REVIEW OF LITERATURE
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Review of available information relevant to such aspect as food and feeding, host biochemical influence on feeding and reproduction of insects, is provided to enable a proper understanding as well as meaningful correlation and discussion of these aspects.

Phytophagous insects select their food largely in response to nutrient and allelochemical quality. The biochemical composition of plants changes with plant and tissue age (Denno and Mc Clure, 1983; Slansky and Scriber, 1985; Mattson and Haack, 1987; Heinrichs, 1988). Many phytophagous insects, compensate for a decline in the nutrient content of their food by feeding more often and or/by consuming larger meals (Slansky, 1992a).

Whittaker and Feeny (1971) postulated that specialist herbivores' by concentrating fewer resources on detoxifying a limited number of allelochemics gain advantage over generalist herbivores which must allocate more reserves to detoxify a large diversity of allelochemicals and therefore carry a higher metabolic load. This idea derived largely from data (Krieger et al., 1971) suggests that polyphagous
species of lepidoptera larvae have a higher level of aldrin epoxidase activity than do monophagous species. Food intake, utilization and assimilation are active, dynamic processes which can be altered by an organism in an adaptive manner in response to extrinsic and intrinsic factors (Slansky and Scriber, 1985). Food consumption varies with insect-host interactions, (nutrient/allelochemical action) life history (specialists Vs generalists, forbivores Vs tree feeders and herbivores Vs carnivores) and most other aspects of insect biology (Slansky and Scriber, 1985; Slansky and Wheeler, 1992; Murugan et al., 1993 a, b). Some phytophagous species appears to be better "compensators" than others (Slansky, 1982 b), but there are few studies which assess the ability of insects to alter food consumption and utilization in response to known variation in food quality and quantity, (Slansky and Wheeler, 1989 and 1992).

Herbivores cope with this variability to achieve adequate nutrient intake and to avoid or reduce ingestion of toxic allelochemicals, in large part through flexible feeding behaviour, including selecting food with high nutritional quality consuming more than one food, refusing to eat foods containing deleterious compounds, neophobia,
food aversion, learning and other aspects of foraging behaviour (Haskell and Southwood, 1978; Mattson, 1980; Ahmad, 1983; Bernays and Graham, 1988; Lee and Bernays, 1988; Waldbauer and Friedman, 1991; Slansky, 1992). Once food is contacted the chemosensory system plays a central role in the initiation and maintenance of feeding, with nutrients such as sugars and amino acids as important phagostimulants (Bernays and Simpson, 1982). Concentrations and proportions of nutrients often vary greatly among species or among different parts of the same plant (Waldbauer and Friedman, 1988, 1991; Naeem et al., 1992). Insects may compensate for nutrients dilution by increasing their intake from a nutrients deficient species or plant parts (quantitative compensation) (Slansky and Wheeler, 1989; Simpson and Simpson, 1990) or by eating a suitably balanced intake from two or more species or plant parts that may both be deficient but are nutritionally complementary (quantitative compensation, i.e., self-selection) (Waldbauer and Bhattacharya, 1973; Waldbauer and Friedman, 1991).

The amount, rate and quality of food consumed by an adult influences its performances, mating success, timing and extent of reproduction, dispersal, ability and
probability of survival (Slansky and Scriber, 1985). Certain insects are able to select either poor quality food or to select high quality food from a variety available to them (Miller and Strickler, 1984; Frazier, 1986; Waldbauer and Friedman, 1988). Food quality also can affect larval growth and development and subsequent adult physiology (Johnson, 1969; Slansky, 1982; Slansky and Scriber, 1985).

Numerous books and reviews have dealt with the huge heterogenous assemblage of secondary chemical expressed by plants, which are interpreted as deterrents or toxicants to herbivores (Rosenthal and Janzen, 1979; Brattsten and Ahmad, 1986; Bernays, 1989). Assays of single substances may reveal dose response and toxicity, but for several reasons they incompletely reflect actual responses to plants in which they naturally occur. First, nutritional value of the plant to a specific herbivore can mitigate or exacerbate the detrimental effects of secondary chemicals (Reese, 1979; Hare, 1987; Broadway and Duffey, 1988). Second, plants invariably contain more than one protective secondary chemical (Berenbaum, 1985). Even the most polyphagous species display feeding preferences that are determined by the presence or absence of particular secondary plant
chemicals (Mulkern, 1967; Chapman, 1990). Poor nutritional quality also can be an effective defence against insects (Reese, 1983; Neuvonen and Haukioja, 1984).

Avoidance of plants with high alkaloid content by insects correlates with a lower occurrence of these compounds in favoured grasses (Bernays and Chapman, 1977), fed to the grasshopper *M. bivittatus*. 1% gramine in the diet reduced feeding rates and significantly reduced adult weight (Harley and Thorsteinson, 1967); 3% gramine in the diet caused 50% reduction of feeding in *L. migratoria*, a predominantly graminivorous acridid (Bernays and Chapman, 1977). In insects dietary protease inhibitors can stimulate the over-production of proteolytic digestive enzymes, resulting in severe protein alteration (Broadway and Duffey, 1986).

Secondary plant compounds that are produced by one organism and affect other organisms are referred to as allelochemicals (Kogan, 1986a). Many of the deleterious metabolic effects of allelochemicals may be due to these interactions. There is increasing evidence that secondary metabolic products exists in a dynamic equilibrium and are involved in cycles that include primary compounds such as
sugars and amino acids (Seigler and Price, 1976). Slansky (1990) reported allelochemicals toxic to one insect species may serve as an attractant or nutrient to another, and some of the chemicals contributing to leaf toughness may also have allelochemical activity. Certain nutrients and allelochemicals serve as feeding stimulants for insects whereas other function as antifeedants (Miller and Strickler, 1984; Stadler, 1984). A very toxic allelochemical may be used as a source of nitrogen by highly coevolved herbivore (Reese, 1979).

Many Lepidoptera have been found to require at least one of the polyunsaturated fatty acids viz, linoleic or linolenic acid in their diets of successful pupal eclosion, wing expansion, larval growth and better reproduction (Vanderzant et al., 1957; Dadd 1961, 1964, 1985; Chippendale et al., 1964; Vanderzant, 1968; Hou and Hsiao, 1978; Sivapalan and Gnanapragasam, 1979).

Lepidoptera tend to reveal fatty acid deficiency dramatically by failure of the pupal/adult ecdysis as in the classical study of Ephistia flourmoths (Fraenkel and Blewett, 1946, 1947) development to the pharate adult is usually completed, but the adult failed to reach the pupal
stage, emerges incompletely and larval growth was often retarded. An apparently critical physiological need for fatty acid at metamorphosis (Grau and Terriere, 1971) was confounded by complete alleviation of pupal adult failure in some lepidopteran provided with linolenic acid only during late larval development (Rock et al., 1965; Kato, 1978). Essential fatty acid deficiency similarly manifests as pupal adult failure in some Hymenoptera and can be alleviated by linolenic acid (Yazgan, 1972). Although Orthoptera are hemimetabolous and lack a pupal stage acridid grasshoppers also express fatty acid deficiency by the emergence of deformed adults at the final moult, sometimes proceeded by markedly retarded nymphal growth (Dadd, 1963; Nayar, 1964). Work with several lepidopteran (Tamaki 1961; Chippendale et al., 1964; Terriere and Grau, 1972; Turunen 1974; Hou and Hsiao, 1978) found that only linoleic acid could avert failure at pupal, adult ec dysis, though linoleic acid was sometimes independently necessary for an optimal larval growth rate, while armyworm, Spodoptera litoralis and Homono coffearia, apparently require both linolenic and linoleic acids for normal adult emergence (Sivapalan and Gnanapragasam, 1979).
Some insects are able to regulate independently their intake of protein and carbohydrate, both adjusting the amount of a given food that they ingest and by selecting between alternative foods (Simpson and Simpson, 1990; Waldbauer and Friedman, 1991).

Plants have compounds that reduce digestibility after being ingested such as the chemicals in the plants that are associated with host suitability once ingested. Different hosts, vary in their suitability after ingestion, even for polyphagous species (Busching and Turpin, 1977; Hough and Pimentel, 1978). The main chemoreceptors responsible for accepting or rejecting food by insect larvae are found on the maxillary palp (Dethier, 1970; Schoonhoven, 1973, 1981). Secondary plant substance so detected usually have a deterring role, but some are phagostimulatory (Kogan, 1977; Rosenthal and Janzen, 1979; Schoonhoven, 1981). A substance that deters a generalist feeder may be a phagostimulant for a specialist. Phytophagous Orthoptera and Lepidoptera especially, benefit from high nitrogen in their food, particularly in the form of easily digestible amino acids (Slansky and Feeny, 1977; White, 1978).
The nitrogen level of food plants has generally been varied by the application of fertilizer or by sampling from a range of food plant species or populations and usually higher nitrogen levels have been found to increase survival (Myers and Post, 1981; Myers, 1985; Ohmart et al., 1985; Taylor, 1988), although in some studies increase in nitrogen have been found to have no effect (Lincoln, 1985; Ohmart et al., 1985) or even a negative effect (Stark, 1965; Myers, 1985). Since nitrogen and water levels are often correlated in plants (Scriber and Slansky, 1981), it is difficult to separate their effects (and, indeed, those of any other factors which change concentration with the application of fertilizer or between plant species or populations) on phytophage survival.

Phytophages have developed numerous mechanisms that enable them to take advantage of nitrogen and water-rich (more "nutritious") food (Simpson and Simpson, 1990). For example, the feeding stage of some insects may exhibit facultative carnivory, feed on the most nitrogen-rich plant part, change in position or plant with season and may alter host plant-chemistry (McNeill and Southwood, 1978; Mattson, 1980). Further more, insects on nutritionally poor diets may maximize their nutrient uptake by increasing feeding
rates or development time (Taylor, 1989; Simpson and Simpson, 1990). Female insects may also selectively oviposit on plants most nutritionally suitable for their off-spring (Williams, 1983; Myfes, 1985; Ng, 1988).

Many studies have demonstrated that increase in the nitrogen content of host plant or diet increases larval survival (Myfes and Post, 1981; Myfes, 1985; Ohmart et al., 1985; Cates et al., 1987; Johnson and Bentley, 1988; Taylor, 1988), although this is not always the case (Stark, 1965; Lincoln, 1985). The ability of ovipositing butterflies to select food plants most suitably for their offspring has been demonstrated by various other studies (Ives, 1978; Jones and Ives, 1979; Rausher, 1981; Rausher and Papaj, 1983; Williams, 1983; Chew and Robbins, 1984; Singer, 1984; Ng, 1988).

Herbivorous insects do not live in a nutritionally homogenous environment as their food is variable in both the quantity and quality of nutrients it contains (Slansky and Rodriguez, 1987). Like vertebrates (Le Magnen, 1985) insects are able to compensate for such variability by altering their feeding behaviour.
They can do this in two ways by altering the amount of food eaten and by selecting between available foods (Simpson and Simpson, 1990; Waldbauer and Friedman, 1991). In some experiments insects were given a single diet in which concentrations of both protein and carbohydrate were varied (Simpson and Abisgold, 1985; Raubenheimer and Simpson, 1990). In others, locusts were given a choice of two diets, one of which had no protein but contained one of a graded series of carbohydrate levels and the other contained no digestible carbohydrate but had one of the series of protein levels (Simpson et al., 1988; Chyb and Simpson, 1990). The third type of assay was involved manipulating the nutritional state of insects by feeding them for a defined period on one of several artificial diets, and then providing them with the opportunity to make good any deficiency incurred by allowing them to select between diets (Booth, 1985; Simpson et al., 1988, 1990), but the combination of all three approaches, along with direct manipulation of blood nutrient titres by injection (Abisgold and Simpson, 1988; Simpson et al., 1990b).

Dietary selection involves behavioural decisions both before and after a food is contacted. Some of these decisions involve associatively or non associatively
learned responses, while others are based on innate preferences or direct physiological feedbacks (Booth, 1985; Baker et al., 1987; Simpson and Simpson, 1990). Simpson and White (1990) showed that locusts learn to associate the odour of a food with its protein content. Nymphs are attracted to such odours when they are deprived of protein, but not when they are deficient in carbohydrate. Once food is contacted the chemosensory systems play a central role in the initiation and maintenance of feeding, with nutrients such as sugars and amino acids acting as important phagostimulants (Bernays and Simpson, 1982).

Abisgold and Simpson (1987, 1988) and Simpson et al. (1990 b) demonstrated, using nutrient injections, that amino acids in the blood provide a nutritional feedback controlling the duration of intermeal intervals in the locust, and that part of this effect is apparently mediated by specific changes in the responsiveness of mouthpart sensilla to stimulation by amino acids. In those studies locusts were fed on artificial diet with the protein component diluted to varying degrees compensation involved eating more of the diluted diets. It was hypothesized that such a mechanism could also control dietary selection behaviour for protein and perhaps via blood sugar levels,
even for carbohydrate (Abisgold and Simpson, 1988). Amino acids and sugars are found in highest concentrations within plant tissues rather than on their surfaces.

The relationship of vitellogenin levels (Agui et al., 1985 a; DeBianchi et al., 1985 b; Adams and Filipi, 1988) with ovarian development during the first cycle of oogenesis in the housefly has been reported. Protein feeding is required for ovarian maturation (Adams and Nelson, 1990; Adams and Gerst, 1991) because it activates the corpus cardiacum -(CC) - egg development neurosecretory hormone (EDNH) pathway (Adams and Nelson, 1990; Adams and Gerst, 1992).

Numerous studies on food utilization by Bombyx mori has been summarized by Legay (1957, 1958) and Yokoyama (1963). Beenakkers et al. (1971) observed differences in the approximate digestability (AD), efficiency of conversion of ingested (ECI) and digested (ECD) food values when fed with nutritionally selected host plants.

Chaplin and Chaplin (1981) supported the hypothesis that monophagous herbivores are more efficient in converting food into tissue than polyphagous species as suggested by
Waldbauer (1968) and Whittaker and Feeny (1971). An apparent exception, the monarch butterfly larva, a specialist on milkweed, has a net production efficiency similar to or lower than polyphagous Lepidoptera. To explain this, Schroeder (1976) suggested that food is not limiting for monarch larvae, and hence, there is selection for rapid growth at low food conversion, rather than slow growth at high efficiency.

Higher degree of efficiency of conversion has been reported for Bombyx mori on Morus alba (Hiratsuka, 1922) and Protoparce sexta on tomato (Waldbauer, 1964), because of the highly nutritious food. Simpson (1981) observed the efficiency of utilization of food throughout the fifth instar of L. migratoria significant variation was observed in the quantitative food intake on diverse host plants during post-embryonic development in some pyrgomorphids (Ananthakrishnan et al., 1985).

In insects living on stored dried food (Fraenkel and Blewett, 1944) the ECD was low. Reynolds et al. (1985) suggested that the feeding behaviour of the caterpillar is adopted to maximise the rate at which nutrient is absorbed by the gut, thus permitting maximal rate of growth.
Phytophagous insects require adequate concentration of nutritionally important chemical substances like proteins, amino acids, carbohydrates, lipids and nitrogen in their diet for growth and reproduction. Growth and reproductive success depend to a large extent on the insect's ability to ingest, digest and convert plant nitrogen efficiently and rapidly. The importance of dietary nitrogen as a factor influencing both the fitness of individual herbivorous insects and the dynamics of insect population has been extensively documented (Slansky and Feeny 1977; McNeill and Southwood, 1978).

Protein is always a prime dietary necessity when the whole life cycle is considered, and in adults that take non-proteinaceous food it is supplied by larvally derived stores, though often requiring exogenous augmentation in the females before reproduction can proceed (Pappas and Fraenkel, 1977). The nutritional value of insect's food depends not only on the quantity of food (Mattson, 1980; Scriber, 1984; Schroeder, 1986) but protein quality is also a critical factor influencing the growth and development of insects (Wicker and Nardon, 1982; Horie and Watanabe, 1983). Protein quality is defined mainly by the amino acid profiles.
and the suitability of food protein depends upon how readily its amino acids are liberated and absorbed by the insect as well as the compliment of amino acid it provides.

Food habits and host plant specificity of insects were postulated to be determined by the effects of "secondary plant chemicals" that attracted or repelled the insects and influenced their locomotor, ovipositional and feeding behaviour. Herbivores consume more or less concentrated forms of nutrient supplements and allelochemicals. Chronic effects of allelochemics on insect growth, development and utilization of food were reviewed by Reese and Beck (1976).

Chemical and ecological interest in the milkweeds as a source of poisons which serve a protective function in insects has recently been forthcoming. The cardenolides are a group of C_{23} steroid derivatives, they usually occur in nature as glycosides (cardiac glycosides) attached through oxygen at C-3 of the genin (where R=H in structure) to one or more sugar moieties. Cardenolides are particularly abundant in the families Apocynaceae and Asclepiadaceae. They have been isolated from 12 genera of the Asclepiadaceae (Hoch, 1961). The structure of calotropin was formulated as
Crout et al. (1963). It has been determined that cardenolide concentrations in *Asclepias nivea* and *A. curassavica*.

The metabolic costs to a plant of producing defensive chemicals are expected to bring commensurate rewards in individual fitness (Cates, 1975). The metabolism of cardiac glycosides in plant is well documented (Gibbs, 1974). Examples of the diversity of plant-derived poisons and their immediate precursors used for defensive purposes by insects about in reviews (Eisner, 1970; Schildknecht, 1971). The grasshopper *Poekilocerus bufonius* feeds exclusively on asclepiad plants and has a poison gland from which the contents may be ejected as a spray at the immature hopper stage, or as a foamy froth in the adult stage (VonEmon et al., 1967).

Pyrrolizidine alkaloids (PAs) are defensive secondary metabolites found in numerous plant groups. They are found in the Compositae, Boraginaceae, Fabaceae and Apocynaceae (Bull et al., 1968; Mattocks, 1986). Ithomine and danaine butterflies are attracted to PAs (Masters, 1968; Pliske et al., 1976). PAs are used by the insects as male pheromone precursors (Edgar, 1982; Edgar et al., 1971, 1973) and as
chemical defense compounds (Brown, 1984; Boppre, 1986). All male danaine butterflies except the monarch, Danaus plexippus, appear to secrete PA-derived pheromones for courtship (Edgar, 1975; Ackery and Vane Wright, 1984). PAs are required as precursors for biosynthesis of the quantitatively dominant pheromone, component danaidone and hydroxydanaidonal necessary for courtship success.

PAs are chemically defined as ester alkaloids composed of an amino alcohol (necine:originating from 1-hydroxy methylpyrrolizidine) and mono-or-dicarboxylic acids (necic acids; often C₇-C₁₀ oxygenated and highly branched acids (Bull et al., 1968). Toppel et al. (1988) have recently shown for crotalaria that in the course of germination PAs are metabolized as a nitrogen source. Hydroxy danaidal previously well known as male pheromone is the airborne signal from a variety of PA sources (Krasnoff and Dussourd, 1989; Bogner and Boppre, 1989; Pliske et al., 1976).

Storage of PAs by Lepidoptera was first demonstrated by Aplin and Rothschild (1968, 1972) and numerous similar studies have been undertaken since the analyses reported by Brown (1984 a, b and 1987) are outstanding for their detail. PAs found in insects do not necessarily represent
finger prints of the PAs found in their host(s); rather there are greater differences in the patterns, both qualitative and quantitative (Culvenor and Edgar, 1972; Aplin and Rothschild, 1972), even sex differences occur in PA storage by larvae that had fed on the very same individual plant.

Although storage of PAs are not inevitably imply a protective function, we know from the mediculous studies of Eisner (1980, 1982) and Brown (1984 a, and b, 1987) that Lepidoptera (Utethesia and Ithomiinae) can be protected from predation (by Nephila spiders) by stored PAs they has gathered, respectively, as larvae or adults.

Dixon et al. (1978) analysed cardenolide content in the plant and indicated that D.plexippus preferred the species with lower cardiac glycoside concentration. Zalucki and Kitching (1982a) also compared oviposition on A.curassavica and A.fruticos in a flight cage, and using published plant glycoside levels (Roeske et al., 1976) concluded the opposite to Dixon et al. (1978) i.e., females preferred high cardenolide plants. None of the above studies, except Cohen and Brower (1982), measured cardiac glycosides in the plants actually used in the oviposition experiments.
**D. plexippus** oviposit and feed exclusively on plants in the Asclepiadaceae, and predominantly on species in the genus *Asclepias* (Ackery and Vane wright, 1984). These plants are notable for their toxicity to vertebrates, because they contain a group of plant secondary compounds known as cardiac glycosides (CG) (Brower, 1984).

Due in part to nerve insensitivity (Vaughan and Jungreis, 1977; Jungreis and Vaughan 1977), an ability of larvae to concentrate cardiac glycosides above their gross concentration in the plants (Malcolm and Brower, 1989; Nelson, 1992), and an ability to conserve the compounds through the adult stage (probably a form of storage excretion Brower et al., 1988) monarchs are considered to have evolved the ability to exploit the chemical defences of the plants. This relation to monarchs has attracted substantial attention particularly with respect to adult CG content, aposematic coloration and predation by birds (Brower et al., 1968, 1988) the monarch-milkweed story has served as the paradigm for ecological chemistry (Brower and Brower, 1964; Brower, 1984; Harbome, 1988; Malcolm and Zalucki, 1992).
More generally, the survival of phytophagous insects on their host plants has attracted much attention in the ecological literature (Dempster, 1983). Although extensive work on host plant resistance in agriculture indicates that various aspects of "plant quality" are related to the mortality of associated herbivores (Todd et al., 1971; Fisk, 1980; Hutchins et al., 1984) most ecologists consider biotic factors such as parasites and predators (Hassell, 1985), and/or the physical environment to play the major role in survival of specialist herbivores. Since females of specialist herbivorous insect species supposedly select hosts to maximise immature survival (Singer, 1984), and since immatures are considered to be highly adapted to feed and survive on these plants, the secondary chemicals in these "hosts" are considered to be of minimal consequence in mortality of these immatures.

Interactions of cardenolides or cardiac glycosides and monarch butterfly has been extensively documented (Brower, 1984). Level of cardiac glycosides and insect preference, non-preference studies by several authors (Brower, 1961; Dixon et al., 1978; Zalucki and Kitching 1982a; Malcolm and Brower 1986; Zalucki et al., 1989).
Cohen and Brower (1982) and Zaluki et al. (1989) measured cardiac glycoside levels in the individual plants on which immatures were found. The easiest parameter to measure in biomass (Malcolm and Brower, 1986; Zalucki et al., 1989) by expressing immatures per unit biomass. However this does not account for differences in appearance which females might perceive including leaf shape, colour and texture (Rausher, 1978). Feeding may change cardiac glycoside levels as occurs in other plant secondary compounds (Edwards and Wratten, 1983) and plant cardiac glycosides in milkweeds vary over time (Roeske et al., 1976).

Comparing distributions of immatures (eggs and larvae) across two plant species and making conclusions regarding oviposition preferences (Malcolm and Brower, 1986; Zalucki et al., 1989) confounds at least three processes - oviposition, survival and interplant movement by larvae. No one has measured survival in the early stages (first and second instar) in relation to these compounds, although no effect has been demonstrated in later instar larvae (Dixon et al., 1978; Cohen, 1983).