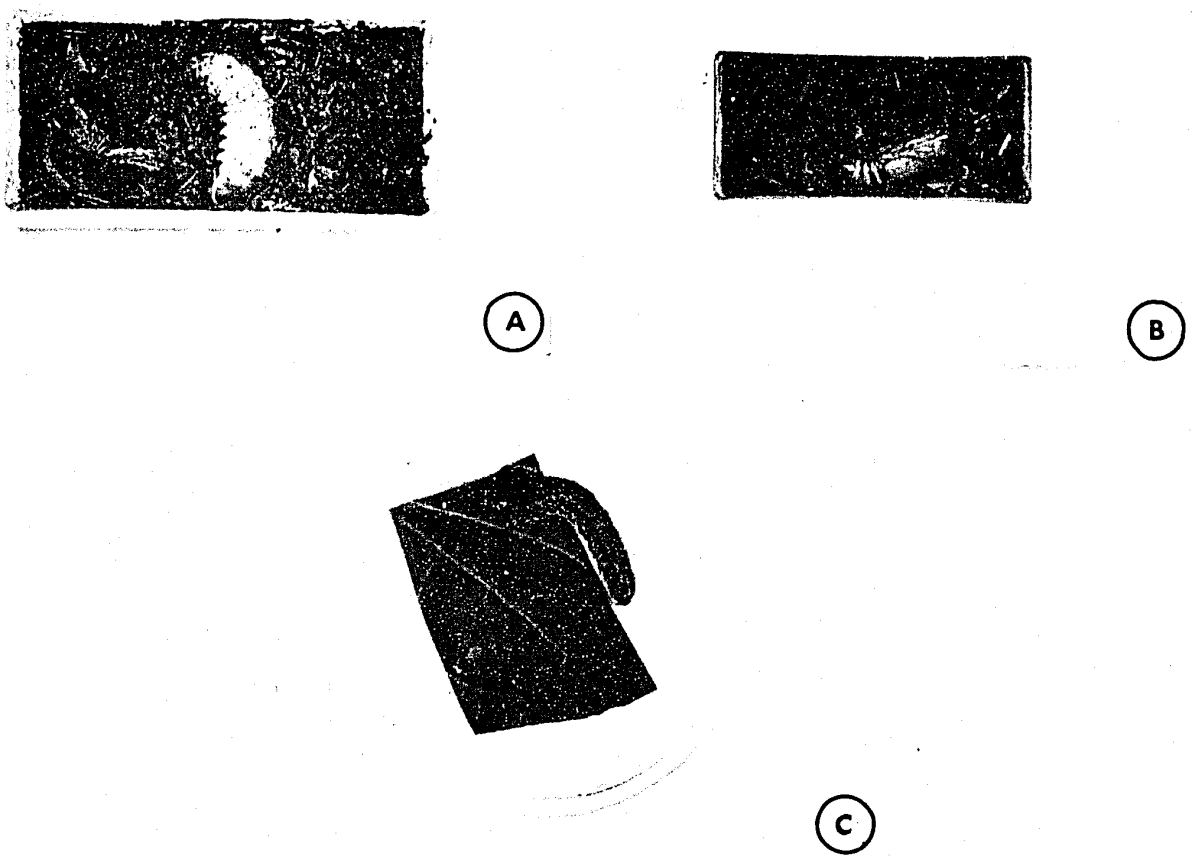


Plate II. Rearing containers for prepupae (A), pupae (B), and Nicotiana tabacum reared larvae (C).

III RESULTS

a) Growth and Development of Larvae Reared on Artificial Diets

The nutritional adequacy of the 8 diets tested, varied with respect to larval growth, development, and survival (Table 3). Meridic test diet VI provided the best medium for use as a substitute for the bean diet in rearing the larvae of E. messoria.

Survival to the pupal and adult stages was greater on the bean diet than on meridic diet I. Changes in the ascorbic acid and protein content of diet I (by increasing the ascorbic acid content to 0.04% in diets II, III, and V and by increasing the protein content with the addition of soybean protein in diets III and V) resulted in an increased number of individuals reaching the pupal and adult stages. By increasing cholesterol from 0.006% to 0.06% in these diets, (IV, V and VI), the improved survival was partially lost. However it was still better than survival on the bean diet. The highest mortality occurred on meridic diet VII, in which soybean protein was used as the sole source of protein. There was 100% mortality in meridic diet VII with the majority dying as first instar larvae during the first 2 weeks of development. A few remaining larvae moulted to the second instar and survived up to 5 weeks.

Larvae reared on the bean diet were significantly heavier ($P \geq 0.05$) at maximum larval weight than larvae reared on the test diets I and IV, but were significantly lighter

($P \geq 0.05$) than larvae reared on diets III, V and VI. The weights of the pupae from the bean diet were also significantly greater ($P \geq 0.05$) than the pupae of diet IV, but were lighter than the pupae of diets III and V. There were few apparent differences in the weights of pupae from diets I, II, and VI and the bean diet.

Larvae reared on the bean diet required significantly fewer ($P \geq 0.05$) days to attain larval maturity than larvae reared on meridic diets I, II, III and IV, but took significantly longer ($P \geq 0.05$) than larvae reared on meridic diet VI. The duration of the prepupal period was significantly shorter ($P \geq 0.05$) for the bean diet than meridic diets II, III, IV, V and VI. The total number of days to pupation and adult emergence was also significantly shorter ($P \geq 0.05$) for those reared on the bean diet than for all of those reared on the meridic test diets. In a comparison of the development times of the meridic test diet groups, diets V and VI required significantly fewer days ($P \geq 0.05$) to develop as larvae and pupae than the groups reared on diets I, II, III, and IV.

Larvae had 6 or 7 instars before pupation on all the artificial diets (Figure 2). The majority of larvae which were reared on the bean diet and meridic diet VI had 6 larval instars, while the majority of the larvae fed test diets I, II, III, IV, and V had 7. There is little apparent difference in the widths of the 6th and 7th instar head capsules when they are the ultimate instar.

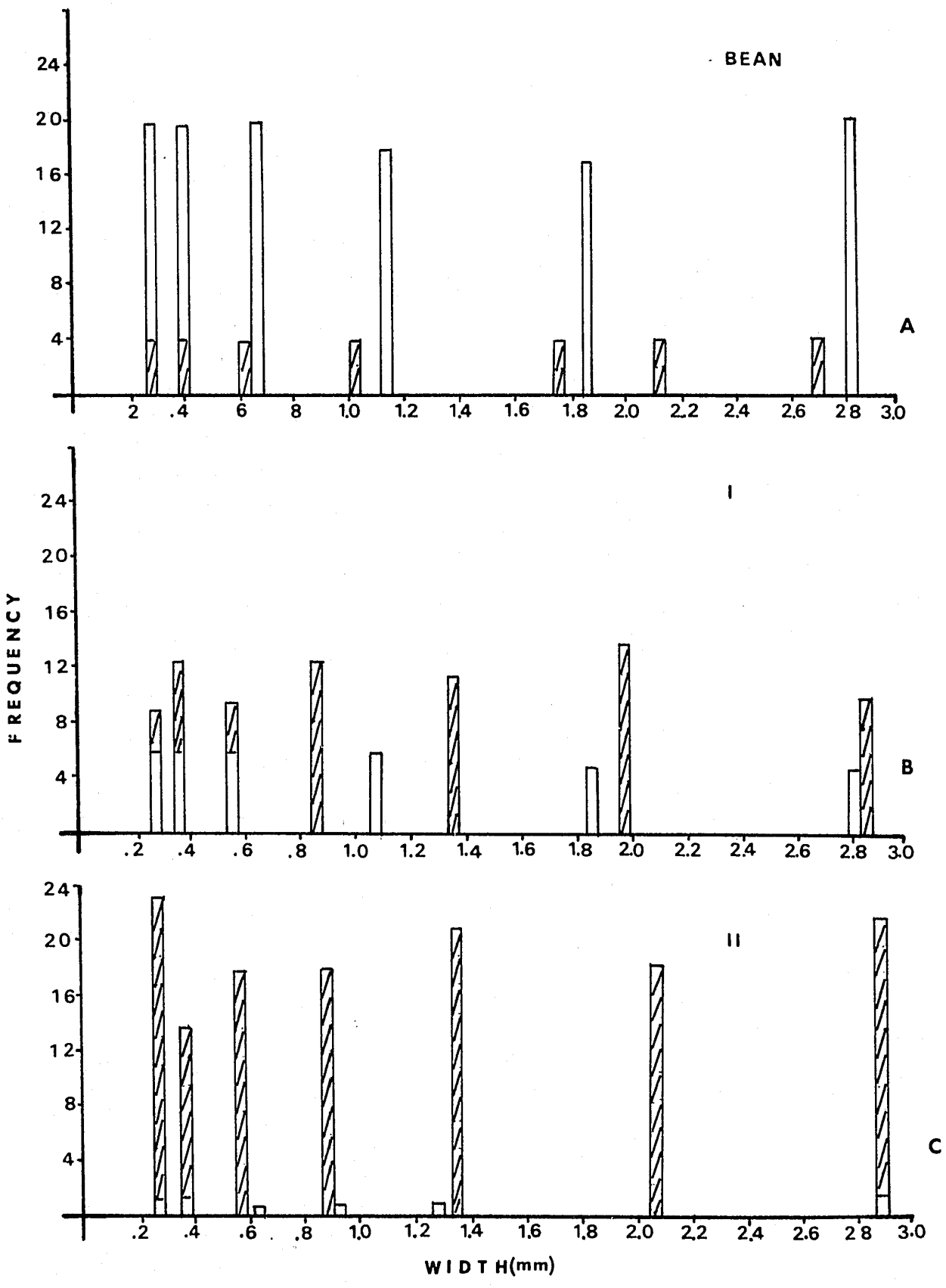
Table 3: Development of Euxoa messoria on 8 artificial diets.

Diet	Number of Days to Larval Maturity	Maximum Larval Weight (mg)	Duration (days) of Prepupal period	Number of Days to Pupation	Pupal Weight (mg)	Duration (days) of Pupal Period	Percent Pupation	Number of Days to Adult Emergence	Percent Adult Emergence
Bean	40.3 a	569.0 a	13.9 a	55.6	270.6 a	26.3 a	73.3	81.1	63.0
sd	2.5	71.6	3.5	5.8	47.8	4.2		3.5	
I	55.3 c	530.8 bc	15.2 ab	76.1 a	261.7 ab	25.7 ab	70.0	99.1 a	56.7
sd	4.6	67.5	3.4	12.3	29.7	3.2		6.3	
II	52.9	558.1 ab	16.5 bc	69.6	260.8 ab	27.2	90.0	96.4 a	86.7
sd	4.4	69.4	3.5	5.1	38.7	2.0		5.1	
III	42.1 b	790.0 d	19.4 de	62.0 b	321.2	29.0	93.4	90.2	86.7
sd	3.8	9.3	7.8	8.1	33.2	3.3		9.2	
IV	56.4 c	520.5 c	24.5	81.0 a	241.5 b	25.7 ab	73.3	106.3	70.0
sd	6.8	80.1	5.6	9.0	49.3	2.7		8.5	
V	40.7 ab	675.8	17.9 ce	60.5 b	297.1	27.3 ac	80.0	85.5 b	80.0
sd	3.4	78.4	3.8	8.4	38.6	2.3		4.5	
VI	36.3	643.8	20.2 d	59.7 b	278.1 ac	27.2 ac	73.3	84.8 b	70.0
sd	2.6	76.2	3.3	7.7	46.8	2.0		4.8	
VII **	-	-	-	-	-	-	0	-	0

* Numbers followed by common letters are not significantly different ($P \geq 0.05$).
** 100 % mortality in the first two instars.

30 first instar larvae were introduced to each of the above diets

Figure 2: Variations in the mean head capsule widths and number of instars of Euxoa messoria reared on 7 artificial diets.
▭ - 6 instars; ▭▭ - 7 instars.
A - Bean B - I, C - II, D - III,
E - IV, F - V, G - VI,


BEAN
A
I
B
II
C
FREQUENCY
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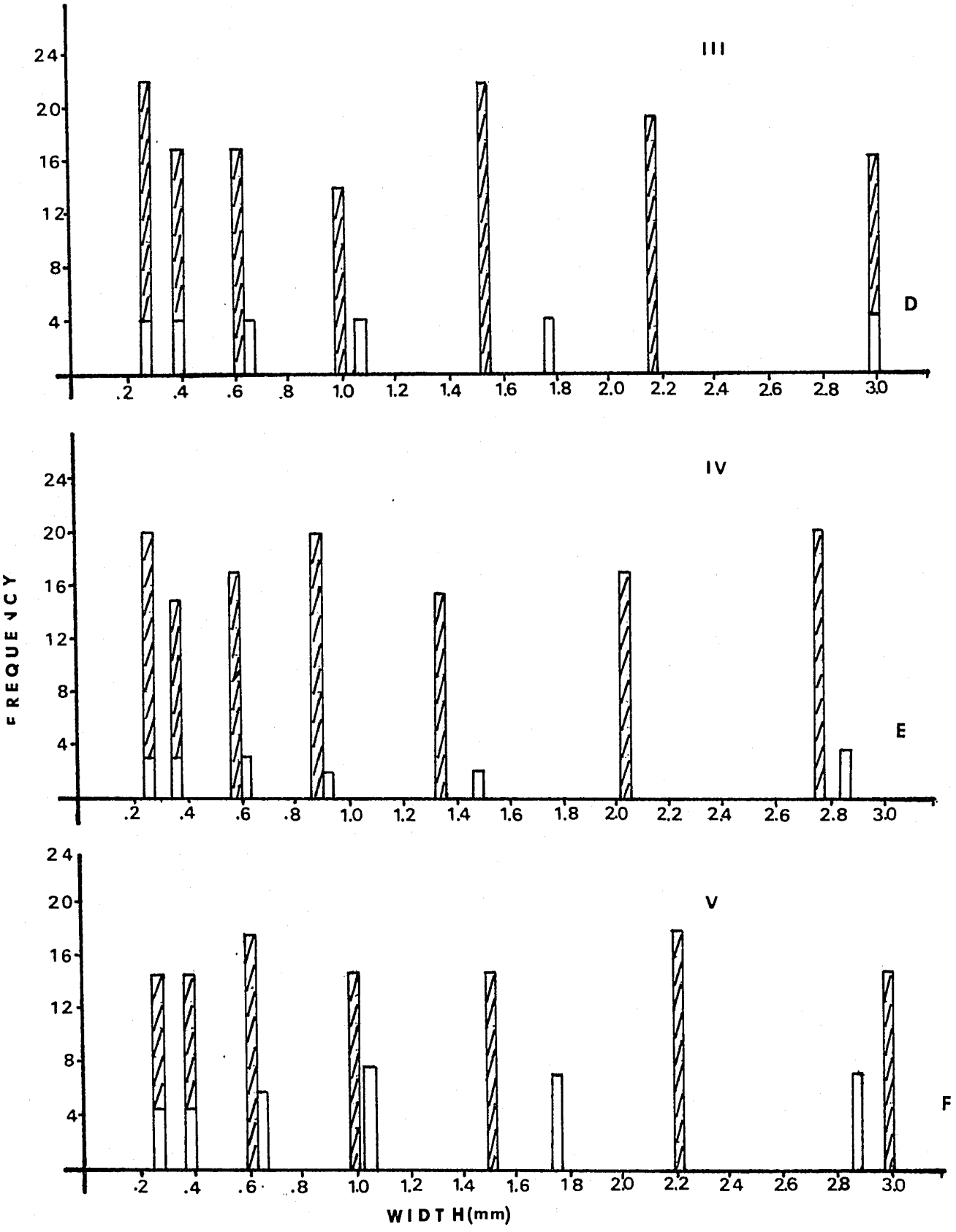
24
20
16
12
8
4
2 .4 6 8 1.0 1.2 1.4 1.6 1.8 2.0 2.2 2.4 2.6 2.8 3.0
.2 .4 .6 .8 1.0 1.2 1.4 1.6 1.8 2.0 2.2 2.4 2.6 2.8 3.0


III
D
IV
E
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FREQUENCY
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.2
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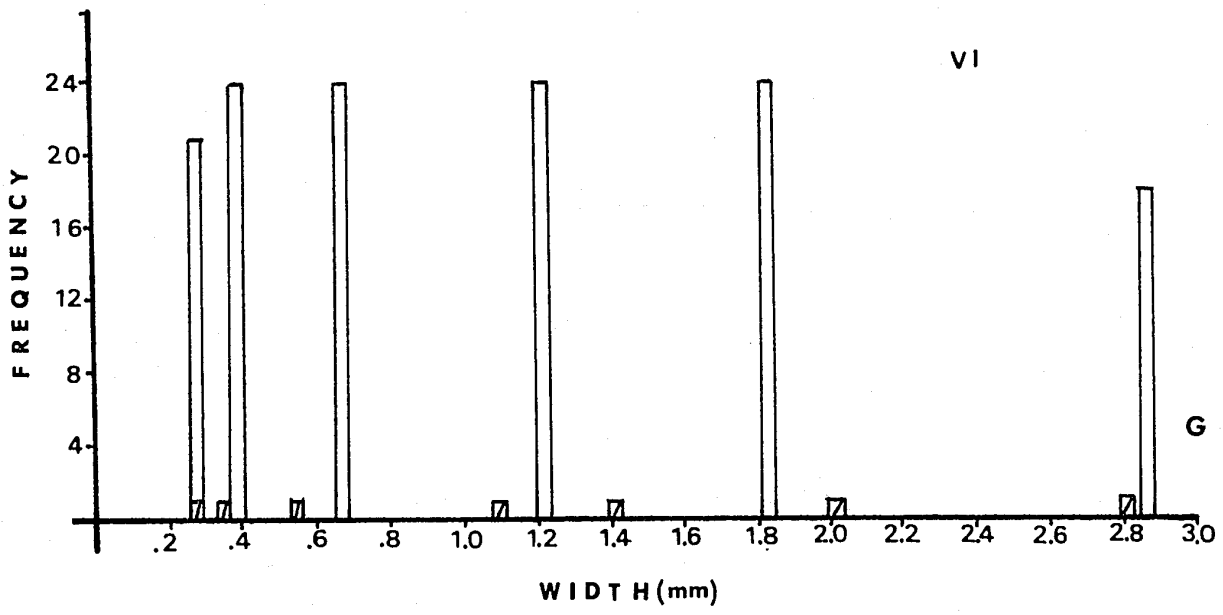
VI
G
FREQUENCY
24
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1.2
1.4
1.6
1.8
2.0
2.2
2.4
2.6
2.8
3.0
WIDTH (mm)

In general, the growth and development of larvae reared on meridic diet VI was very uniform. Most of the larvae moulted to each successive instar on the same day, while in groups fed the other 6 artificial diets, moulting was spread over 2-3 days.

The meridic test diets spoiled much faster than the bean diet. The test diets were white in colour when freshly prepared but became brown after 2 days of exposure to room temperature.

b) Influence of Alkaloids on Survival and Growth

(i) Veratrine

At all concentrations tested the addition of veratrine to the diet resulted in 100% mortality of the first instar larvae during the first week of development. The control group developed normally, with 70% of the larvae surviving to the adult stage.

(ii) Berberine

Growth and development of larvae reared on the control and berberine diets were significantly different, and varied depending upon the level of berberine present in the diet (Table 4). Of the five concentrations of berberine tested, 0.30% and 1.00% greatly reduced survival to the pupal and adult stages; 0.03% and 0.10% slightly reduced survival, while 0.01% slightly increased survival. The reduced survival of the berberine-fed larvae was associated with a high mortality in the early instars and the pupal stage.

Table 4: Development of Euxoa messoria on control diet and diets containing berberine.

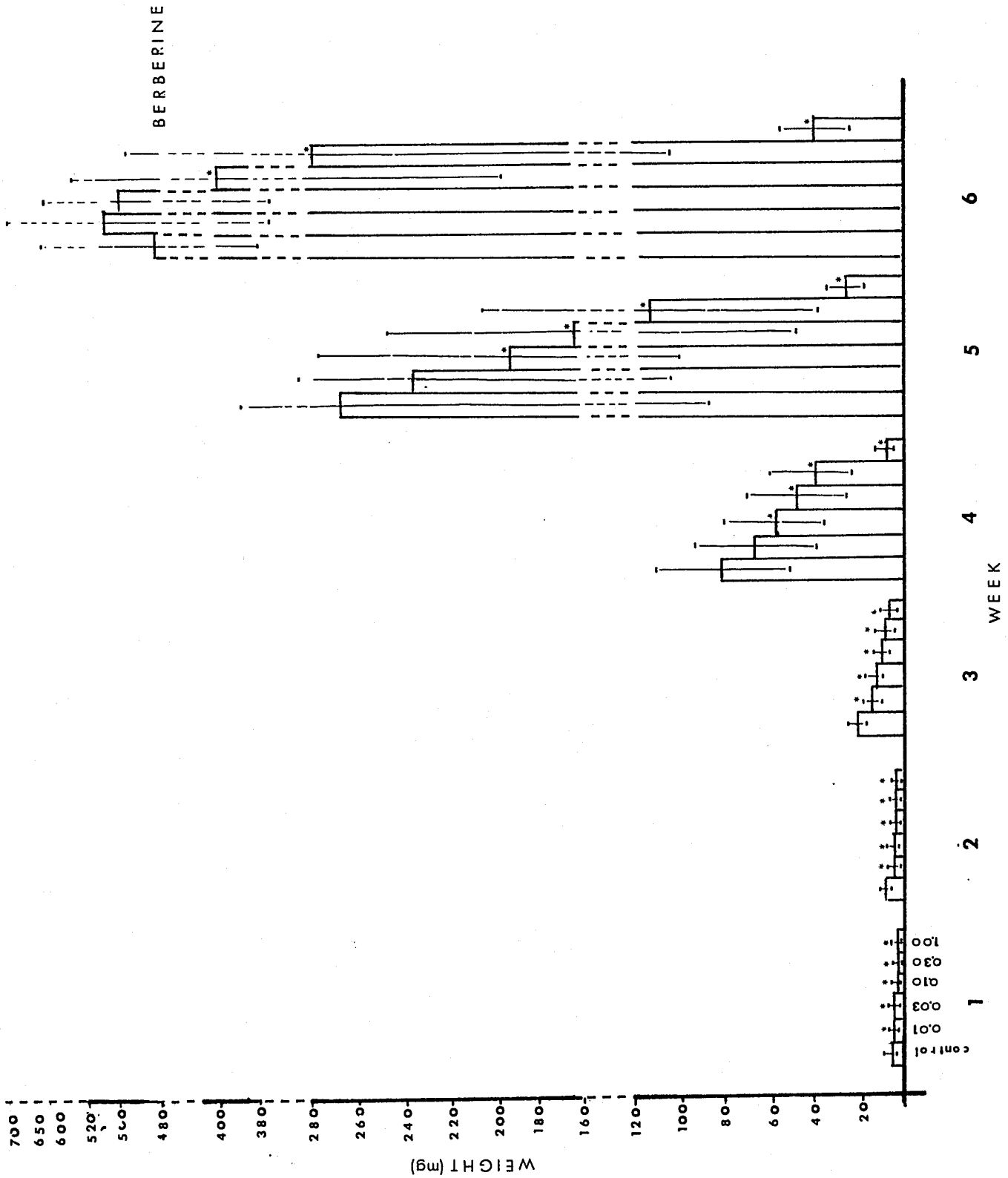
Diet	Number of Days to Larval Maturity	Maximum Larval Weight (mg)	Duration (days) of Prepupal Period	Number of Days to Pupation	Pupal Weight (mg)	Duration (days) of Pupal Period	Percent Pupation	Number of Days to Adult Emergence	Percent Adult Emergence
Control	42.8	638.8	16.6	56.2	324.5	25.7	87.0	82.0	80.0
sd	5.6	69.0	4.0	7.3	36.3	3.0		7.2	
0.01 %	42.9	640.8	16.4	59.7a	335.0	26.0	87.0	86.6a	83.0
sd	5.2	104.9	4.8	6.1	53.5	8.0		11.0	
0.03 %	43.7	627.5	14.5a	57.8	317.4	27.7	73.0	85.3	73.0
sd	4.0	59.1	4.2	5.9	29.4	6.4		9.0	
0.10 %	45.1	597.4	13.9a	59.1	307.2	25.5	77.0	84.0	73.0
sd	4.5	72.9	2.8	6.0	40.6	6.4		7.9	
0.30 %	45.9	561.7a	13.8a	63.9a	259.3a	26.6	50.0	86.7	30.0
sd	5.0	61.1	2.5	9.9	57.5	6.4		9.5	
1.00 %	-	-	-	85.0	-	-	7.0	-	0

* Numbers followed by the letter a are significantly different ($P \geq 0.05$) from the controls.

Feeding on increasingly higher concentrations of berberine extended the larval period and reduced larval size. There were significant differences ($P \geq 0.05$) between the mean weights of larvae reared on the control and berberine diets during larval development (Figure 3). At each weekly observation of the larval weights, larvae reared on 0.10%, 0.3% and 1.0% berberine were significantly smaller than the controls. Larvae fed 0.01% and 0.03% berberine diets were initially smaller than the controls, but by the 4'th and 6'th week respectively, there were no apparent differences in weights. Levels of 0.1%, 0.3% and 1.0% berberine, which reduced larval size during development, also significantly reduced ($P \geq 0.05$) the maximum larval weights. At 0.01% and 0.03% berberine has no apparent influence on size at larval maturity. Pupal weights are not affected by dietary levels of 0.01%. 0.03%, and 0.1% berberine. Larvae fed 0.3% andl.0% berberine diets formed significantly smaller pupae and at 1.0% there were only 2 pupae; they were small, malformed individuals which had not completely shed the larval cuticle.

Before the cuticle hardens and darkens, the colour of the pupae is normally white. Pupae from the berberine diets were yellow, showing a similar colour to their diets. As the colour of the diet deepened with increasing concentrations of berberine, the pupal colour also tended to deepen. The cuticle of the pupae of the 1.0% berberine diet group was extremely fragile. Upon normal handling of the larvae with blunt forceps, the cuticle was easily damaged, causing a

Figure 3: Mean weekly weights of Euxoa messoria reared on control and berberine diets. * Significantly different from the controls ($P \geq 0.05$).


BERBERINE
WEIGHT (mg)
WEEK
control
0.01
0.03
0.10
0.30
1.00

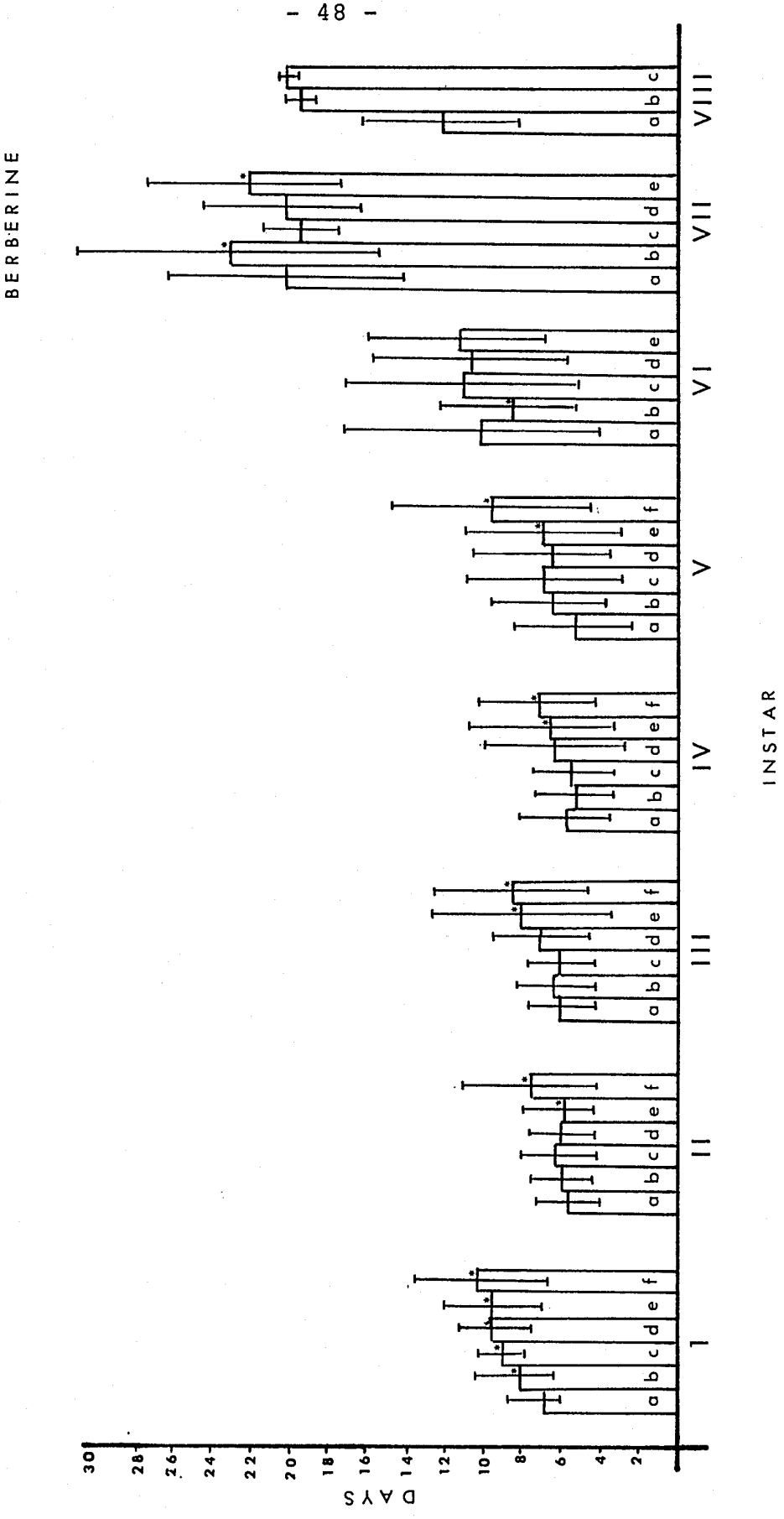
loss of haemolymph. For this reason, the pupal weights were not measured and the pupae were not handled. The pupae died within a few days of the larval-pupal ecdysis. The haemolymph which was oozing from the injured pupae was also a yellow colour, contrasting to the normally colorless pupal haemolymph.

There were significant differences in the duration of instars between the control and berberine fed larvae (Figure 4). At each level of berberine tested, the duration of the first instar was significantly increased. ($P \geq 0.05$). At 0.01%, berberine significantly increased ($P \geq 0.05$) the period of instars VII and at 0.1%, instar III. Dietary levels of 0.3% and 1.0% also significantly increased ($P \geq 0.05$) the number of days spent in instars II, III, IV, V, and VII. There were no significant differences in the duration of instars II-VII in larvae reared on 0.03% berberine.

Berberine had no apparent effect on the length of time required to reach larval maturity (Table 4), but at dietary concentrations of 0.03%, 0.1%, and 0.3%, the duration of the prepupal period was significantly reduced ($P \geq 0.05$). The total number of days to pupation were significantly increased ($P \geq 0.05$) by concentrations of 0.01% and 0.3% berberine, and the total number of days to adult emergence was significantly increased at 0.01%. There were no apparent differences in the number of days to pupation and adult emergence between the controls and the remaining berberine diets.

There was little apparent difference in the growth of

Figure 4: Mean number of days/instar of Euxoa messoria reared on control and berberine diets.
a - control, b - 0.01%, c - 0.03%
d - 0.10%, e - 0.30%, f - 1.00%.
* Significantly different from the controls ($P \geq 0.05$).


BERBERINE
DAYS
INSTAR
I
II
III
IV
V
VI
VII
VIII

males and females of the control and the berberine groups (Table 5). The females were heavier at larval maturity but produced lighter pupae than the males in the control 0.01%, and 0.03% berberine groups. The reverse was true for larvae fed either 0.10% or 0.30% berberine, there was no difference in weight at larval maturity, but the females were larger than the males at pupation. The females emerged before the males in all the groups except the 0.03% berberine group.

On all diets, the majority of the larvae had 7 larval instars (Figure 5). The controls, 0.01% and 0.03% berberine groups had a small number with 8 instars. Generally, berberine increased the proportion of larvae having 7 instars. There was little apparent difference between the mean head capsule widths of the ultimate larval instar of the control and 0.01% 0.03% and 0.10% berberine reared larvae, but larvae fed 0.30% and 1.00%, had smaller head capsule widths in the ultimate instar.

(iii) Nicotine

Larvae reared on nicotine containing diets were variably and significantly different from the controls, depending on the level of nicotine present (Table 6). Nicotine at 0.01% and 0.03% had little effect on survival to the pupal and adult stages, but at concentrations of 0.1%, 0.3% and 1.0% survival decreased. The dietary level of 1.0% nicotine caused 100% mortality in the first instar, during the first week of development. The decrease in survival of larvae fed 0.1% and 0.3% nicotine was associated with a higher mortality in the first three instars.

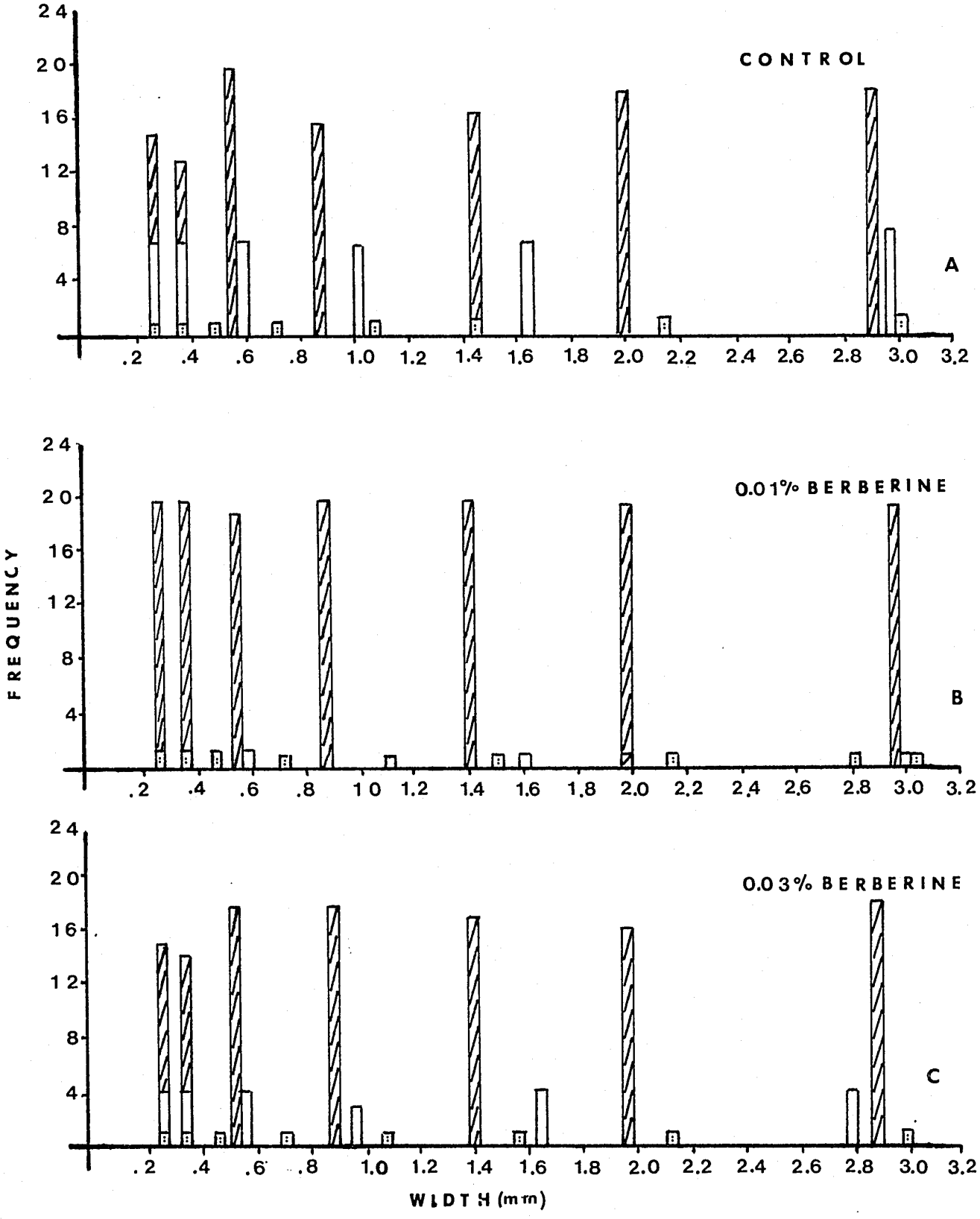
Table 5. Development of males and females of Euxoa messoria on control diet and diets containing berberine.

Diet	Number of Days to Larval Maturity		Maximum Larval Weight (mg)		Number of Days to Pupation		Pupal Weight (mg)		Number of Days to Adult Emergence		Number of	
	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂
Control	42.3	42.7	631.2	598.2	55.7	53.9	319.3	330.1	79.6	83.2	9	17
0.01 %	42.7	43.4	648.5	639.8	59.0	61.6	335.0	334.6	86.1	88.4	20	5
0.03 %	43.4	43.1	640.8	618.4	60.0	56.6	306.2	320.0	87.0	82.8	7	14
0.10 %	46.4	44.3	578.4	619.4	60.2	57.8	307.7	286.5	85.0	85.2	10	11
0.30 %	45.7	46.3	567.0	563.0	59.1	60.7	268.5	269.5	86.3	88.0		
1.00 %*	-	-	-	-	-	-	-	-	-	-	-	-

* In this group, 2 out of 30 larvae reached the pupal stage, but due to malformations, it was not possible to sex them.

Figure 5 : Variations in the mean head capsule widths and number of instars of Euxoa messoria reared on control and berberine diets.
▭ - 6 instars, ▨ - 7 instars, ▭ - 8 instars.

A - control B - 0.01 %
C - 0.03 % D - 0.10 %
E - 0.30 % F - 1.00 %


CONTROL
A
0.01% BERBERINE
B
0.03% BERBERINE
C
FREQUENCY
WIDTH (mm)
24
20
16
12
8
4
.2
.4
.6
.8
1.0
1.2
1.4
1.6
1.8
2.0
2.2
2.4
2.6
2.8
3.0
3.2

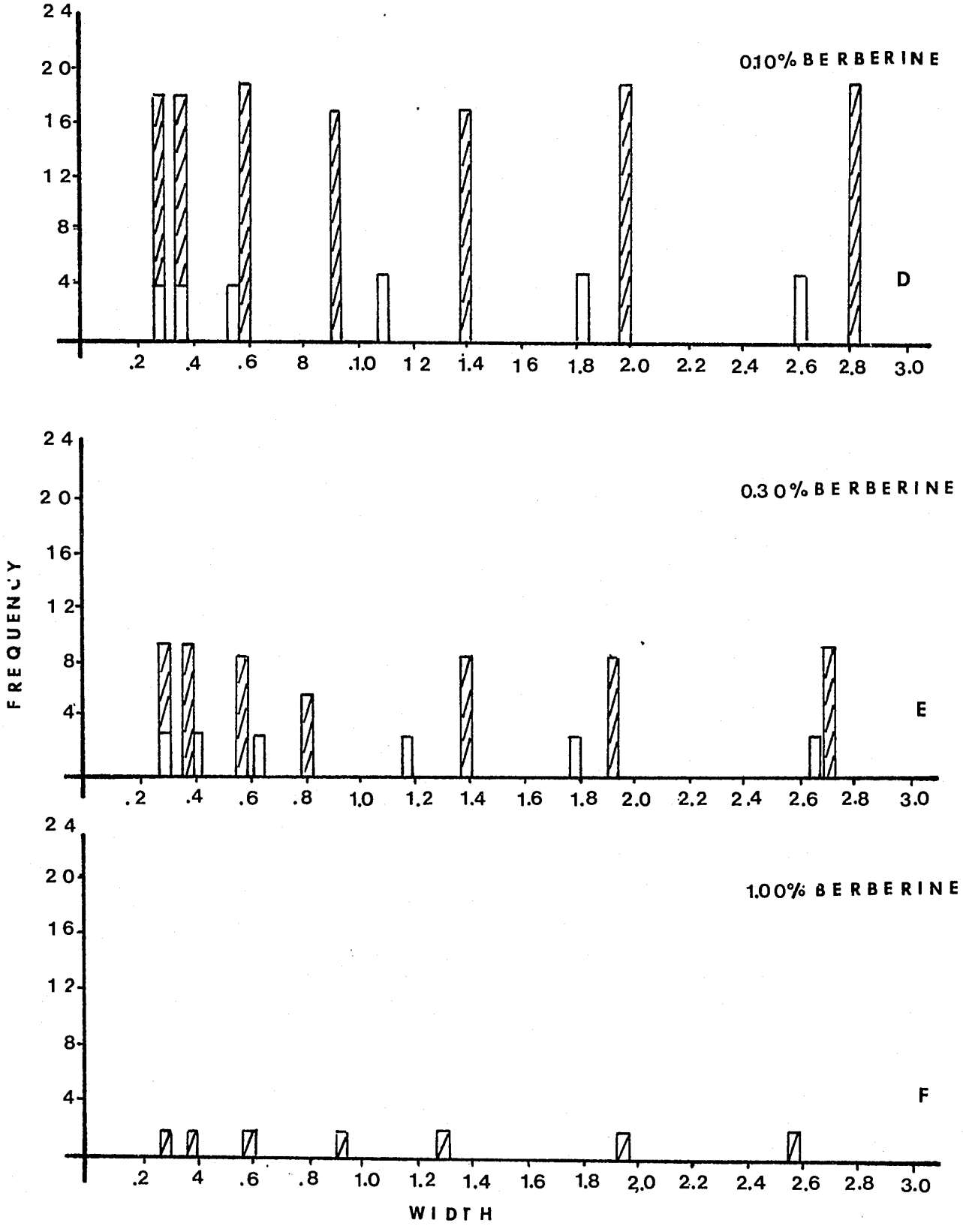

0.10% BERBERINE
D
0.30% BERBERINE
E
1.00% BERBERINE
F
FREQUENCY
WIDTH
24
20
16
12
8
4
.2
.4
.6
.8
1.0
1.2
1.4
1.6
1.8
2.0
2.2
2.4
2.6
2.8
3.0

Table 6: Development of Euxoa messoria on control diet and diets containing nicotine.

Diet	Number of Days to Larval Maturity	Maximum Larval Weight (mg)	Duration (days) of Prepupal Period	Number of Days to Pupation	Pupal Weight (mg)	Duration (days) of Pupal Period	Percent Pupation	Number of Days to Adult Emergence	Percent Adult Emergence
Control	39.5	699.0	49.5	90.6	297.8	26.0	77.0	113.7	70.0
sd	2.5	98.7	11.0	12.5	33.6	5.0		12.6	
0.01 %	38.9	703.0	51.6	87.9	300.3	27.1	90.0	111.4	67.0
sd	3.1	94.5	14.1	14.4	43.2	6.0		10.2	
0.03 %	40.2	677.7	48.4	89.5	295.6	26.1	77.0	117.1	70.0
sd	3.6	135.0	11.5	12.3	55.4	3.2		11.0	
0.10 %	43.4a*	705.4	45.4	89.5	306.9	25.9	50.0	115.9	50.0
sd	2.9	123.0	9.7	8.7	53.6	3.0		8.9	
0.30 %	45.8a	688.1	44.0	91.7	326.8	27.9	30.0	118.9	30.0
sd	4.1	116.2	10.8	9.9	63.4	1.2		9.6	
1.00 %**	-	-	-	-	-	-	0	-	0

* Numbers followed by the letter a are significantly different ($P \geq 0.05$) from the controls.
** On this diet there was 100 % mortality during the first three instars.

There were significant differences ($P \geq 0.05$) in the mean weekly weights of larvae reared on the control and nicotine diets (Figure 6). At each weekly observation of the larval weights, the mean weight of larvae fed 0.1% and 0.3 % nicotine were significantly smaller ($P \geq 0.05$) than the controls. Larvae reared on 0.03% nicotine were smaller than the controls during the first and second weeks of development but there were no apparent differences in weight during the remaining development period. At 0.01% nicotine the larvae were significantly heavier ($P \geq 0.05$) than the controls at the 2 nd and 5 th weekly observations but there were no apparent differences at the other observations. Dietary levels of 0.01%, 0.03%, 0.1% and 0.3% nicotine had no effect on the maximum larval weights and pupal weights (Table 6).

There were significant differences in the duration of instars and development times between the controls and the nicotine-fed larvae. Nicotine at 0.1% and 0.3% significantly increased ($P > 0.05$) the number of days required to reach larval maturity (Table 6). This increase in larval development time was the result of significantly longer duration of each of the first 3 instars (Figure 7). Nicotine at 0.01% and 0.03% had no apparent influence on development time to larval maturity. At the following concentrations: 0.01%, 0.03%, 0.1%, and 0.3% nicotine there was no effect upon the number of days to pupation or adult emergence (Table 6). Larvae reared on 0.1% and 0.3% nicotine had increased larval development times; they also spent less time as prepupae with

Figure 6 : Mean weekly weights (mg) of Euxoa messoria reared on control and nicotine diets.
* Significantly different from the controls ($P \geq 0.05$).

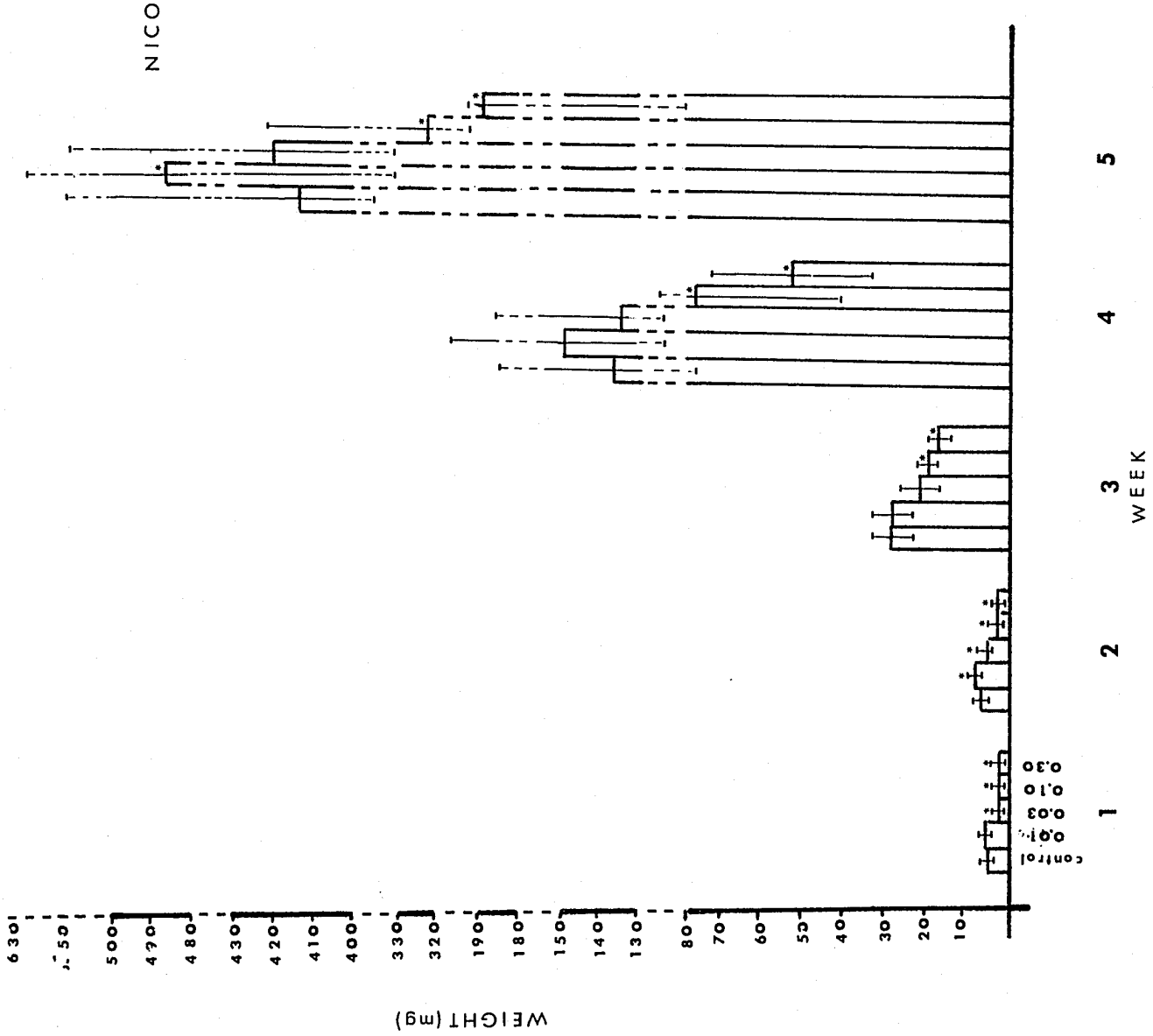
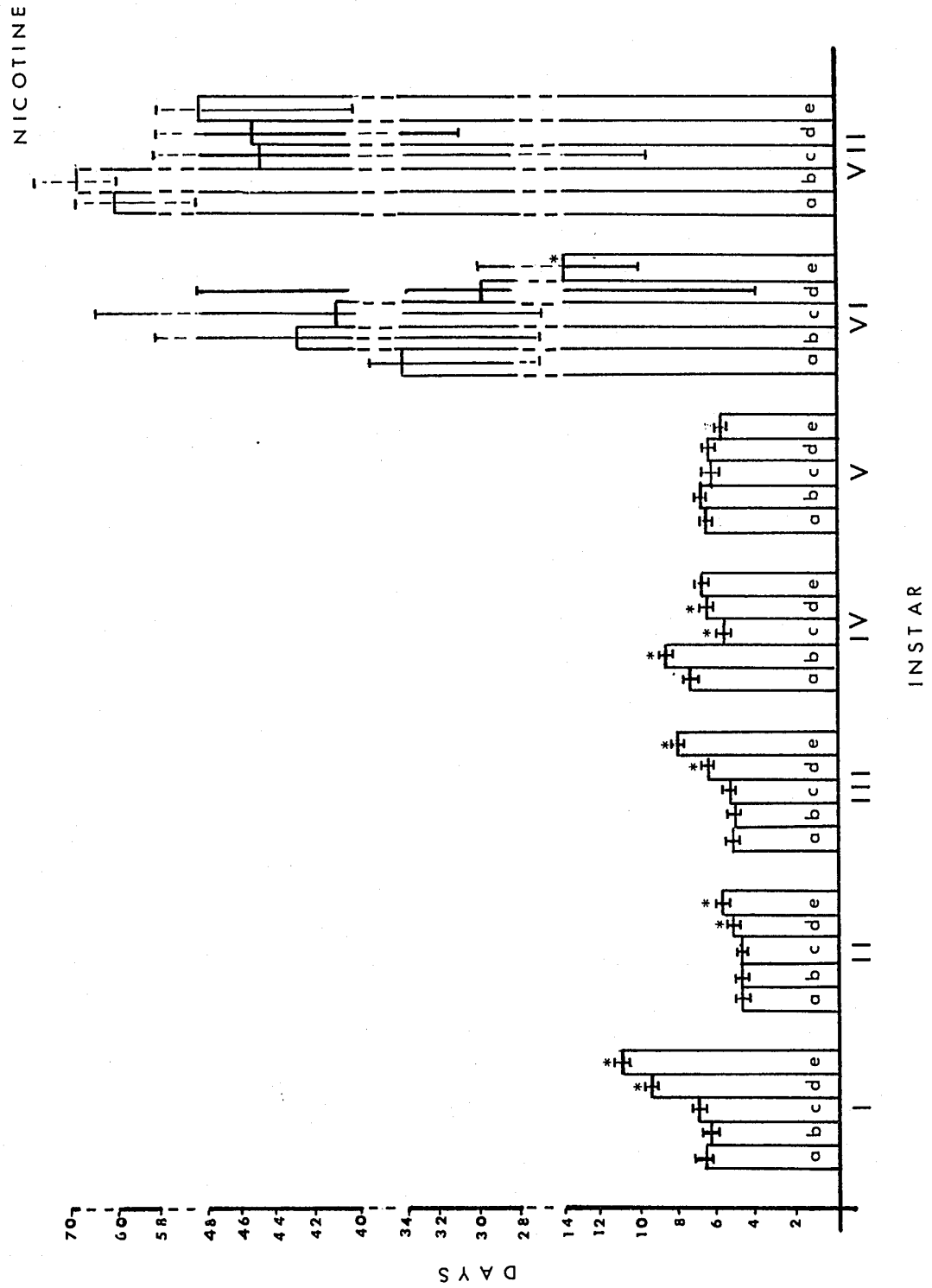

NICOTINE
WEIGHT (mg)
WEEK
control
0.01
0.03
0.10
0.30
1
2
3
4
5
10
20
30
40
50
60
70
80
130
140
150
180
190
320
330
400
410
420
430
480
490
500
630

Figure 7 : Mean number of days / instar of Euxoa messoria reared on control and nicotine diets.
a - control, b - 0.01 % nicotine, c - 0.03 % nicotine, d - 0.10 % nicotine, e - 0.30 % nicotine.
* Significantly different than the controls ($P \geq 0.05$).


NICOTINE
DAYS
INSTAR
I
II
III
IV
V
VI
VII
a b c d e

the result that the overall time from eclosion to pupation or emergence of the adult was the same.

The females of the control group weighed less than the males at larval maturity and as pupae, whereas the females of the nicotine fed groups were larger than the males (Table 7). The females of both the control and 0.01% nicotine group emerged 10.0 and 11.7 days (respectively) later than the males. Higher concentrations of nicotine influenced this period between male-female emergence by decreasing the number of days separating the emergence of them, thus at concentrations of 0.03% and 0.1% nicotine the females emerged before the males.

Larval instars were determined by head capsule measurements (Figure 8). The control and 0.01%, 0.03%, 0.1% and 0.3% nicotine reared groups had 6 or 7 larval instars. The majority of the larvae reared on the control 0.01%, and 0.03% nicotine diets had 6 instars. Higher concentrations of nicotine (0.1% and 0.3%) increased the number of larvae having 7 instars, but at 0.01% the proportion of larvae with 7 instars decreased, even lower than those reared on the control diet. There was little apparent difference in the widths of either the ultimate instar head capsule (6 or 7 moulters) or the nicotine reared individuals.

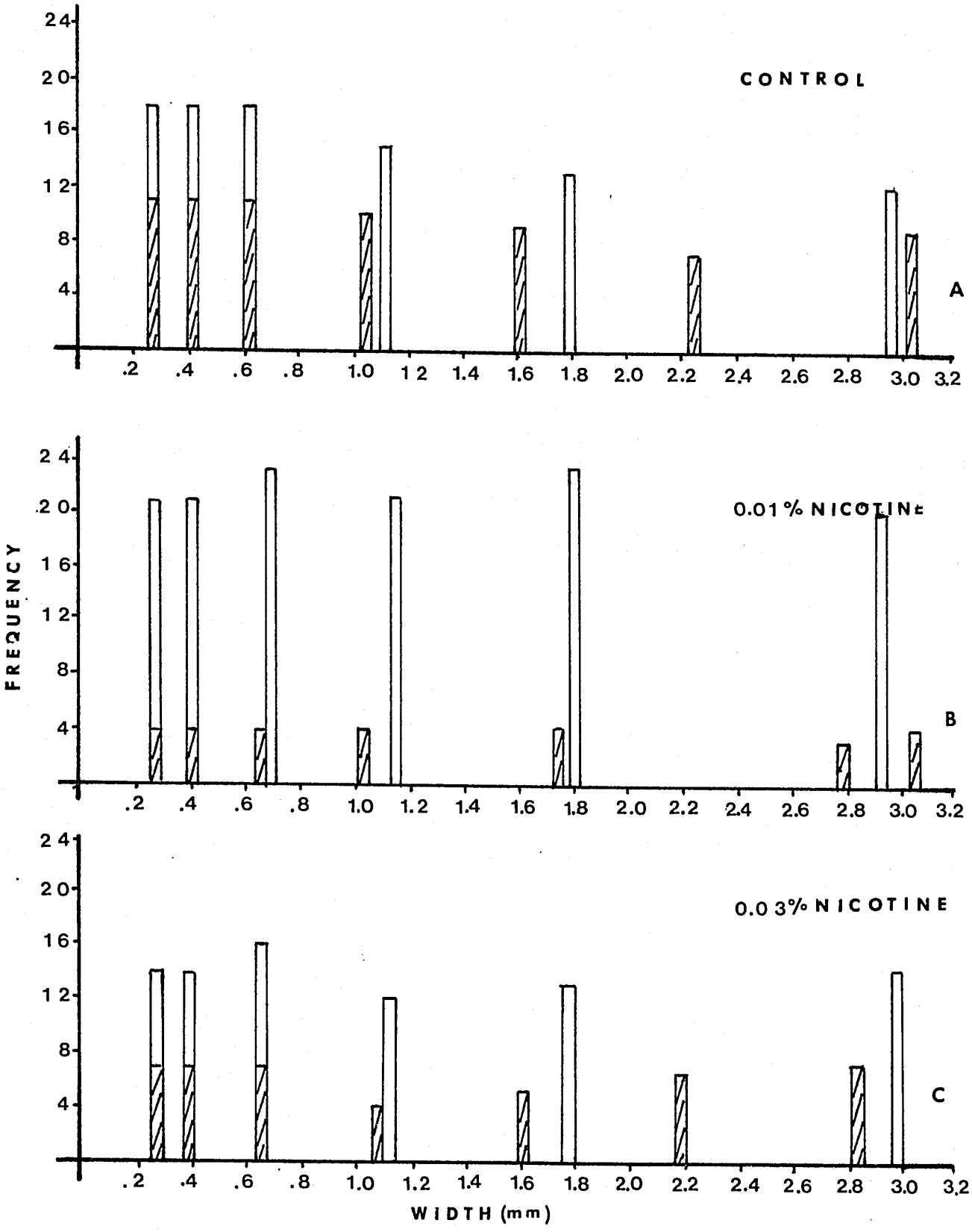
(iv) Atropine

Larvae reared on the atropine diets show significant differences in growth, development and survival compared to the controls (Table 8). At all the concentrations tested

Table 7. Development of males and females of Euxoa messoria on control diet and diets containing nicotine.

Diet	Number of Days to Larval Maturity		Maximum Larval Weight (mg)		Number of Days to Pupation		Pupal Weight (mg)		Number of Days to Adult Emergence	
	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂
Control	39.3	39.7	685.9	695.6	93.8	88.6	287.3	307.2	118.6	108.6
0.01 %	39.0	39.2	709.8	698.3	88.8	83.8	301.7	294.1	118.4	106.7
0.03 %	41.6	39.2	650.1	666.0	83.8	89.7	306.5	287.6	116.0	118.2
0.10 %	42.7	43.9	733.3	705.4	87.0	90.0	319.0	297.8	113.0	117.8
0.30 %	43.7	46.4	740.0	661.3	94.0	88.6	356.3	309.0	121.0	115.3
1.00 %	-	-	-	-	-	-	-	-	-	-

Figure 8 : Variations in the mean head capsule widths (mm) and number of instars of Euxoa messoria reared on control and nicotine diets.
▭ - 6 instars, ▭▭ - 7 instars.
A - control B.- 0.01 %
B - 0.03 % C - 0.10 %
D - 0.30 %


CONTROL
A
0.01% NICOTINE
B
0.03% NICOTINE
C
FREQUENCY
WIDTH (mm)
24
20
16
12
8
4
.2
.4
.6
.8
1.0
1.2
1.4
1.6
1.8
2.0
2.2
2.4
2.6
2.8
3.0
3.2

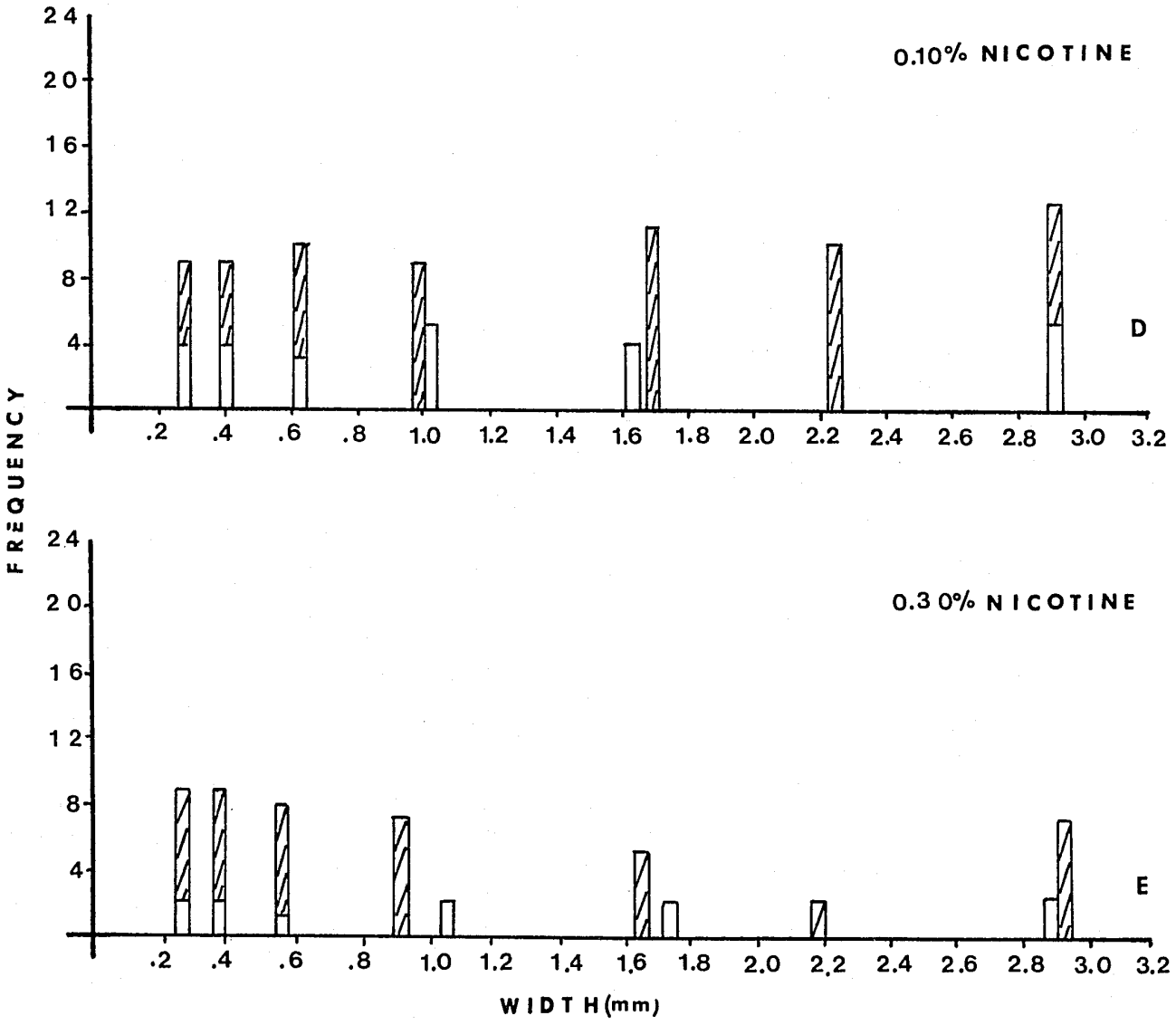

0.10% NICOTINE
D
0.30% NICOTINE
E
FREQUENCY
WIDTH (mm)
24
20
16
12
8
4
.2
.4
.6
.8
1.0
1.2
1.4
1.6
1.8
2.0
2.2
2.4
2.6
2.8
3.0
3.2

Table 8: Development of Euxoa messoria on control diet and diets containing atropine.

Diet	Number of Days to Larval Maturity	Maximum Larval Weight (mg)	Duration (days) of Prepupal Period	Number of Days to Pupation	Pupal Weight (mg)	Duration (days) of Pupal Period	Percent Pupation	Number of Days to Adult Emergence	Percent Adult Emergence
Control	33.0	652.6	32.7	64.9	287.2	27.0	70.0	91.9	63.0
sd	2.9	87.5	11.3	10.3	46.2	7.2		11.7	
0.01 %	31.4a*	667.8	39.4a	71.3	279.8	25.8	90.0	96.8	83.0
sd	2.8	97.8	12.6	15.2	50.6	3.1		12.3	
0.03 %	31.0a	737.9a	39.1a	70.1	276.8	26.3	83.0	96.8	83.0
sd	2.3	98.2	12.6	15.2	29.6	3.1		14.8	
0.10 %	30.2a	720.3a	35.3	64.8	302.1	27.6	90.0	92.6	87.0
sd	1.8	88.6	10.2	9.7	50.9	2.7		12.3	
0.30 %	32.4	711.1a	40.9a	74.0	285.2	28.0a	93.0	102.1a	87.0
sd	3.8	71.5	16.0	15.4	35.8	2.7		16.2	
1.00 %	34.0	689.7	39.1	72.7	279.8	26.6	87.0	100.1a	80.0
sd	2.6	76.1	18.6	17.4	40.3	2.7		17.8	

* Numbers followed by the letter a are significantly different (P≥0.05) from the controls.

atropine increased survival to pupation and adult emergence. There were significant differences in the mean weekly weights and maximum larval weights of the controls and atropine fed larvae. At concentrations of 0.03%, 0.1%, and 0.3%, atropine significantly increased ($P \geq 0.05$) the mean weekly weights during the development period (Figure 9), and also maximum larval weights (Table 8). In the first week of growth 1.00% atropine reduced the larval weight, but there were no apparent differences in weight during the remaining period of development. At a concentration of 0.01%, atropine had no effect on the weekly or maximum larval weights. Pupal weight was unaffected by atropine at any of the levels tested.

There were significant differences ($P \geq 0.05$) in the development times between the controls and the atropine-reared larvae (Table 8). At 0.01%, 0.03%, and 0.1% atropine significantly decreased the development time to larval maturity, due to the shorter duration of some of the early instars (Figure 10). At levels of 0.3%, and 1.0% atropine there was no effect on the total number of days required to reach larval maturity, but the first instar was significantly reduced ($P \geq 0.05$) at a concentration of 0.3% atropine and prolonged at 1.0%.

All concentrations of atropine increased the prepupal period, which was significantly longer ($P \geq 0.05$) in the groups fed 0.01%, 0.03% and 0.3%. Larvae reared on 0.3% atropine took significantly longer ($P \geq 0.05$) to reach the pupal stage. The remaining levels of atropine had no apparent

Figure 9 : Mean weekly weights (mg) of Euxoa messoria reared on control and atropine diets.
* Significantly different from the controls ($P \geq 0.05$).

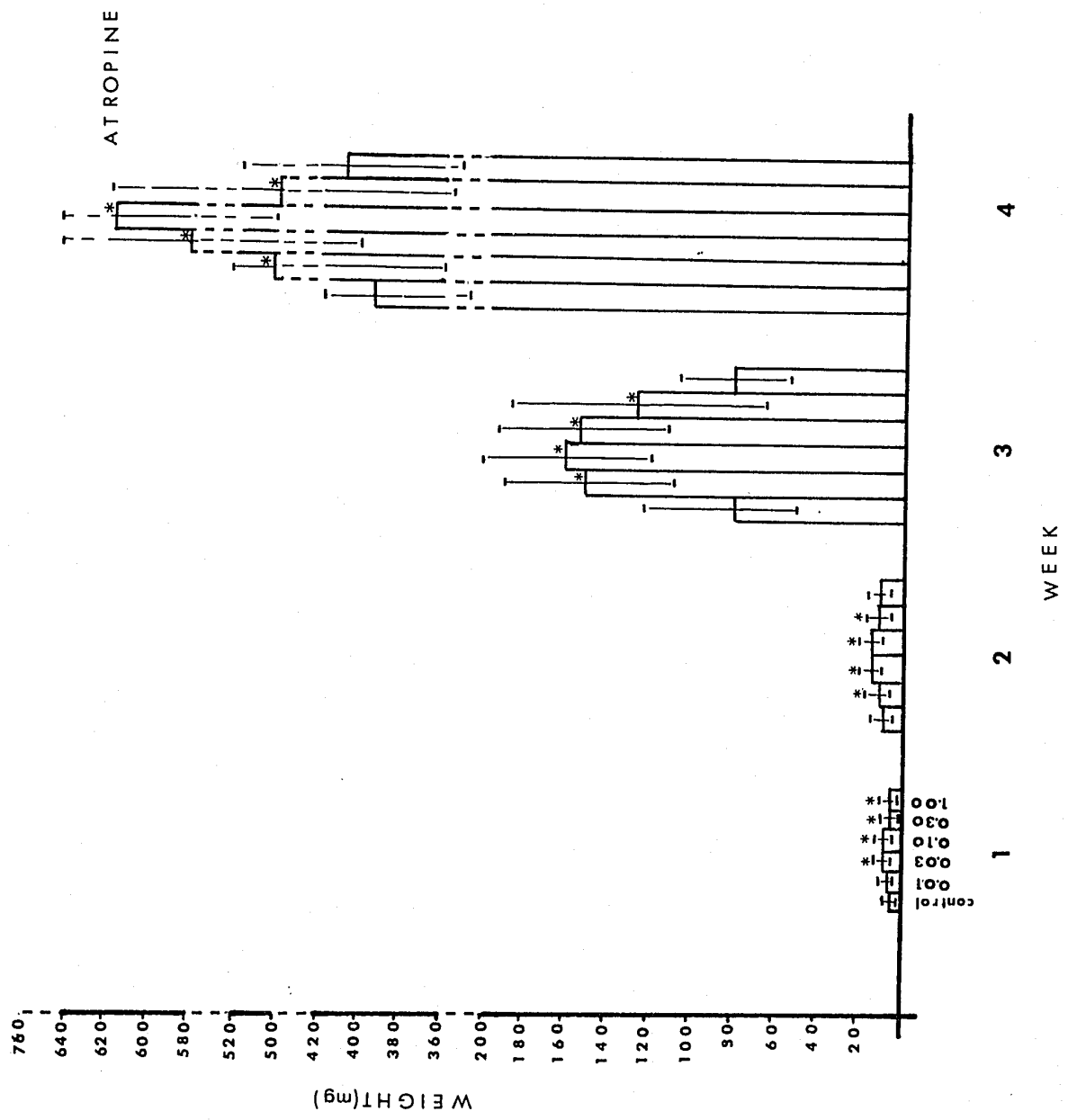
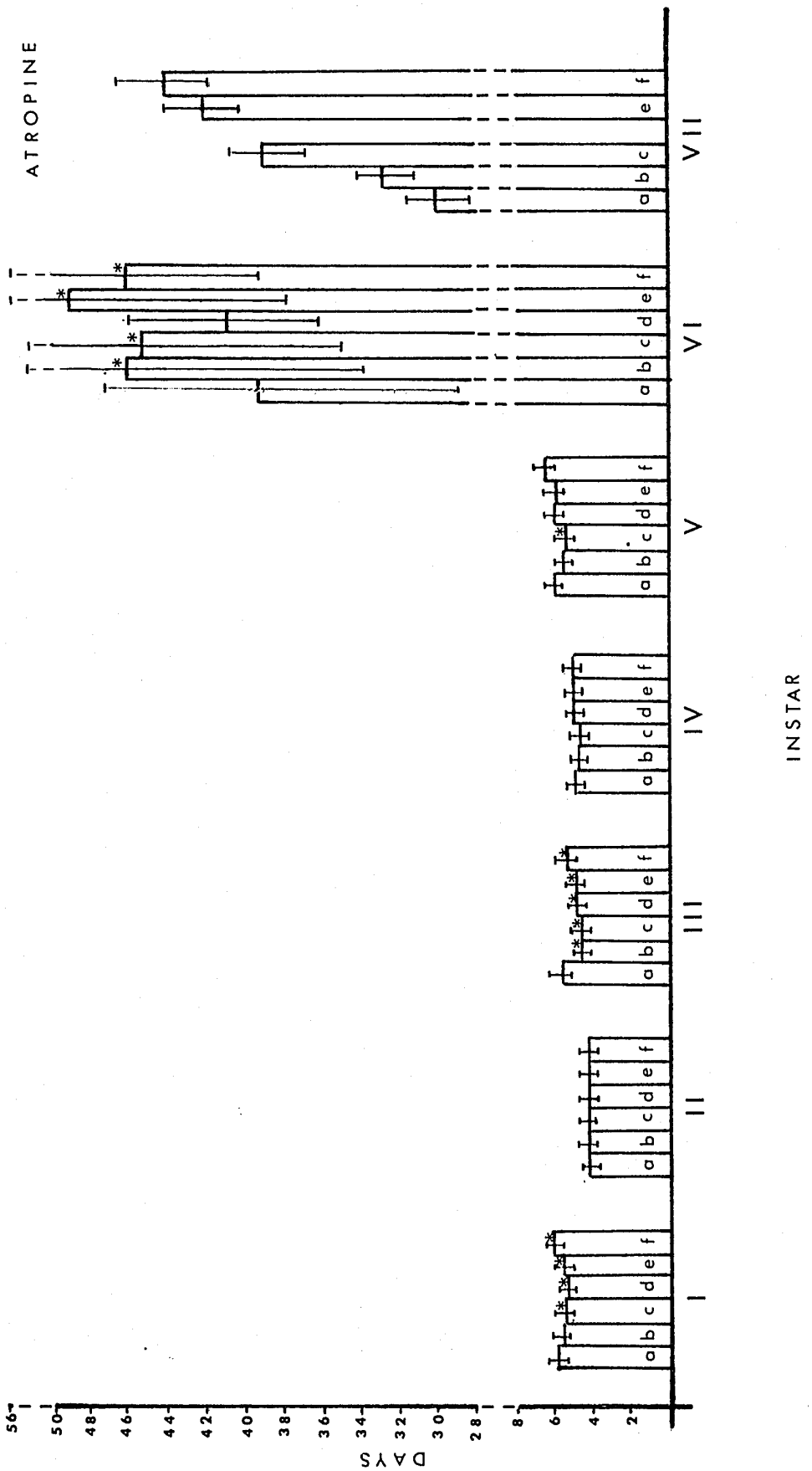

WEIGHT(mg)
760
640
620
600
580
520
500
420
400
380
360
200
180
160
140
120
100
30
60
40
20
control
0.01
0.03
0.10
0.30
1.00
1
2
3
4
WEEK
ATROPINE

Figure 10 : Mean number of days / instar of Euxoa messoria reared on control and atropine diets.
a - control, b - 0.01 % atropine, c - 0.03 % atropine, d - 0.10 % atropine. e - 0.30 % atropine, f - 1.00 % atropine.
* Significantly different from the controls ($P \geq 0.05$).


ATROPINE
DAYS
INSTAR
I
II
III
IV
V
VI
VII

influence on time to pupation. The total number of days to adult emergence was significantly greater ($P \geq 0.05$) for groups reared on 0.3% and 1.0% atropine whereas the lower concentrations (0.01%, 0.03% and 0.1%) had no effect on the total development time.

Females of the control and 0.01%, 0.03%, 0.1% and 0.3% atropine groups were smaller than the males at larval maturity and pupation, while females of the 1.0% atropine group were larger than the males (Table 9). Females of the control and all atropine groups pupated, and emerged as adults, after the males.

Variations in the number of head capsules and mean head capsule widths for each instar and instar class are illustrated in Figure 11. The controls, 0.01%, 0.03%, 0.3% and 1.0% atropine reared larvae had 6 or 7 larval instars before pupation, with the majority of individuals having 6 instars. All larvae reared on 0.1% atropine had only 6 instars. The widths of the ultimate instar head capsules were essentially the same for the two instar classes and for the control and atropine groups.

c) Development on Nicotiana tabacum varieties Lonibow and Delhi-34

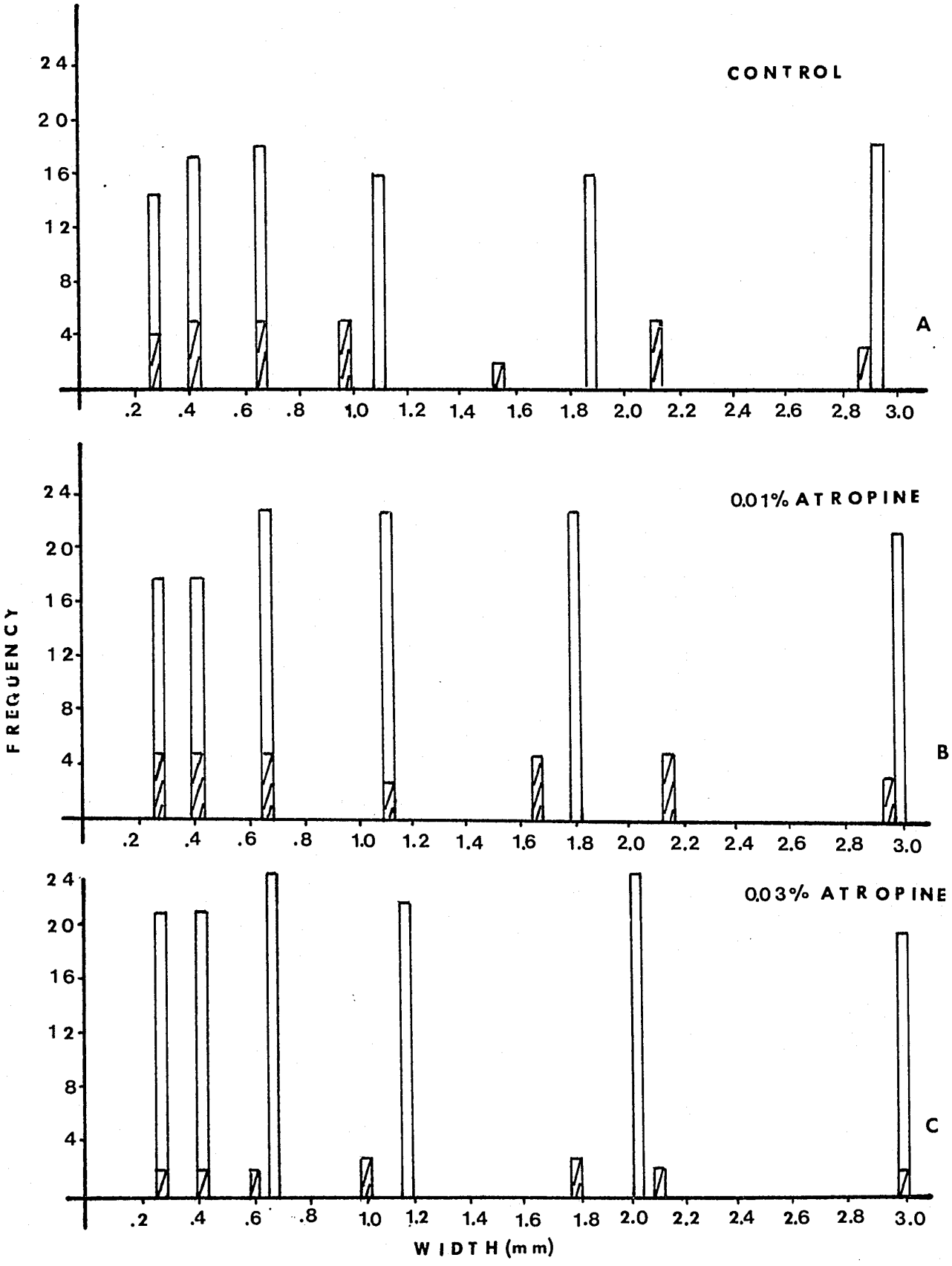
Larvae reared on the Nicotiana tabacum varieties, Lonibow and Delhi-34 and on a meridic diet had different developmental characteristics (Table 10). The survival to the pupal and adult stages was abnormally low for the diet-reared group. In five groups of larvae which had been reared on this diet,

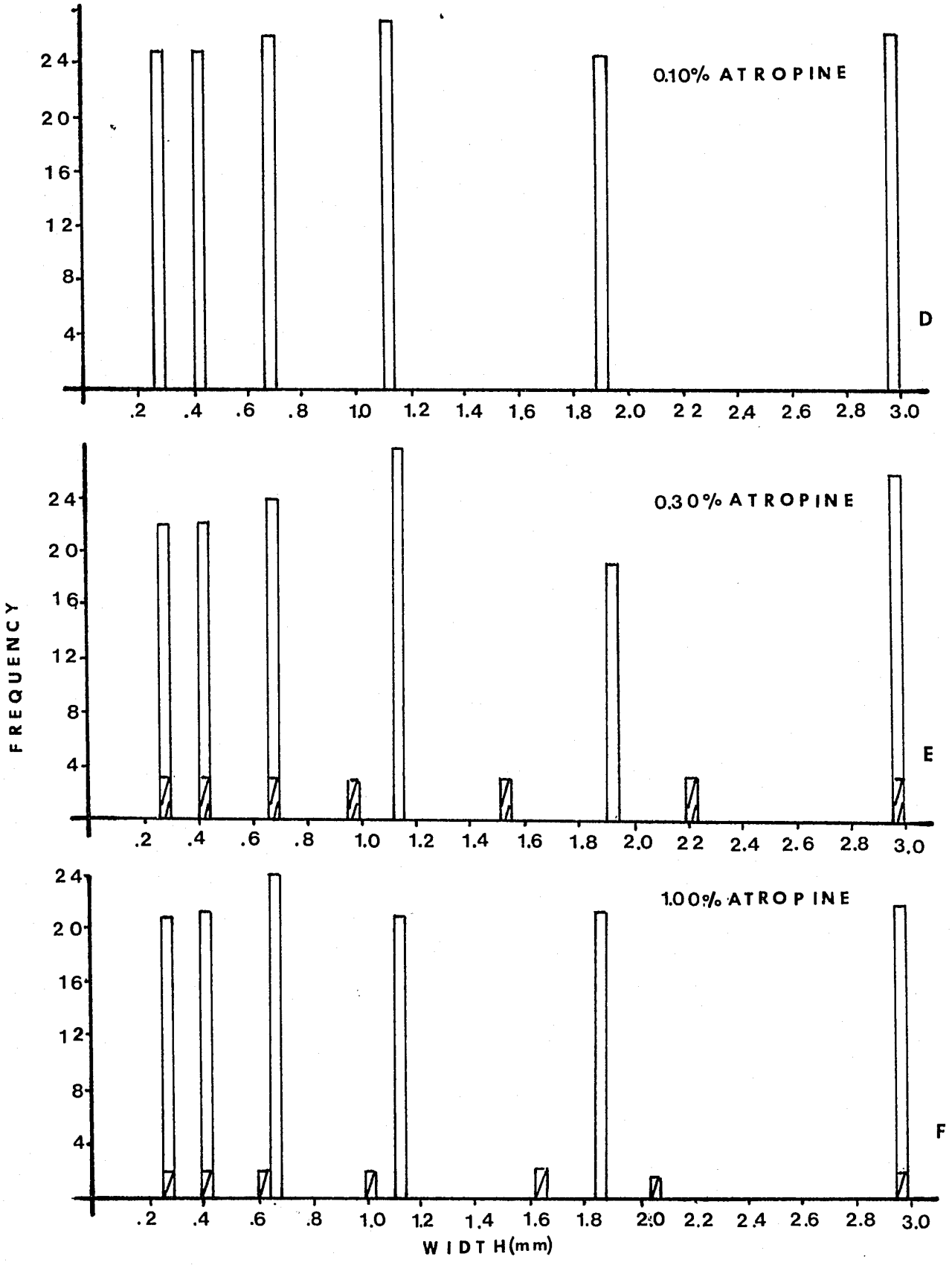
Table 9. Development of males and females of Euxoa messoria on control diet and diets contining atropine.

Diet	Number of Days to Larval Maturity		Maximum Larval Weight (mg)		Number of Days to Pupation		Pupal Weight (mg)		Number of Days to Adult Emergence	
	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂
Control	32.1	33.4	625.6	647.2	70.5	61.4	286.0	288.1	95.9	89.4
0.01 %	32.0	30.7	657.3	683.6	80.7	61.9	281.6	293.0	106.1	85.2
0.03 %	30.0	30.5	722.4	744.2	72.8	62.3	277.4	276.3	97.2	90.7
0.10 %	30.8	29.7	681.5	759.0	66.2	63.3	280.4	302.0	95.9	89.2
0.30 %	31.5	33.4	661.6	719.0	81.4	65.0	266.7	296.5	113.8	92.8
1.00 %	33.8	28.6	707.6	634.9	81.6	62.0	290.0	274.0	107.8	89.4

Figure 11 : Variations in the mean head capsule widths (mm) and number of instars of Euxoa messoria reared on control and atropine diets.
▭ - 6 instars, ▭▭ - 7 instars.

A - control B - 0.01 %
C - 0.03 % D - 0.10 %
E - 0.30 % F - 1.00 %


CONTROL
A
0.01% ATROPINE
B
0.03% ATROPINE
C
FREQUENCY
WIDTH (mm)
4
8
12
16
20
24
.2
.4
.6
.8
1.0
1.2
1.4
1.6
1.8
2.0
2.2
2.4
2.6
2.8
3.0


0.10% ATROPINE
D
0.30% ATROPINE
E
1.00% ATROPINE
F
FREQUENCY
WIDTH(mm)
4
8
12
16
20
24
.2
.4
.6
.8
1.0
1.2
1.4
1.6
1.8
2.0
2.2
2.4
2.6
2.8
3.0

the average survival to pupation was 77% and to adult emergence was 70%. Survival on the N. tabacum varieties was lower for the Delhi-34 fed group than the Lonibow-reared group.

There were significant differences in the weights of larvae reared on the N. tabacum varieties and the artificial diets during larval development. Larvae reared on Delhi-34 were significantly smaller ($P \geq 0.05$) on a weekly basis than both the Lonibow and artificial diet-reared larvae (Figure 12). Lonibow-fed larvae were significantly heavier ($P \geq 0.05$) than the diet-fed individuals in the 2nd, 3rd, and 4th weeks of growth. During the 5th week, the weights of the Lonibow and diet-reared larvae were essentially equal. Delhi-34 reared larvae were significantly smaller ($P \geq 0.05$) at larval maturity than both the Lonibow and diet reared larvae (Table 10). There was little apparent difference in the maximum larval weights between the Lonibow and diet-reared larvae. At pupation, the Delhi-34 reared pupae weighed significantly less ($P \geq 0.05$) than either the diet or the Lonibow-reared pupae. However, the Lonibow-fed group weighed significantly more as pupae ($P \geq 0.05$) than the diet-reared group.

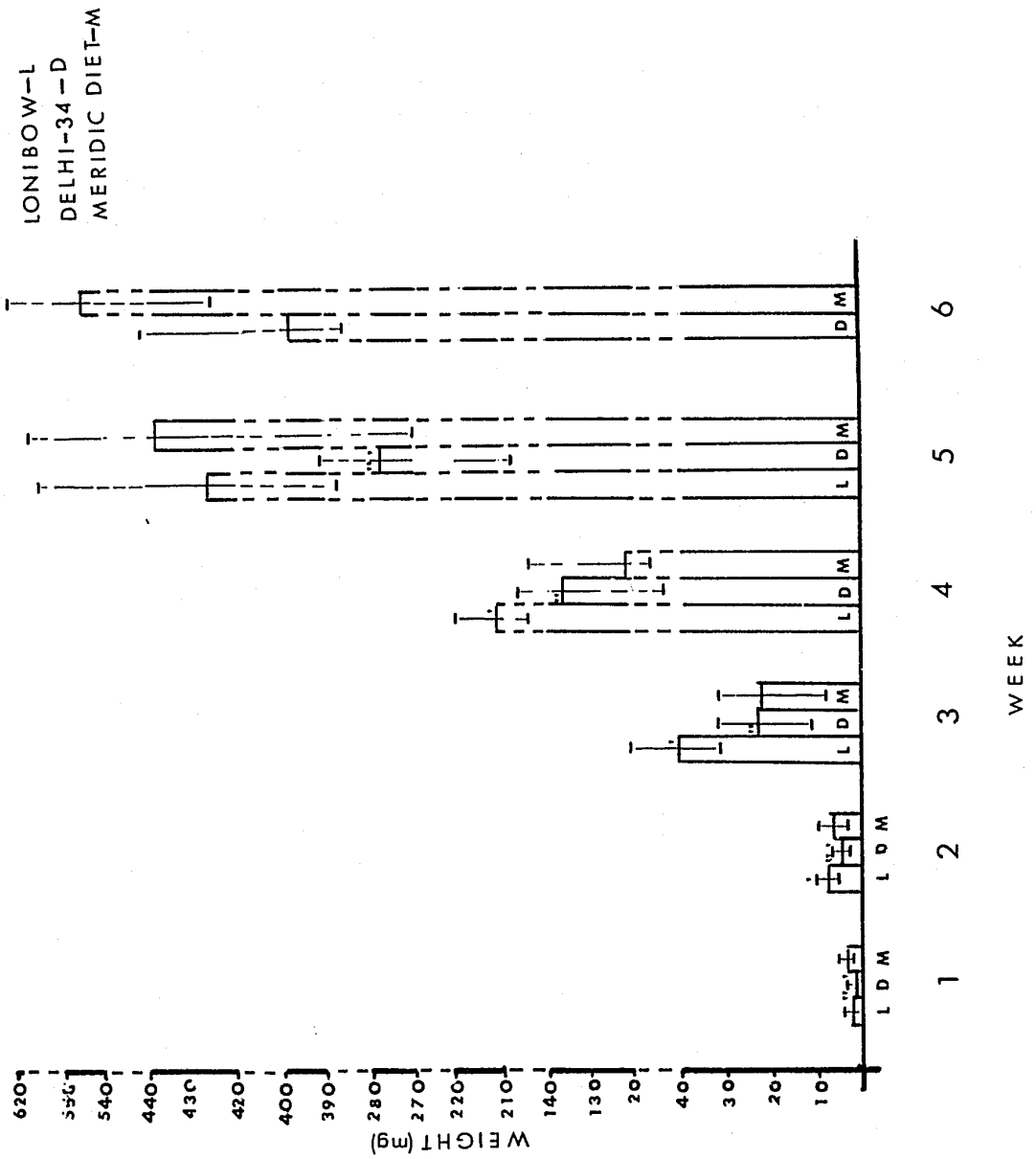
Larvae reared on Delhi-34 took significantly longer ($P \geq 0.05$) to reach larval maturity than the larvae which were fed Lonibow or meridic diet. The prepupal period was significantly longer ($P \geq 0.05$) in meridic diet-fed larvae than in the N. tabacum - fed larvae. The total time to pupation and adult emergence was also significantly longer ($P \geq 0.05$) in the diet-reared group compared with the groups fed tobacco

Table 10: Development of Euxoa messoria on two varieties of Nicotiana tabacum, Lonibow and Delhi-34, and a meridic diet.

Diet	Number of Days to Larval Maturity	Maximum Larval Weight (mg)	Duration (days) of Prepupal Period	Number of Days to Pupation	Pupal Weight (mg)	Duration (days) of Pupal Period	Percent Pupation	Number of Days to Adult Emergence	Percent Adult Emergence
Meridic Diet	38.4a*	652.1a	24.4ab	62.8ab	281.8a	27.3	77.0**	90.5a	70.0**
sd	4.0	87.0	5.8	3.3	37.8	2.9		5.3	
Lonibow	39.4b	649.5b	17.1a	57.0a	301.6a	28.1	70.0	84.7ab	63.3
sd	1.2	53.0	4.3	4.3	25.3	3.0		2.8	
Delhi-34	43.0ab	553.9ab	16.5b	58.8b	234.1a	27.4	57.0	87.6	53.3
sd	4.0	91.7	3.2	3.8	40.6	1.9		4.8	

* Numbers followed by a common letter are significantly different ($P \geq 0.05$).
** Values are based on the average survival of five groups reared on this diet.
sd - standard deviation.

Figure 12 : Mean weekly weights (mg) of Euxoa messoria reared on Nicotiana tabacum varieties Lonibow and Delhi-34 and a meridic diet.
L - Lonibow
D - Delhi-34
M - Meridic diet
' significantly different from the controls (P≥0.05).
" Significantly different from the Lonibow (P≥0.05).


LONIBOW-L
DELHI-34-D
MERIDIC DIET-M
WEIGHT (mg)
620
540
440
430
420
400
390
280
270
220
210
140
130
20
40
30
20
10
L D M
1
2
3
4
5
6
WEEK

leaves. Lonibow-fed larvae took significantly less time ($P \geq 0.05$) to emerge as adults than the Delhi-34 reared group.

The females of the synthetic diet-reared group weighed more than the males at maximum larval weight, but this situation was reversed in both of the groups fed tobacco leaves (Table 11). As pupae, the females of all three groups were larger than the males. The females of the meridic diet and Delhi-34 groups emerged 6.7 and 3.6 days later (respectively) than the males, while in the Lonibow-fed group both developed at approximately equal rates.

The majority of the larvae reared on the artificial diet had 6 larval instars and a few had 7 instars before pupation (Figure 13). The majority of larvae in the Lonibow and Delhi-34 groups had 7 instars and a small proportion (8% and 18% respectively) of the population had 8 instars. The Lonibow group also had a few larvae (12%) with 6 instars. The mean head capsule widths of the ultimate instar head capsules were essentially equal for the larvae reared on Lonibow, Delhi-34, and meridic diets and the 3 instar classes (6,7, or 8).

d) Feeding Preference

(i) Alkaloids

The response of E. messoria to the alkaloid diets is summarized in Table 12. The veratrine diets at all concentrations tested were totally unpalatable to the larvae. Feeding activity on the veratrine discs was very limited and was mainly confined to discs containing the lowest concentrations (0.01% and 0.03%).

Figure 13 : Variations in the mean head capsule widths (mm) and number of instars of Euxoa messoria reared on a meridic diet and two varieties of Nicotiana tabacum, Lonibow and Delhi-34.

▭ 6 instars, ▭▭ 7 instars, ▭ 8 instars.

A. Meridic Diet
B. Lonibow
C. Delhi-34

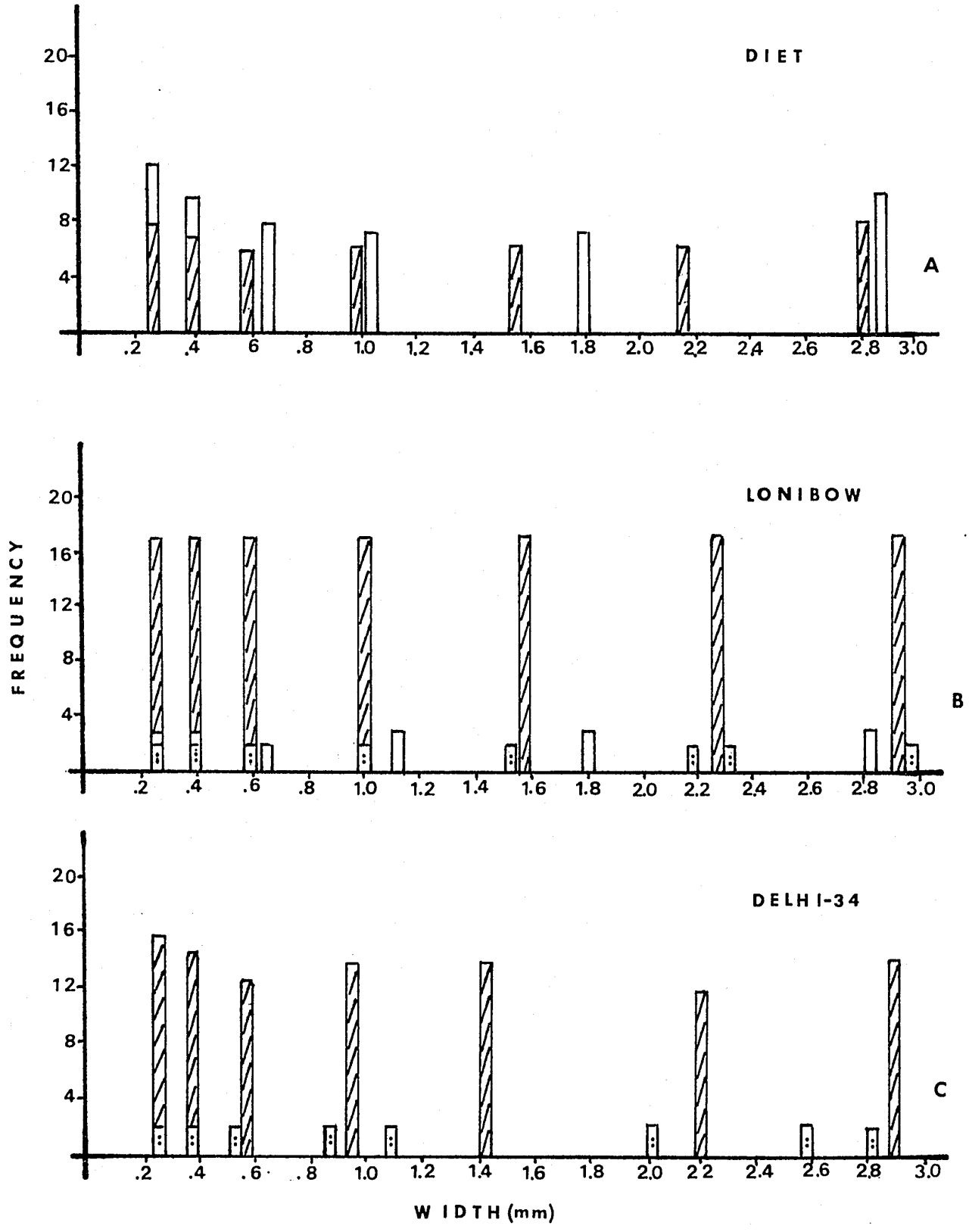

DIET
A
LONIBOW
B
DELHI-34
C
FREQUENCY
WIDTH (mm)
20
16
12
8
4
.2
.4
.6
.8
1.0
1.2
1.4
1.6
1.8
2.0
2.2
2.4
2.6
2.8
3.0

Table 11. Development of males and females of Euxoa messoria reared on two varieties of Nicotiana tabacum, Lonibow and Delhi-34, and a meridic diet.

Diet	Number of Days to Larval Maturity		Maximum Larval Weight (mg)		Number of Days to Pupation		Pupal Weight (mg)		Number of Days to Adult Emergence	
	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂
Meridic Diet	38.2	37.1	665.4	587.4	64.9	61.2	319.2	278.4	94.3	87.6
Lonibow	39.7	39.2	630.7	660.0	58.6	55.8	346.1	275.9	84.3	84.8
Delhi-34	42.9	46.7	597.6	558.5	60.5	57.9	255.2	223.6	89.8	86.2

Table 12 : Palatability of alkaloid diets.

Diet	Palatability*	Diet	Palatability*
Veratrine		Berberine	
0.01 %	---	0.01 %	0
0.03%	---	0.03%	-
0.10 %	---	0.10 %	--
0.30 %	---	0.30 %	--
1.00 %	---	1.00 %	---
Nicotine		Atropine	
0.01 %	+	0.01 %	++
0.03 %	-	0.03 %	+++
0.10 %	+	0.10 %	+++
0.30 %	+	0.30 %	++
1.00 %	+	1.00 %	++

* Palatability:
  --- full unpalatability - the amount consumed of the test disc is less than 10 % of the amount consumed of the control disc.
  -- strong deterrent - the amount consumed of the test disc = 10 - 30 % of the amount consumed of the control discs.
  - Slight deterrent - the amount consumed of the test disc = 30 - 80 % of the amount consumed of the control discs.
  0 no deterrent or stimulant effects - the amount consumed of the test discs = 80 - 100 % of the amount consumed of the control discs.
  + slight stimulant - the amount consumed of the control disc = 10 - 80 % more than the amount consumed of the control discs.
  ++ strong stimulant - the amount consumed of the test disc = 80 % or more than the amount consumed of the control discs.

Larvae reacted in a variety of ways to the test discs impregnated with berberine-containing diet according to the concentrations of the alkaloid. At 0.01% berberine there was no visible deterrent or stimulative effects. Approximately equal amounts of the control and 0.01% berberine diet discs were consumed. At higher concentrations, berberine acted as a feeding deterrent. The level of 0.03% slightly reduced feeding and at 0.1%, 0.3%, and 1.0% berberine was a strong feeding deterrent.

Nicotine appeared to stimulate feeding. At all concentrations tested, except 0.03%, feeding activity on the nicotine diet discs was slightly greater than the control discs. Feeding on the 0.03% nicotine discs was however, slightly lower than the controls.

Atropine was a strong phagostimulant at all concentrations tested, particularly at the levels of 0.03% and 0.1%.

In order to examine the influence of the alkaloids alone on the feeding response of E. messoria, solutions of the alkaloids were prepared and presented to the larvae. Each alkaloid was tested at the five diet concentrations of 0.01%, 0.03%, 0.1%, 0.3% and 1.0% (Table 13). Presenting the alkaloids in solution had no influence on feeding. There was little or no feeding activity on any of the water or water-alkaloid discs over a period of 24 hours. The berberine, nicotine and atropine discs showed some evidence of very light feeding, but the veratine discs were left completely untouched.

Table 13. Feeding response of Euxoa messoria to solutions of veratrine, berberine nicotine, and atropine. Values are given as the percent of the discs consumed.

Alkaloid	Distilled Water Control	0.01%	0.03%	0.10%	0.30%	1.00%
Veratrine	0.0	0.0	0.0	0.0	0.0	0.0
Berberine	1.4	0.0	0.0	0.0	0.0	0.0
Nicotine	3.0	0.8	0.7	1.4	4.2	0.1
Atropine	0.1	0.4	0.1	0.0	2.9	0.0

The possible influence of the nutrient content of the diet and the alkaloids on feeding was tested by combining sucrose with atropine (Table 14). Sucrose was examined for its possible influence on feeding. The concentration of 3.2% was tested, as this was the concentration of sucrose in the diet used. Sucrose proved to be a strong phagostimulant to the larvae of E. messoria. When sucrose was combined with atropine, the atropine-sucrose discs were strongly preferred, at all the atropine concentrations tested (0.01%, 0.03%, 0.1%, 0.3%, and 1.0%), to the control sucrose discs. These results were similar to the feeding preference of E. messoria to the atropine diet discs.

(ii) Plants

Three varieties of N. tabacum (Lonibow, Delhi-34, and Burley 21) and one garden variety of Nicotiana (N. alta, white bidder) were presented in a choice experiment along with a control of distilled water (Table 15). The larval feeding response to Lonibow and Delhi-34 were approximately equal but Burley 21 was less acceptable to the larvae. The garden variety of Nicotiana was the least preferred.

The three varieties of N. tabacum were tested again with Atropa belladona and a distilled water control (Table 15). A. belladona was strongly preferred over the three varieties of tobacco.

Five garden plants were also tested for feeding preference. The plants presented were tomato, Lycopersicum esculentum L, ageratum, Ageratum sp., delphinium, Delphinium grandiflora

Table 14. Feeding response of Euxoa messoria to sucrose and sucrose-atropine solutions. Values are given as the percent of the disc consumed.

A.

Distilled water control	3.2% Sucrose
0.7	47.3

B.

3.2% Sucrose	Sucrose-atropine	0.01%	0.03%	0.1%	0.3%	1.0%
13.8		38.7	34.1	28.8	31.8	19.6

Table 15. Feeding response of *Euxoa messoria* to: *Nicotiana tabacum* var Lonibow. Delhi-34 and Burley 21. and *N. alta*, white bidder; *Atropa belladona*; and five common garden plants. Values are given as the percent of the discs consumed.

A. *Nicotiana*

Distilled Water Control	Lonibow	Delhi-34	Burley 21	White bidder
0.0	57.3	48.7	26.0	10.6

B. *Atropa*; *Nicotiana*

Distilled Water Control	*Atropa belladona*	Lonibow	Delhi-34	White bidder
0.2	41.9	15.5	15.8	14.8

C. Garden Plants

Distilled Water Control	Tomato	Ageratum	Delphinium	Salvia	Marigold
0.0	0.0	34.3	11.9	10.3	46.2

L.var, salvia, Salvia splendens (Ker-Gawl) var, and marigold, Tagetes erecta L., using distilled water as control (Table 15). The larvae of E. messoria showed a definite preference towards certain plants; the order of preference for these five garden plants was: Marigold,>Ageratum>Delphinium=Salvia>Tomato.

It was observed that soon after the larvae were placed in the centre of the feeding arena they would move towards the green discs which had leaf material on them, but never towards the white distilled water control discs. The larvae did not always start eating the discs as soon as they came into contact with them but would often rest underneath the discs or wander around the edges of the arena, often crawling over the test discs. The majority of the feeding activity occurred at night.

(iii) Extirpation of sensory structures

Veratrine diets were chosen as the test medium in these experiments because of their consistent unpalatibility to intact larvae.

a) Bilateral antennectomy

Removal of the antennae increased the amount of feeding activity on the veratrine diets (Table 16). Intact larvae generally avoided the veratrine discs. Larvae with their antennae removed still showed a strong preference for the control discs but some feeding activity occurred on the veratrine discs, particularly at concentrations of 0.01% and 0.03%. By evaluation of the area consumed on the veratrine discs, as

Table 16. Effects of bilateral antennectomy and maxillectomy on the feeding response of *Euxoa messoria*. Values are given as the percent of the discs consumed.

I. Veratrine Diets

A. Bilateral Antennectomy.

Control	0.01%	0.03%	0.10%	0.30%	1.00%
83.9	14.7	2.2	0.6	0.3	0.1

B. Bilateral Maxillectomy.

Control	0.01%	0.03%	0.10%	0.30%	1.00%
19.9	1.8	0.2	0.3	0.1	0.0

C. Combined Bilateral Antennectomy and Maxillectomy.

Control	0.01%	0.03%	0.10%	0.30%	1.00%
6.3	2.1	1.1	0.2	0.0	0.0

II. Sucrose: Bilateral Maxillectomy.

Distilled water	3.2% Sucrose
1.1	7.5

III. Sucrose - Atropine Solutions: Bilateral Maxillectomy.

Distilled Water	3.2% Sucrose	Sucrose: 0.01% berberine	0.01% veratrine	0.01% nicotine	0.03% atropine
0.0	17.5	12.4	0.0	17.4	13.4

a percentage of the area consumed on the control discs. It appears that 0.01% veratrine becomes a strong deterrent while the remaining concentrations remain totally unpalatable.

b) Bilateral Maxillectomy

The feeding activity of maxillectomized larvae was generally suppressed and the larvae required 48 hours exposure to elicit any feeding responses (Table 16). During this period some feeding occurred on the 0.01%. 0.03%. 0.1% and 0.3% veratrine discs but 1.0% veratrine discs were always left untouched. The larvae still showed a preference towards the control discs, followed by the 0.01% veratrine discs.

c) Combined Antennectomy and Maxillectomy

As was observed previously with larvae which had their maxillae removed, feeding was suppressed and the larve required 48 hours exposure to elicit any feeding responses. At the end of this period very little measurable activity was evident on the test discs (Table 16).

The bilateral maxillectomy trials were repeated to examine the possible influence of substances with strong phagostimulative effects to intact larvae. Test solutions of distilled water and sucrose, and sucrose-alkaloid mixtures were presented to the maxillectomized larvae (Table 16). As was observed previously, feeding activity was suppressed and the larvae were left for 48 hours. During this period, only limited feeding occurred. Larvae presented with a choice between distilled water and 3.2 % sucrose

solution still showed a preference for the sucrose discs. When presented with a choice of distilled water, 3.2% sucrose, sucrose + 0.01% berberine, sucrose + 0.01% nicotine, sucrose + 0.03% atropine, and sucrose + 0.01% veratrine, the larvae did not show a strong preference for any particular solution but did avoid the distilled water control and sucrose + 0.01% veratrine discs.

IV. DISCUSSION

a) Influence of diet on growth of E. messoria

The meridic diet VI, containing soybean protein, casein and wheat germ provided the most suitable medium to be used as a substitute for the bean diet in rearing E. messoria. The growth performance of the larvae on the inadequate diets demonstrated some nutritional requirements of this insect. All the test diets except diet VII (containing only soybean protein) permitted growth and development to the adult stage. The nutritional adequacies of the remaining diets varied with the content of ascorbic acid, cholesterol, protein and wheat germ.

The poor growth and low survival of E. messoria on diet I (ascorbic acid level of 0.27% provided by Vanderzant vitamin mixture) is partially the result of the inadequate level of ascorbic acid in this diet because, with increasing the content to 0.4% in diet II, survival, growth and development rates greatly improved. This may be due to E. messoria having a quantitative requirement for this nutrient, which has long been recognized as essential for phytophagous insects (Dadd 1973; Vanderzant 1974; Navon 1978). Excessive or inadequate levels of essential nutrients create metabolic imbalances which result in abnormal growth and development (House 1965). Ascorbic acid deficiencies, which are characterized by ecdysis failure, larval mortality, reduced yield of adults and malformed individuals have been observed in many phytophagous insects (Dadd 1960; Vanderzant et al, 1962; Chippendale and

Beck 1965; Rock 1967; Navon 1978). Navon (1978) has shown that ascorbic acid is associated with the moulting stage of the codling moth, Carpocapsa pomonella (L) and believes that deficiencies of this nutrient interfere with melanization and sclerotization causing morphological abnormalities which impaired food ingestion. The inadequacy of a diet containing 0.27% ascorbic acid for E. messoria is demonstrated by the correction of deficiency symptoms (of low survival, small size and slow growth) associated with the increased level of 0.4%. It is not known if this quantity provides the optimal level of dietary ascorbic acid for E. messoria.

Cholesterol fulfills the dietary sterol requirements of most insect (Dadd 1973) but has proven to be an unsuitable source for Crambus trisectus (Zencker) which suffered high mortality and malformed adults when used as its sterol source (Dupnik and Kamm 1970). The normal development of E. messoria on diets containing 0.006% cholesterol demonstrates that cholesterol is an adequate sterol source. However 0.06% caused suboptimal growth (reduced survival, slower development rates and low larval and pupal weights) indicating that excessive quantities can be detrimental to this insect. This could be the result of a nutrient imbalance caused by the excess of cholesterol interrupting the normal metabolic processes of the insect. In experiments with Celerio euphorbiae (Linn) , , House (1965) found that a diet containing imbalanced amounts of various nutrients caused a decrease in consumption and weight gain.

The diets which permitted the best growth were the oligidic bean diet and meridic diets III, V, and VI. The superior growth, characterized by shorter development times and larger size, is associated with the protein source and total protein content (Table 17). It is evident that soybean protein alone is inadequate for growth and development of E. messoria. This is in agreement with the observations of Vanderzant and Davich (1961) on Anthonomus grandis (Boh.). Similarly, Creswell et al (1971) found that soyflour was not an adequate source of amino acids for the Nantucket pine tip moth, Rhyacionia frustrana Comst. Raw soybeans are known to contain toxic substances and the protein is poorly utilized (Vanderzant 1974). By heating soybean products, the nutritional quality improves, possibly by eliminating the toxic properties (Vanderzant 1974) or as Brewer and Tidwell (1978) suggested, by reducing the concentration of anti-nutritional enzymes. However, soybean products have provided satisfactory protein sources for some lepidopterous larvae, such as the cotton leaf-worm Spodoptera littoralis (Alabama argillacea Hübner) (Levinson and Navon 1969) the bollworm, Heliothis zea Boddie (Brewer and Tidwell 1978) and the sugar cane borer, Diatraea saccharalis Fabr. (Brewer 1977).

Although inadequate as the sole source of protein, soybean protein combined with casein improves the growth of E. messoria. From this, it appears that the soybean protein complements casein by compensating for possible amino acid imbalances.

The addition of wheat germ to synthetic diets is often required for normal growth (Chippendale and Beck 1964; McMorran 1965; Vanderzant 1967; Beck et al, 1968). Its importance probably lies in the nutrient balance it provides to a diet and in the strong phagostimulant effects it has on many phytophagous insects (Vanderzant 1967; Beck et al, 1968). Wheat germ contains minerals, amino acids, protein, lipids, fatty acids and sterols (Pomeranz, 1971). The addition of wheat germ to the diet for E. messoria (diet VI) improved the diet with respect to development times and uniformity of growth, but it was also detrimental to the larval and pupal sizes. The detrimental effects on growth could possibly be due to the increased sterol level of the diet, since it was previously observed that excessive levels of sterol were detrimental to E. messoria. Wheat germ would account for an increase of approximately 0.012% of sterol in the diet, raising the total sterol content to 0.072%.

Brewer (1977) has shown the effects of different protein sources on the growth and development of the sugar cane borer D. saccharalis and the bollworm H. zea. The developmental characteristics of E. messoria on the artificial diets tested also demonstrates a dependance on protein source (Table 17). The number of days required for development to the adult stage decreased with the increasing protein contents of the diets. The longest development periods were associated with meridic diets I, II, and V (protein content of 2.9%) followed by diets III and V (protein content 5.7%) diet VI (protein content 6.9%) and the bean diet (protein content 8.2%).

Table 17. Total protein content of 8 artificial diets.

Diet	Protein source	Percent Protein
Bean	beans, wheat germ, yeast	8.2
I	casein	2.9
II	casein	2.9
III	casein, soybean protein	5.7
IV	casein	2.9
V	casein, soybean protein	5.7
VI	casein, soybean protein, wheat germ	6.4
VII	soybean protein	2.6

Although the total development times are associated with the total protein content, larval development times are not, since larvae reared on diet VI reached larval maturity before larvae fed the bean diet. It appears that diet VI may have nutrient deficiencies which delay development in the prepupal and pupal periods.

Further evidence of possible deficiencies or imbalances of this diet are also seen in a comparison of growth characteristics of larvae reared on this artificial diet (VI) and on the Nicotiana tabacum variety Lonibow. Although the larval and pupal sizes and development rate to larval maturity are similar, the meridic diet caused an increase in development time in the prepupal and pupal stages, suggesting that some nutrients may be missing or are at inappropriate levels in this synthetic diet, resulting in suboptimal growth and development.

b) Number of instars

The larvae of E. messoria reared for these experiments had 6, 7 or 8 instars before pupation. Extra instars have been attributed to the following factors: genetic constitution, population density of the larvae, food deprivation, temperature, nutrition and decrease in vigour. (Leonard 1968, 1970; Poitout and Cayrol 1969; Zenner-Polania and Helgesen 1972). Physical variables were controlled in these experiments with E. messoria and the larvae used in each experiment (i.e. rearings for meridic diets; each alkaloid and N. tabacum)

were from the same parental stock thus ensuring that the genetic constitution of the larvae in a particular experiment was constant. The only variables present were nutrient content, alkaloids and varietal influences N. tabacum var Lonibow and Delhi-34. Nutrient quality appears to influence the number of instars required for normal development since, in the meridic diets tested, larvae fed on diets which caused poorer growth usually required 7 instars to complete growth while on nutritionally adequate mediums, the majority of larvae required only 6. Schmidt and Lauer (1977) demonstrated the importance of nutrient content in determining the number of instars larvae required for normal development in Choristoneura spp. The alkaloids berberine, nicotine and atropine variously influenced the number of instars the majority of the larvae required. Berberine and nicotine ingested at levels which were physiologically growth-inhibiting (0.3%, 1.0% and 0.1% and 0.3% respectively) resulted in a tendency for the larvae to require 7 instars instead of 6. This appears to indicate that extra moults are a consequence of ingesting physiologically detrimental levels of dietary compounds. However, in the group reared on berberine, an 8th instar was observed on the control, 0.01% and 0.03% berberine diets but not at the higher levels, suggesting that the previous statement is not totally applicable in this case. But, the absence of 8th instar individuals at the higher concentrations could also be the result of the ultimate moulting individual being more susceptible to the inhibiting levels of berberine and are therefore eliminated

before larval development was complete. Differences in growth of larvae having 6, 7 or 8 instars was evident in early development, usually showing up at the 3rd instar, since head capsule widths were smaller for larvae having 7 or 8 instars.

The growth stimulating effect of atropine at 0.10% tended to decrease the number of instars required for normal development, since the entire group matured in only 6 larval instars while the remaining atropine groups and the controls experienced 6 or 7 instars.

From these effects, it appears that the number of instars required by E. messoria is affected by both growth-stimulating and growth-interfering chemicals, where fewer instars are associated with the more favorable growth situations. Perhaps this indicates a mechanism adapted by E. messoria whereby extra instars are a response to physiologically detrimental effects of ingested compounds and are necessary to allow complete development.

The influence of N. tabacum varieties on instar number, indicates possible chemical influences of tobacco (either nutrients, secondary plant compounds or both) which make it necessary for E. messoria to have extra instars for normal development. The differences in alkaloid content do not appear to influence the number of instars required.

c) Influences of alkaloids on growth, development and survival of E. messoria.

The ability of E. messoria to survive and utilize the diets with added alkaloids indicates that exposure to alkaloids

has two important agronomic implications. Firstly, the alkaloids affect the survival of E. messoria and secondly chronic exposure to them during the larval period, variously influences growth and development of the insect by acting as growth stimulants or antibiosis agents.

(i) Survival

The survival of E. messoria on the various alkaloid diets indicates that the larvae are adapted to tolerate some alkaloids better than others. Also, the concentrations that can be tolerated varies with the alkaloid. At the lowest concentration tested (0.01%) veratrine caused 100 % mortality, so too did nicotine at the concentration of 1.00%. Mortality rates such as these which occurred in very early development, clearly demonstrate the sensitivity of E. messoria to these alkaloids at these dietary levels. The remaining alkaloids and concentrations of alkaloids were tolerated with varying degrees of success.

Berberine

It appears that E. messoria can tolerate diets containing up to 0.1% berberine since 70 % or more of the larvae became adults. However, they are unable to cope successfully with levels of 0.3 % and 1.0 %, as indicated by the marked drop in survival and the absence of adults in the 1.0 % group. The greatest mortality of the larvae reared on the berberine diets occurred in the early instars (I - III) which would suggest that the larvae are most sensitive to this alkaloid during early development, and in particular at the levels of 0.3% and 1.0 %.

Nicotine

Nicotine at 0.01% may act as a stimulant to the larvae of E. messoria since the survival to pupation was increased, although some consequences of ingesting this diet are evident during the pupal stage, which was characterized by high pupal mortality. Similarly, stimulant effects of sublethal levels of some insecticides have been observed (Dajoz, 1969) and is possibly the reason for the elevated larval survival on 0.01% nicotine. Because survival to the adult stage in 0.01% and 0.03% nicotine groups is roughly equivalent to survival in the controls, E. messoria appears to be well suited to deal with the ingestion of this alkaloid at these conentrations. However, larvae showed a much greater sensitivity to nicotine at the dietary levels of 0.1% and 0.3 %, since the survival sharply dropped with these increases in concentration suggesting that levels greater than 0.03% are increasingly toxic to E. messoria. As was observed with berberine, larvae seem to be more sensitive to the toxic effects of nicotine in early development.

Atropine

In contrast to the detrimental effects of veratrine, berberine, and nicotine, at all concentrations atropine increased the number of larvae forming adults. This clearly illustrates that at the five levels tested, atropine is not toxic to E. messoria but instead, enhances survival.

Information on the effects of plant chemicals on survival

of insect pests such as E. messoria has potential agronomic use. A food plant containing concentrations of secondary plant chemicals sufficient to reduce survival or cause 100% mortality in the insects which attack it has an effective defensive mechanism against that insect. With E. messoria, it would appear that if ingested plant materials contained levels of compounds sufficiently toxic to the larvae, such as 0.01% veratrine or 0.3% and 1.0% berberine or 0.1%, 0.3% or 1.0% nicotine, the success of this insect would be drastically impeded. Evidence that this could indeed be a mechanism of resistance by a plant against E. messoria was shown in the rearings of the N. tabacum varieties Lonibow and Delhi-34. On a wet weight basis, the total alkaloid levels of Lonibow and Delhi-34 are roughly 0.02-0.03% and 0.2-0.3% respectively which correspond to the range of nicotine diets used in these experiments. In both instances, survival on the lower alkaloid containing diets, (Lonibow and 0.01%, 0.03% nicotine) were similar to the non-alkaloid controls whereas survival on the high alkaloids diets (Delhi-34, 0.1%, 0.3%, 1.00% nicotine) was reduced. This supports the observation that E. messoria is well suited to cope with lower concentrations of this alkaloid but less well equipped to survive on higher dietary levels. Moreover, the apparent elevated sensitivity of E. messoria to these alakaloids in early development could be advantageous to a plant by successfully reducing or eliminating this pest during a period where collectively they do less damage due to their small size. This information could

possibly be applied to the control of E. messoria as a pest in tobacco areas. The usual course of this insect's development involves first feeding on rye until it is ploughed under and then moving to tobacco (Beirne 1971). By using a variety of rye or some other suitable plant which could cause a reduced survival of E. messoria during its early stages of development, the population could be reduced, thereby decreasing the number of insects which move over to the tobacco seedlings and thus potentially reduce the damage to this economic crop.

(ii) Influence of chronic exposure to alkaloids on growth and development

All the alkaloids which permitted survival, affected larval development. It is of interest that the alkaloids berberine, nicotine and atropine differently affected the size and/or development times of the larvae, suggesting that the larvae of E. messoria adapt differently to each of these compounds, or conversely that these chemicals influence different processes of this insect.

Berberine

Berberine appears to inhibit larval size with either drastic effects in the early stages of growth or chronically throughout the development period. Although larvae reared on 0.01% and 0.03% berberine were initially smaller than the controls, berberine at these dietary levels had no influence on the ultimate size at larval maturity or pupation since the controls were of equal size. One explanation of this

initial diminutive effect on the larvae is that a lag occurred in the development to full activity of the protective physiological mechanism(s). Rafaeli-Bernstein and Mordue (1978) found that Zonocerus variegatus L.passively excreted the cardiac glycoside ouabain but with prolonged exposure, ouabain excretion was induced to the extent that it was actively excreted against a concentration gradient by the Malpighian tubules. Perhaps a similar situation exists in E. messoria whereby a period of induction is required to fully activate the protective system after which the berberine is removed or reduced to non-toxic or uninhibiting proportions. The longer period of reduced growth with 0.03% berberine could possibly be the result of the higher level of berberine which might have accumulated and would therefore require a longer period to reduce the berberine to a physiologically acceptable level. The recovery of growth observed at the lower concentration of berberine was not observed with the levels of 0.1%, 0.3% and 1.0%, suggesting that the protective mechanisms of the larvae are not able to handle higher concentrations of this compound. The consequences of these limitations of the activity of the protective mechanism(s) is that the larvae are exposed to physiologically inhibiting levels of berberine throughout larval development.

Although 0.1% berberine inhibited the maximum larval weight, it had no apparent influence on pupal size. This is possibly explained by the observed tendency of 0.1% and 0.3% berberine reared individuals to lose less weight during the

prepupal period. It further suggests the possible interference of berberine in the normal prepupal process of weight loss, or it may also indicate another aspect of tolerance of E. messoria to ingested berberine whereby smaller larval size is compensated for during the prepupal period so that the pupal size is unaffected.

Because of the malformed pupae from the 1.00% group, it appears that berberine possibly influences the normal moulting cycle. However the small number of observations does not clearly indicate this influence. Berberine has no significant influence on the total development time of E. messoria except at 0.01%. This can be explained by the fact that this group had an abnormally high percentage of females (20 out of 25). At the lower concentration of berberine (0.03%) there was a general trend towards increased development times for the females compared to the males. Because of the large number of females in the 0.01% group, the total development time to the adult stage was higher relative to the remaining diets.

Even though development times to the adult stages are not influenced by berberine, the larval development times (during the instars II, III, IV, V and VII) are increased by 0.1%, 0.3% and 1.0% berberine. However, the expanded periods of these instars are largely compensated for by a shorter duration of the prepupal stage. The ultimate result of these changes, is that individuals are able to emerge as adults synchronously, regardless of the dietary content of berberine.

Nicotine

Although the size at larval maturity and pupation and the number of days required to complete development were not influenced by 0.01%, 0.03%, 0.1% or 0.3% nicotine, these dietary levels did have some influences during larval development. At 0.01%, and 0.03% nicotine increased the duration of the first instar; caused a decrease in the initial larval weights at 0.03%; and increased size at the 3rd and 5th weeks at 0.01%. However, subsequent growth was unaffected since development was comparable to the controls. Because of this, it can be concluded that nicotine at these levels has no over all negative or positive influence on E. messoria. The periodic occurrence of the elevated weights of the 0.01% group could possibly be due to a stimulating effect which is often associated with sublethal levels of some chemicals. The depression of weight in early development by 0.03% nicotine along with the general increased duration of the first instar may signify a period of induction which is necessary for the detoxification system to become fully operative. With the ingestion of 0.1% and 0.3% nicotine it appears that E. messoria does exhibit some sensitivity towards this alkaloid since the development times to larval maturity are increased, thereby slowing down the rate of growth. This slow growth could possibly indicate that with the ingestion of 0.1% and 0.3% nicotine, the load on the detoxification system is greater than it can handle, thus allowing physiologically inhibiting levels to accumulate.

The slow down in development in 0.1% and 0.3% reared groups is the result of an increased duration of the first 3 instars, which suggests that the larvae are more vulnerable to the negative effects of ingested nicotine in early development.

Despite the increased time required to mature by larvae of 0.1% and 0.3% groups, the total time to adult emergence was not affected because the prepupal period was shortened. This development character adopted by E. messoria insures that, regardless of the concentration of nicotine ingested (up to 0.3%) individuals have synchronous development rates to the adult stage.

Atropine

Atropine has a growth stimulating influence on both larval size and development times in E. messoria, since larvae grew faster and were heavier on all the atropine diets than the controls. This response was particularly evident at the concentrations of 0.03% and 0.1% atropine. Although the atropine-fed larvae weighed more at larval maturity, there were no apparent differences in pupal weights between the atropine and control reared pupae. This loss of growth-stimulating effects of atropine was due to changes which occurred during the prepupal period, where atropine-fed larvae tended to lose more weight than the controls. This suggests that larvae are sensitive to the effects of ingested atropine during the prepupal stage. Besides causing a loss of weight, atropine-fed larvae also experienced an

extended prepupal period. This could also be responsible for the observed increase in weight loss. The end result of this increased period required by atropine-reared prepupae was to coordinate the emergence of adults in the controls, 0.01%, 0.03% and 0.10% atropine groups. However, adult emergence was extended by 0.3% and 1.0% atropine. From this, it is indicated that E. messoria demonstrates some sensitivity to 0.3% and 1.00% atropine but at all other levels tested, the insect demonstrates a very effective tolerance to this compound.

Conclusions

From the chronic exposure of E. messoria to the alkaloids atropine, berberine, and nicotine, it is evident that while this polyphagous insect can cope with an array of alkaloids (and concentrations of alkaloid) it does have definite limitations in its capabilities to grow on alkaloid-containing diets. These factors which interfere or enhance the success of this insect in utilizing its food are of particular interest with respect to potential agricultural situations.

It appears that E. messoria has developed a mechanism to cope with dietary secondary plant compounds which influence the larval development periods. On the alkaloid and non-alkaloid diets, if the larvae experienced increased or decreased development periods (0.1% berberine, 0.1%, 0.3% nicotine; atropine at all levels) the prepupal period is correspondingly decreased or increased with the overall effect that development time to pupation and adult emergence on most diets are

synchronized. This represents an important adaptative mechanism for polyphagous insects such as E. messoria as it would ensure that regardless of the food plant used by the larvae, the adults would emerge at roughly equal times thus ensuring the correct timing of developmental cycles in a population. A plant containing secondary plant compounds in sufficient quantities to interfere with the adult emergence times (such as 0.30% and 1.0% atropine) would ultimately interfere with the reproductive cycle of the insect and possibly reduce the total insect population of subsequent generations. That E. messoria possesses a mechanism to deal with these effects, for some plant compounds, is a good example of insect-plant coevolution.

The concentration of the alkaloids is an important factor in determining the susceptibility of E. messoria to the antibiosis effects of berberine, atropine and nicotine. The growth response of this insect on diets containing 0.01-0.03% nicotine; 0.01%, 0.03%-0.10% berberine and 0.01%, 0.03%-0.10% atropine, clearly demonstrates this insect's capabilities to tolerate these ingested compounds. Of interest to the agriculturalist is the level at which the insect can no longer cope effectively with these compounds. At this level the compound becomes an antibiosis agent for the plant, defending against insect injury. For E. messoria and the alkaloids examined the larvae becomes susceptible to nicotine between 0.03% and 0.10%; berberine between 0.1-0.3%, and atropine at 0.1-0.3%. Veratrine is completely intolerable at 0.01%

and it is not known what the influence of lower concentrations would be. The potential usefulness of information on the level at which a compound becomes detrimental to an insect is seen in the comparison of the larvae of E. messoria reared on the high and low alkaloid-containing varieties of tobacco, Delhi-34 and Lonibow. The developmental characteristics of the two groups clearly showed that Lonibow was a more suitable host for E. messoria since the larvae and pupae of the Delhi-34 group were smaller and took longer to develop. These differences in the developmental characteristics of E. messoria when reared on these two varieties of tobacco demonstrates the importance of the influence a plant can have on an insect population. Delhi-34 is somewhat resistant to E. messoria due to the antibiosis effects on growth, development rates, and survival. As a result of these detrimental effects, this variety would possibly suffer less damage from this insect. In contrast, Lonibow appears to be susceptible to injury by E. messoria since the insect had no apparent detrimental effects resulting from the ingestion of this plant. On the basis of the resistance - susceptibiliy characteristics of these two varieties, Delhi-34 would be the most suitable choice for use in tobacco production.

It is not clear if the differences in growth observed between these two varieties of tobacco are entirely due to the differences in alkaloid content. It is possible that nutritional quality may also have some influence.

d). Influence of alkaloid diets on males and females of E. messoria.

In the control groups, the females generally weighed less than the males at pupation, however, in the groups fed the nicotine and berberine diets, the females tended to be heavier than the males. From this it appears that the females of E. messoria are possibly better suited than the males to tolerate diets containing these alkaloids. The greater tolerance of the females is associated with prepupal development; at this stage, females tend to lose less weight than males. This may indicate the existence of a sexual difference in the efficiencies of the physiological mechanisms associated with tolerance. This phenomenon of sexual dimorphism with respect to physiologically inhibiting chemicals has been observed by Rothschild (1973), who reported greater concentrations of lethal chemicals in females of Aphis caja and the golden tail moth, Euproctis similis. Atropine is tolerated equally well by both sexes of E. messoria since the developmental characteristics do not appear to be affected.

e) Feeding Preference

The feeding preference experiments with the alkaloid diets, solutions, and test plants clearly demonstrated that E. messoria responds to both feeding stimulants and deterrents or repellents and it shows a definite preference in host-plant selection.

Veratrine was a strong antifeedant to the larvae at all the

concentrations tested. This antifeedant effect could explain why the larvae failed to grow on artificial diets to which veratrine had been added.

The observed reduction in feeding on diets containing berberine at concentrations greater than 0.01 % implies that this is the threshold for its antifeedant effect on E. messoria. The acceptance of berberine at 0.01 % and the rejection at dietary levels of 0.03 - 1.00 % is possibly due to differences in the activity of the chemoreceptors when stimulated with these concentrations. Ma (1977) showed that in the African armyworm, Spodoptera exempta (Hubner), the antifeedant effects of warburganal were associated with bursting discharges in several receptor cells. When this compound was applied to the sensilla of the armyworm in subthreshold levels the bursting discharge occured only after long periods of exposure.

Nicotine had a slight phagostimulant effect at all the levels tested except 0.03 %, suggesting that at this concentration nicotine has a slightly negative influence on feeding. However, the general feeding response of the larvae to 0.01 %, 0.1 %, 0.3 %, and 1.0 % nicotine implies that the larvae of E. messoria have adapted to or are in the process of adapting to the nicotine content of it host plants (Nicotiana) in which nicotine is the principal alkaloid. The receptors of this insect may be sensitive to nicotine and will elicit a feeding response in the larvae when they are stimulated by a variety of concentrations. Possibly at the concentration of 0.03%

nicotine activates the receptors in such a manner that the stimulus is interpreted as an antifeedant and thus reduces the feeding response. However, the reason for this insect's response to this concentration is not clear and could possibly represent an artifact of the experimental situation. Cook (1976) observed that the apparent preference for 0.625 M sucrose over 0.125 M sucrose by Locusta migratoria could have been influenced by sensory adaptations from feeding on the higher concentration discs first, which then influenced the feeding response to the the feeding response to the lower concentration discs.

The feeding response of the larvae to the N. tabacum varieties Lonibow and Delhi-34 suggests that these varieties are equally accepted despite their differences in total alkaloid content. This supports the observation of equal responses to the diets of 0.01 %, 0.1 %, 0.3 %, and 1.0 % nicotine in which concentration does not appear to influence the feeding response. The response to the variety of Burley 21 and to N. alta (white bidder) indicates some feeding deterrent effects are present in these plants. The characters responsible for discouraging the feeding on Burley 21 and White Bidder discs could be the result of the relative proportion of stimulant and deterrent compounds or it could be due to nutritional differences. From the larval feeding preferences to these plants, it appears that Nicotiana species possess the potential for resistance to E. messoria by inducing an avoidance reaction by the larvae (i.e. antixenosis). Thus, Nicotiana

species appear to possess two mechanisms of resistance useful against this insect; firstly, the antibiosis effects, which were observed in the rearings with Lonibow and Delhi-34 , and secondly the behavioural - or antixenosis effects. Thus there are at least two mechanisms which could be used to obtain strains of N. tabacum with resistance to E. messoria.

Atropine is a very strong phagostimulant to the larvae of E. messoria, particularily in the range of 0.03 - 0.1 %. The response to increasingly higher concentrations of this alkaloid implies that it enhances feeding over a certain range. If the trend of feeding activity continued with concentrations above 0.1 %, it is possible that atropine could become a deterrent at levels exceeding 1.0 %. The strong phagostimulating effect of atropine is possibly a part of the reason for the strong preference the larvae demonstrated towards Atropa belladona.

The response of E. messoria to a choice of A. belladona and the varieties of N. tabacum (Lonibow, Delhi-34, and Burley 21) shows the larvae preferred A. belladona. This preference could be useful in the practice of attracting larvae in the field by the use of trap plants. Bucher and Cheng (1970) demonstrated that cutworms would aggregate in small areas in a rye field where a few tobacco plants were placed. The response of E. messoria to a choice of A. belladona over 3 varieties of tobacco demonstrates the potential usefulness of this plant as a trapping agent. The use of this plant or one with related properties, introduces the prospect of improving on the suggestions of Bucher and Cheng (1970).

Results from aggregating this pest into one small area could facilitate collecting of the larvae for laboratory studies and for monitoring the population density of the insect. Furthermore, it could restrict the treatment of crops with pathogens or insecticides to small areas.

The feeding response of the larvae towards the 5 garden plants tomato, marigold, delphinium, salvia, and ageratum, further confirms that in its polyphagous habit, E. messoria is not an indiscriminate feeder, but rather demonstrates a preference for some plants over others.

The lack of (or reduced) response of the larvae towards the alkaloid solutions suggests the importance of a nutrient matrix in determining the response of E. messoria to these compounds. Similarily, in Pieris brassicae sinigrin alone had only a small effect on food intake, but in combination with sucrose, it strongly enhanced feeding; this synergistic response of sucrose was also seen with amino acids and ascorbic acid (Ma, 1976; Schoonhoven, 1976). Sucrose is a strong phagostimulant to E. messoria, as it is to many phytophagous insects. The importance of this nutrient in the feeding behaviour of E. messoria was demonstrated in the experiments with atropine - sucrose solutions. Sucrose proved to have a synergistic effect with atropine, and enhanced the feeding response of the larvae. Although the results of the feeding activity in the atropine - sucrose experiments and the atropine diet experiments are similar, there was generally more feeding on the diet discs. This suggests that other nutrients

may also influence the feeding response.

When the larval preferences for the alkaloid diets are compared with the effects of these diets on growth, development, and survival, it is evident that larval food choice does not guarantee that they will choose a diet suitable for normal development (Table 18). Veratrine was totally unpalatable to the larvae, and the larvae were also incapable of utilizing the veratrine diets as a food source. The failure of the larvae to thrive on these diets could be due to the strong antifeedant effects of this alkaloid or, it could have been the result of ingestion of the diet after a long period of food deprivation, and the subsequent toxic effect of veratrine on the larvae.

The response of E. messoria to berberine would be such that the larvae would be inhibited from feeding on diets containing levels of 0.03 %,and 0.1 %, due to the antifeedant effects of these concentrations, and thus the larvae would be kept from an adequate food source. However, larval responses to 0.01 %, 0.3 % and 1.0 % berberine would correctly lead the insect in accepting food which would - or rejecting food which would not - support growth, development, and survival.

The stimulating effect of nicotine on the larval feeding could cause the insect to accept a diet containing physiologically inhibiting or toxic levels of this alkaloid. Therefore, it's response to nicotine is not a reliable guide for the insect to an adequate food source.

The feeding response of the larvae towards 0.01 %, 0.03 %,

Table 18. Suitability and palatibility of alkaloid diets for Euxoa messoria.

Diet	Palatibility**	Suitability*
Veratrine		
0.01 %	---	--
0.03 %	---	--
0.10 %	---	--
0.30 %	---	--
1.00 %	---	--
Berberine		
0.01 %	0	0
0.03 %	--	0
0.10 %	--	0
0.30 %	--	-
1.00 %	--	-
Nicotine		
0.01 %	+	0
0.03 %	+	0
0.10 %	-	-
0.30 %	+	-
1.00 %	+	--
Atropine		
0.01 %	++	0
0.03 %	+++	+
0.10 %	+++	+
0.30 %	++	-
1.00 %	++	-

* -- no growth or development to the adult stage.
- moderate growth and development
0 normal growth and development
+ enhanced larval growth, and normal development to the adult stage.

** See table 12.

and 0.1 % atropine would ensure that the larvae would ingest an adequate diet for normal growth and development. However, the response towards 0.3 % and 1.0% would result in the larvae ingesting quantities of atropine sufficient to delay adult emergence and could thus be detrimental to the insect's reproductive potential.

f) Role of sensory structures in feeding

Both the antennae and maxillary palps are important in the food selection process, and both nutritive and secondary plant compounds are involved. Because the feeding activity on the veratrine diets was slightly increased in the antennectomized larvae, it appears that the olfactory receptors are involved in food selection. However, feeding was still strongly inhibited which implies the presence of other receptors sensitive to veratrine.

It appears that for E. messoria the maxillary palps are essential for normal feeding activity since feeding was inhibited in maxillectomized larvae. Such inhibition of feeding is contrary to what has been observed in other lepidopterous larvae, in which removal of the maxillary palpi reduced larval ability to discriminate between host and non-host plants, often resulting in the insect accepting plants which are normally rejected (Waldbauer and Fraenkel, 1961;Waldbauer, 1962; Hanson and Dethier, 1973). Inhibition of feeding following the removal of the maxillary palps in E. messoria could possibly be the result of trauma caused by the extirpation

of an organ. Similarily, when more than 50 % of the antennae were removed from adult Plodia enterpunctella (Hubner) fecundity was inhibited; this Deseo (1976) attributed to trauma. However, it has been found that in lepidopterous larvae recovery from the extirpation of sensory structures does occur after a short period of time (Waldbauer and Fraenkel, 1961). Also, the larvae of E. messoria did not experience similar inhibitory effects when the antennae were removed since the control diet discs were readily consumed. This indicates that the larvae can survive the procedure with no permanent ill effects.

Although the removal of the maxillary palps reduced the feeding activity towards sucrose, the larvae still demonstrated a preference for this nutrient. This may be explained by the presence of gustatory sensilla sensitive to sucrose located on structures other than the maxillary palps. Ma (1969) found that in the African armyworm, S. exempta, receptors sensitive to sucrose are located on the maxillary palps, the labrum, and in other parts of the buccal cavity. In maxillectomized larvae of E. messoria the sucrose-sensitive receptors that remain do not appear to have as strong an influence on feeding as the maxillary palp receptors, since the response to sucrose discs by intact larvae was much greater than by maxillectomized individuals. Therefore, it appears that the primary receptors for the phagostimulating effects of sucrose are located on the maxillary palps. Similarily, Dethier (1973) demonstrated that the receptor cells of the tobacco hornworm, M. sexta have over-

lapping spectra of sensitivities to compounds and each cell responds to a compound in a unique manner.

The synergistic effect of the sucrose - 0.03 % atropine solutions was not observed in the maxillectomized larvae, indicating that the receptor site(s) involved had been removed. Dethier and Kuch (1971) suggested that synergistic reactions are specific to certain sensilla, and probably involve a number of receptor cells. From the feeding experiments with E. messoria it appears that the receptor cells critical to the synergistic effects are located on the maxillary palps.

The lack of response to the veratrine-sucrose solutions by the maxillectomized larva demonstrated that the larvae are still sensitive to the deterrent effects of this alkaloid. This is probably the result of the antennal receptors detecting veratrine, but it may also involve receptors in the buccal cavity.

g) Response of the larvae to colour

It was observed that larvae would first approach the green coloured discs of plant materials, often coming to rest beneath these discs before feeding occurred. This indicates the larvae have a preference for this colour, (as compared to the white control discs) and that possibly the colour of the food is an arrestant or attractant for the larvae. Similarily dyes used to improve the attractiveness of poison baits for S. exempta were observed to have an arrestant affect on the larvae (Meisner and Ascher, 1973). Lepidopterans have been

shown to demonstrate a sensitivity to colour, particularily to green and near ultra violet spectra (Schoonhoven, 1972). However, the significance of colour sensitive responses in E. messoria is not clear since this insect is a nocturnal feeder and stays beneath the surface of the soil during daylight hours.

V. SUMMARY AND CONCLUSIONS

Experiments on the effects of 8 artificial diets, diets with 5 concentrations of 4 different alkaloids, and 2 varieties of Nicotiana tabacum (Lonibow and Delhi-34) on the development of E. messoria and experiments to examine the feeding behaviour of the larvae showed that:

1.- Larvae have a quantitative requirement for ascorbic acid.

2.- Excessive quantities of cholesterol are detrimental to the growth and development of the larvae.

3.- Soybean protein is an inadequate source of amino acids for E. messoria, but is useful as a supplement to casein.

4.- Wheat germ provides an unidentified nutritional quality to the meridic diet.

5.- The number of instars before pupation is influenced by the nutritional and alkaloid content of the diet ingested.

6.- Head capsule widths of the ultimate instar larvae are not influenced by the number of instars (6,7,or8) or diet, with the exception of berberine at the dietary level of 0.3 % and 1.0 %, which reduced the head capsule sizes.

7.- Alkaloid diets of veratrine, atropine, berberine, and nicotine have various effects on the survival of E. messoria ranging from complete inhibition (at 0.01 % veratrine, 1.0 % berberine, and 1.0 % nicotine) to enhancing survival (atropine at all levels tested).

8.- Chronic exposure to alkaloid diets demonstrated that

E. messoria can tolerate ingested levels of 0.01 %, 0.03 %, 0.1 % berberine, 0.01 %, 0.03 % nicotine, and 0.01 %, 0.03 %, 0.1 % atropine with no detrimental effects. When these levels were exceeded the ingested compounds exerted various physiological effects which influenced survival, growth and development rates (antibiosis effects).

9.- Berberine inhibits larval and pupal sizes at 0.3 % and 1.0 %.

10.- Nicotine at 0.1 %, and 0.3 % slowed the rate of larval growth, but did not affect the ultimate size at larval maturity or pupation.

11.- Atropine stimulated larval growth and development at all the concentrations tested, however at 0.3 % and 1.0 % development times to adult emergence were increased.

12.- Veratrine diets did not allow growth to take place.

13.- Larvae were most vulnerable to antibiosis effects of the alkaloids berberine and nicotine in the early stages of development.

14.- It appears that E. messoria has developed a mechanism to synchronize the development rates of the larvae so that adult emergence times are not necessarily interfered with by levels of alkaloids which inhibit or enhance larval development rates. This is an advantagous mechanism for a polyphagous species which will utilize a variety of food plants since it would ensure a uniformity in adult emergence times in a population despite the different influences chemicals of various food plants might have.

15.- Feeding preference tests and growth characteristics of larvae fed two varieties of N. tabacum, Lonibow (low alkaloid) and Delhi-34 (high alkaloid), indicate that both are equally acceptable but Delhi-34 is less suitable as a food source for the larvae due to various antibiosis affects (lower survival, smaller size, slower rates of development).

16.- Feeding behavioural experiments indicate that E. messoria shows a definite preference for some food sources over others, and that both nutritive and secondary plant compounds are involved in the selection process.

17.- At the lowest concentration tested, veratrine was a strong antifeedant to the larvae.

18.- Nicotine was a mild phagostimulant to the larvae.

19.- Berberine at 0.01 % exerts no influence on the feeding behaviour but has a negative influence at higher concentrations. The threshold level for the antifeedant effect of berberine appears to be 0.01 %.

20.- Atropine was a strong phagostimulant to the larvae, particularily at the concentrations of 0.03 % and 0.1 %.

21.- Sucrose was a phagostimulant to the larvae.

22.- The response to the alkaloids appeared to be dependant on the presence of a nutritional medium. Sucrose, when mixed with atropine had a synergistic affect on the feeding response of the larvae.

23.- Larvae demonstrated a preference amongst the varieties and species of Nicotiana tested.

24.- Atropa belladona was strongly preferred to 3 varieties of tobacco.

25.- Larval food preferences do not guarentee that the larvae will select a diet suitable for normal growth and development.

26.- Both the antennae and maxillary palps are important in host selection. The maxillary palps appear to be essential for normal feeding to occur since their removal inhibited feeding.

27.- Extirpation experiments showed that sucrose receptors occur on the maxillary palps and in the buccal cavity.

28.- Receptors responsible for synergistic effects of sucrose-atropine solutions also appear to be located on the maxillary palps.

VI. Appendix

Browning of the meridic test diets.

It was observed that the colour of the meridic test diets changed after two days of exposure to room temperatures. Colour changes in insect diets have been observed by several workers (Vanderzant et al 1962; Bridges and Norris, 1977). Bridges and Norris (1977) found that the browning of a casein diet used to rear Xyleborus ferrugineus (F.) was due to a non-enzymic reaction of ascorbic acid with the dietary casein. Further, the casein - ascorbic acid reactions were found to reduce the nutritive value of the casein, which resulted in inhibiting reproduction of X. ferrugineus. It is possible that the browning that was observed in the meridic diets used to rear E. messoria was due to this same reaction, and that the resultant reduction of the nutritive value of the dietary protein may have had a detrimental influence on the growth and development of the larvae. The improved growth of E. messoria on the diets with higher protein contents may be related to the observation made by Bridges and Norris (1977) that the effects of the browning were overcome by increasing the casein content of the diet.

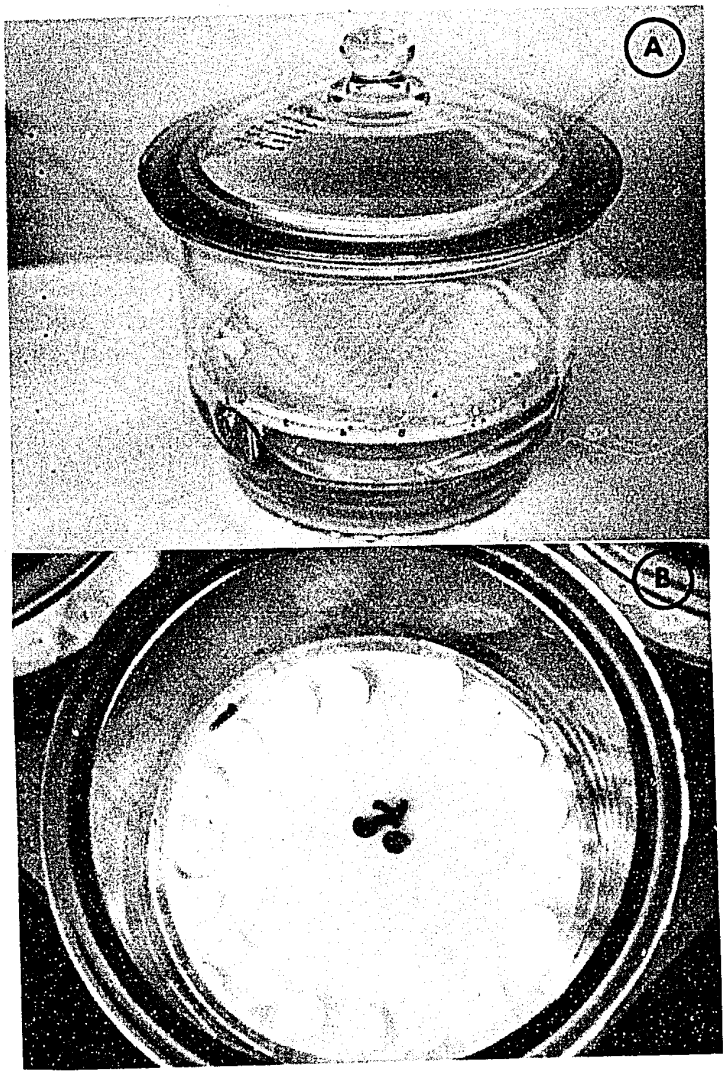


Plate III. A.- Glass dessicator modified to form an arena for feeding preference experiments.

B.- Arrangement of test discs in arena.

Plate IV. Electron micrographs of the antennae and maxillary palps of Euxoa messoria.

A. Ventral view of right side of head (magnified 50X).

B. Antennae (magnified 500X).

C. Maxillary palp (magnified 500 X).

1. antennae, 2. mandible
3. maxillary palp, 4. labrum,
The broken lines indicate where either the antennae or maxillary palps had been ablated.

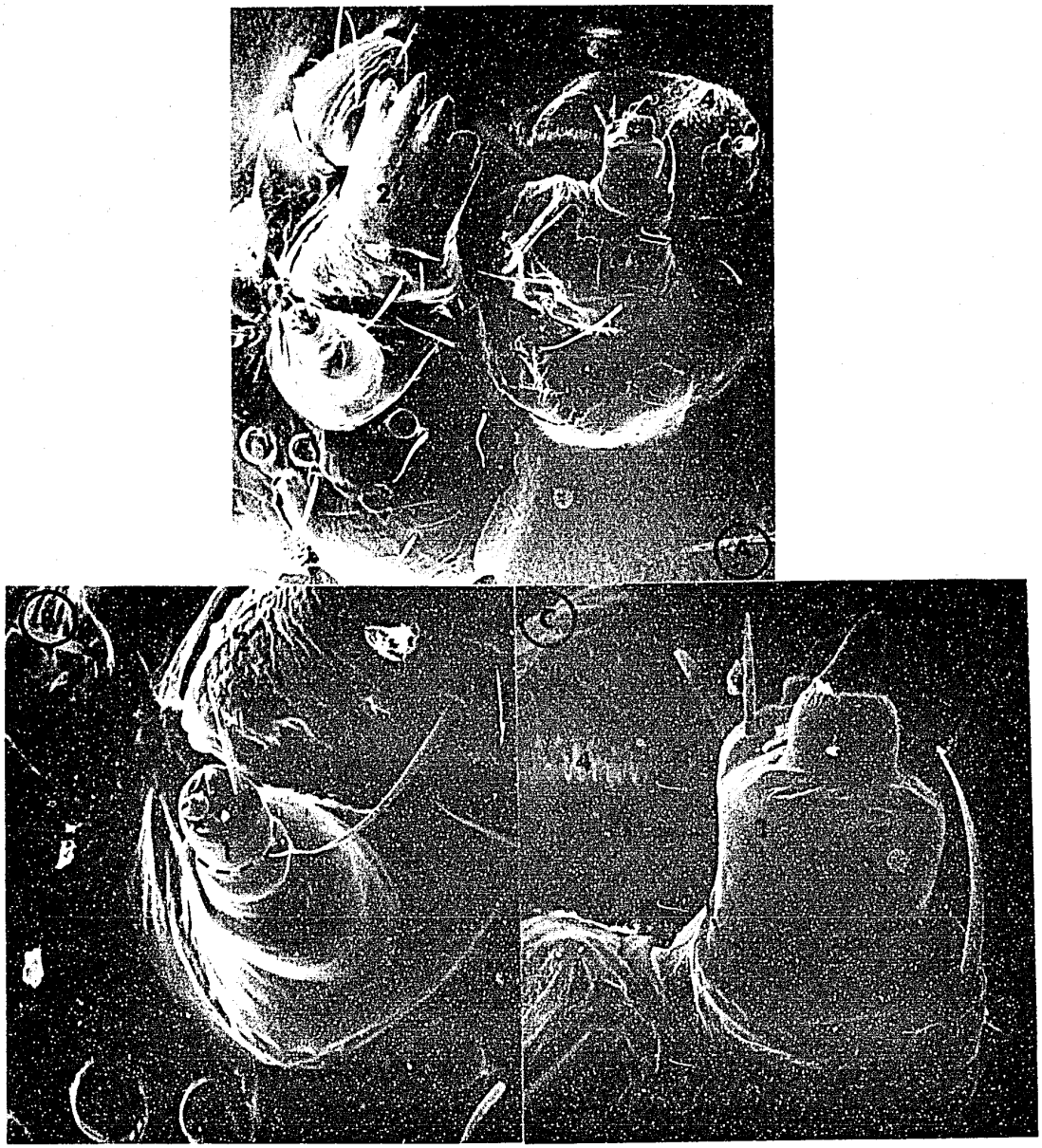
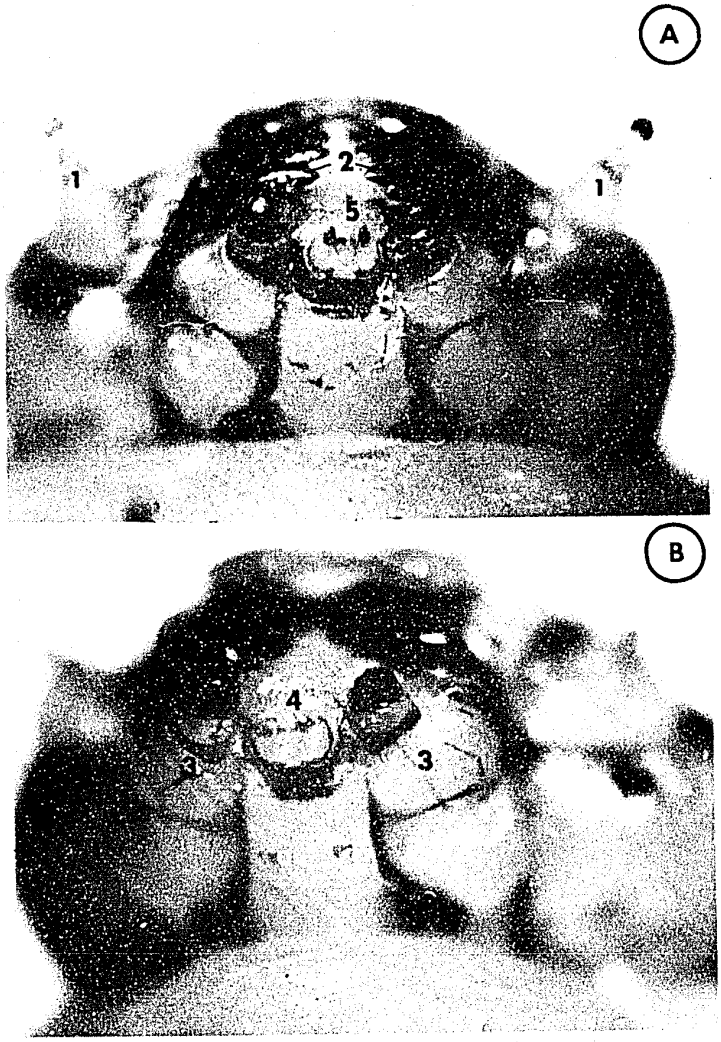


Plate V. Operated larvae of Euxoa messoria after 24 hours of recovery.

A. Antennectomized larva.

B. Maxillectomized larva.

1. remnants of antennae
2. mandibles
3. remnants of maxillary palps
4. labrum
5. area of labrum and maxillary palps.


A
1
2
5
1
B
4
3

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