

Bioenergetics in insect-plant interactions

J MUTHUKRISHNAN

School of Biological Sciences, Madurai Kamaraj University, Madurai 625 021, India

Abstract. Homeostatic mechanisms involving the regulation of the rates and efficiency of food consumption and utilization are reviewed. Adjustment in the rates and efficiencies of consumption and utilization of food during switching on from one host plant to another as well as the compensatory tactics among the consumer species are discussed.

Keywords. Plant chemical composition; insect bioenergetics.

1. Introduction

The origin of phytophagous insects from their detritivorous ancestors and the emergence of terrestrial plants from aquatic habitat and their establishment on land took place simultaneously (Southwood 1972). The phytophagous insects found a better source of nutrients in terrestrial plants than in the nutritionally poor detritus, on which their ancestors were dependent. Consequently, the plants were subjected to a heavy feeding pressure not only by the insects but also by vertebrates. Since then the chemical war between the coevolving groups of plants and insects resulted in a series of morphological, physiological and ecological adaptations in them (Feeny 1976). Many plants have modified their metabolic pathways and evolved a variety of toxic secondary chemicals in defense against herbivores (Schoonhoven 1981). On the other hand, in addition to improving their chemosensory system to enhance host finding and host assessment efficiency, the insects evolved detoxification mechanisms (mixed function oxidases) to counteract the toxic plant chemicals (Brattsten 1979) and homeostatic mechanisms involving regulation of the rates and efficiencies of consumption and utilization of food, to meet their qualitative and quantitative nutritional requirements (Scriber and Slansky 1981).

The spectrum of host plants ingested by insects consists of 10 or more families for generalists (= polyphagous), 2–10 families for intermediates (= oligophagous) and only one family for specialists (= monophagous) (Scriber 1983). Irrespective of the width of the spectrum of host plants, host finding, assessment and acceptance mostly depend on nutrient composition especially protein, water and allelochemicals. When adequate concentrations of the nutrients are not available in the host plant, the insects switch over from one host to other or from one part of the host to other of the same host such as leaf to flower or seed. The switch over is generally followed by adjustments in the rates and efficiencies of consumption and utilization of food. Occasionally, availability of the preferred host plant may be restricted calling for compensatory tactics among the consumer species (Muthukrishnan and Delvi 1974; Muthukrishnan *et al* 1978). The present article highlights the influence of insect-host plant interactions on bioenergetics.

1.1 Bioenergetics

It deals with quantitative aspects of food consumption (C), egestion (F), excretion (U), assimilation (A), metabolism (R) and production (P = conversion) by cells, organisms or populations. The IBP formula of Petruszewicz and MacFayden (1970) usually represented as

$$C = F + U + R + P, \quad (1)$$

is followed in bioenergetics studies. Although energy is not a primary requirement for phytophagous insects, acquisition of sufficient food energy is determined by the various phagostimulants (e.g. protein, water, sugar etc.) and feeding deterrents (e.g. secondary plant substances) present in the food, which evoke positive or negative feeding responses in the consumer. Gravimetric method (Waldbauer 1968) is followed for the quantitative estimation of C , F and P in terms of dry weight, which is converted into energy terms considering the energy equivalents of appropriate samples. Assimilation (A) is calculated as the difference between C and F

$$A = C - F, \quad (2)$$

and metabolism (R) as the difference between A and P .

$$R = A - P. \quad (3)$$

Efficiencies of assimilation (Ae) and gross (Pe_1) or net (Pe_2) production are calculated by relating A to C and P to C or A respectively and expressed in percentage.

$$Ae(\%) = \frac{A}{C} \times 100. \quad (4)$$

$$Pe_1(\%) = \frac{P}{C} \times 100. \quad (5)$$

$$Pe_2(\%) = \frac{P}{A} \times 100. \quad (6)$$

Rates of feeding (Cr), assimilation (Ar), production (Pr) and metabolism (Mr) are calculated by dividing C , A , P and R by the product of mid-body weight (g) of the insect and feeding duration (day)

$$Cr, Ar, Pr \text{ or } Mr = \frac{C, A, P \text{ or } R \text{ (J)}}{\text{Mid-body wt. (g)} \times \text{Feeding duration (day)}}. \quad (7)$$

The procedure described above can also be followed for drawing the budgets for specific compounds or elements present in the food (Muthukrishnan and Pandian 1987). Besides mass and energy budgets, nitrogen and water budgets of insects are usually calculated. Energy budgets are useful to understand the adaptive strategies of organisms. Physiological trade-offs between Cr , Ae and Pe_2 in response to nutritional/environmental stress are not uncommon among phytophagous insects and they have helped them to achieve their ideal final body weight at an optimal growth rate.

2. Host plant parameters of bioenergetics significance

2.1 Nitrogen

Host plant characteristics vary with growth form of plants such as trees, shrubs, forbs or grasses. For leaf feeding insects, leaf chemistry rather than growth form of plant plays a decisive role. Of the many plant characteristics, nitrogen content is vitally important to herbivores. It ranges from 0.03–7% dry wt for different plants and averages 2.1% for 400 species of woody plants (Russell 1947). Within the same species, it differs significantly between seasons, ontogenetic stages, and tissues. During senescence, 20–40% decrease from the maximum level observed in the actively growing season has been reported (Mattson 1980). Tender leaf is richer in N than senescent leaf (e.g. tender *Ricinus communis* leaf 4.83% and senescent leaf 2.08%; Senthamizhselvan and Muthukrishnan 1989). Plant sap has less N (0.004–0.6%) than flowers (92–4%) or seeds (0.5–6.6%) (see figure 1A). C₄ grasses inhabiting xeric N poor soil have less N than the C₃ plants. Competition for the limited soil N between densely populated plants results in low N. Application of N fertilizer to soil increases leaf N by over 4 times. On the other hand, N content of herbivores including insects and mites is several times higher than that of plants and ranges from 7–14% (Scriber 1983). Therefore, N is a limiting nutrient for many phytophagous insects and increase in rates and efficiencies of ingestion and utilization of N may benefit them to realise optimum growth and reproductive success.

2.2 Water

For most terrestrial insects food is the major source of water. Water content of insects is usually higher than their host plants. For instance, most lepidopteran larvae maintain a water content as high as 85–92%. Maintenance of high water contents especially in desiccating terrestrial environment has been a challenging factor for most insects (Edney 1957). For a majority of phytophagous insects low leaf water content has been a major evolutionary hurdle (Southwood 1972). Leaf water

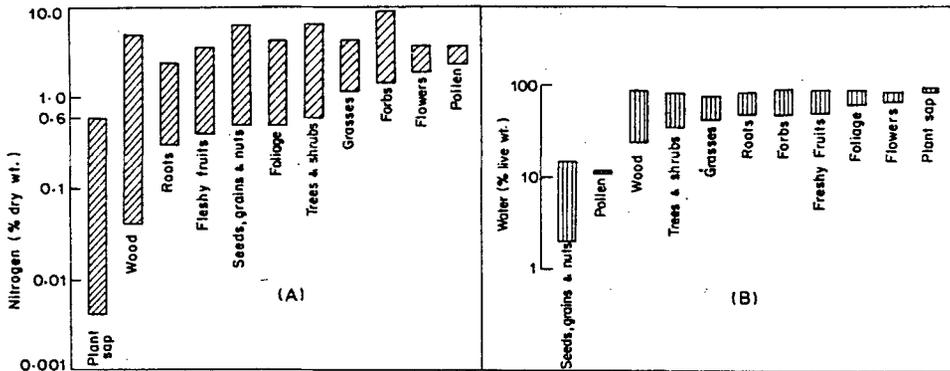


Figure 1. Nitrogen content (% dry wt.) (A) and water content (% live wt.) (B) of host plants.

content covaries with N content in different growth forms, seasons and tissues of plants. It ranges from 75–95% in forbs, 60–85% in grasses and 45–75% in trees (figure 1B). It varies widely in young leaves compared with mature leaves.

2.3 Allelochemicals

These are chemicals evolved by plants to defend themselves against herbivores. However, some of them such as the calotropin of *Calotropis gigantea* have made them vulnerable to insect attack. Although they are considered as non-nutrients, some of them are utilized as nitrogen source by specialist insects (e.g. L-canavanine: Rosenthal *et al* 1982). Toxic amino acids, cyanogenic glycosides, alkaloids, toxic lipids, glucosinolates, sesquiterpene lactones and other terpenoids, saponins, phytohaemagglutinins, protease inhibitors, flavenoids, phenols, tannins and lignins, and insect hormones and antihormones are the major classes of allelochemicals (see Rosenthal and Janzen 1979). Broadly they are classified into two groups—qualitative chemicals which are susceptible to detoxification by specialist insects and quantitative chemicals such as fibers, lignins, silica, tannins, waxes and resins which are dose dependent and capable of reducing the digestibility of ingested food (Feeny 1976). Allelochemicals are capable of seriously impairing food utilization of phytophagous insects. Although nitrogen, water and allelochemicals of host plants are capable of independently influencing the rates and efficiencies of food utilization, it is difficult to quantify their independent influence. Fed on same host plant the performance of different species of insects significantly varies according to their life style, duration of larval development and final body weight attained. Similarly, performance of the same insect fed on different parts of the same host plant also significantly varies depending on the quality of the ingested parts.

3. Food consumption

Insects are capable of varying widely the total quantity of food consumed and the rate at which it is consumed. Besides host plant characteristics such as N, water and allelochemical contents, availability of the preferred host plant and the ability of insects to vary the final body weight are responsible for the observed variations in *C* and *Cr* of same species. Extensive experiments of Slansky and Feeny (1977) revealed that *Cr* of *Pieris rapae* fed on a variety of cultivated and wild plants with 2–5% of N varied from 80–40 J/mg/day. Their results showed a significant negative correlation between N content of host plant and *Cr* (figure 2). The chrysomelid beetle *Phaedon cochleariae* fed on 8-week old turnip leaf containing 49% less N than the leaf of the 4-week old plant displayed 28% increase in *Cr* over that feeding young leaf rich in N (Taylor and Bardner 1968). For the polyphagous *Pericallia ricini* fed on different host plants, Krishnan (1984) also obtained a negative correlation between *Cr* and N content of leaf.

On the other hand Senthamizhselvan and Muthukrishnan (1990) obtained a significant positive correlation between N content of *R. communis* leaf and *Cr* of *Ergolis merione* and *Porthesia scintillans* larvae (figure 3). They found an increase in the fertilizer (urea) dose applied to soil increased the N content of *R. communis* leaf and correspondingly the *Cr* of *E. merione* from 5.06–7.28 kJ/g/day and of

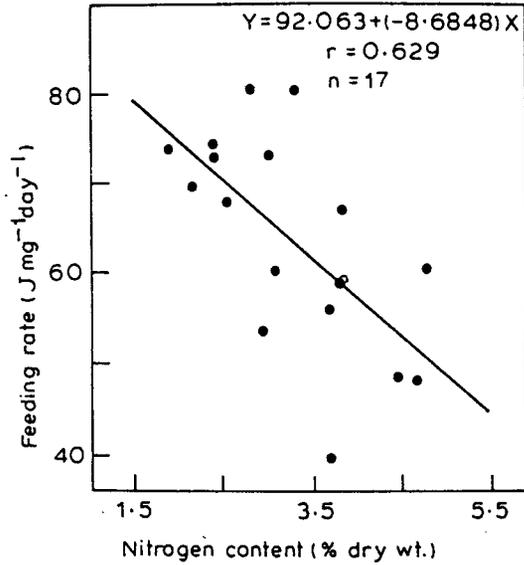


Figure 2. Feeding rate (Cr) of *Pieris rapae* as a function of N content of host plants (from Muthukrishnan and Pandian 1987).

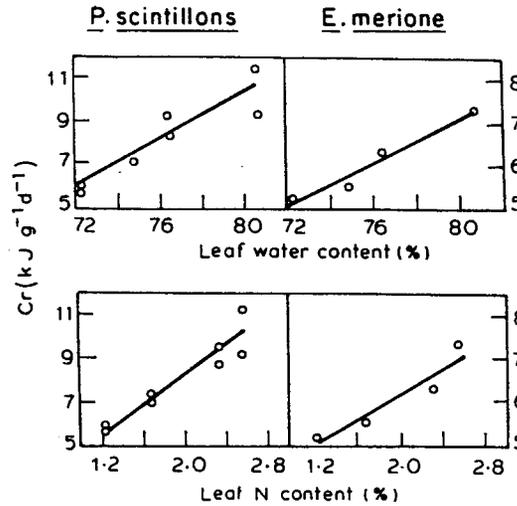


Figure 3. Feeding rate of *P. scintillans* and *E. merione* as a function leaf water and nitrogen contents (from Senthamizhselvan and Muthukrishnan 1990).

P. scintillans from 5.71–10.18 kJ/g/day. Faster *Cr* enabled the larvae to ingest more food. Similarly, higher N content of tender *Moringa olifera* leaf (4.83%) compared with that of senescent leaf (2.08%) doubled the *Cr* of *Eupterote mollifera* larva from 2.758–5.57 kJ/g/day (Senthamizhselvan and Muthukrishnan 1989). Penultimate instar *Papilio glaucus* larva feeding on forbs with 3% N content displayed 30% higher *Cr* (1.7 mg/mg/day) over that (1.31 mg/mg/day) feeding on tree foliage with 2.2% N (Scriber and Feeny 1979). Consideration of water content of the leaf in

addition to N content may explain the contrasting trends in *Cr* in relation to leaf N reported above. *R. communis* leaf raised on higher doses of fertilizer is not only rich in N but also water and energy contents (table 1). The tender *M. olifera* leaf contained more water (74.7%) and energy (20.06 J/mg) than the senescent leaf (water: 50.04%; energy: 14.95 J/mg) (Senthamizhselvan and Muthukrishnan 1989). Similarly the foliage of forbs contains more water than that of trees (figure 1B).

Pandian *et al* (1978) demonstrated the significance of leaf water content on feeding. They found that a minimum of 25% water content is obligatory to evoke feeding in the final instar *Danaus chrysippus* larva; 50% leaf water content enabled the larva to feed adequately to undertake pupation; 60% was the critical minimum water content for successful emergence. Corresponding to increase in the leaf water, *Cr* of the larva also increased. However, *Cr* of the IV instar *Hyalophora cecropia* larva fed on *Prunus serotinia* leaf with 70, 59, 55 and 49% water and 2.7–2.8% N content did not significantly vary (Scriber 1977). Scriber and Feeny (1979) proposed that N content of leaf is more important than water content for forb feeders, while water content is more important than N content for tree foliage feeding insects. Besides N and water, allelochemicals also significantly vary *Cr*, especially of polyphagous insects.

Whereas feeding as well as other bioenergetic parameters of a specialist insect are not seriously hampered by allelochemical with which it was associated during the coevolution, those of generalists widely fluctuate according to the nature and concentration of the allelochemical. *Cr* of *D. chrysippus* fed on *C. gigantea* leaf treated with up to 0.3% concentration of caffeine significantly decreased; further increase in the concentration to 0.5% resulted in an increase in the *Cr* (Muthukrishnan *et al* 1979). However, theophylline had a negative impact on *Cr* of *D. chrysippus*. Fed on *R. communis* leaf treated with 0.1, 0.3 and 0.5% ether extract of the neem kernel. Several plant chemicals possess antifeedant property. Flower extract of *Delonix regia*, seed extract of *Erythrina indica* and kernel extract of *Azadirachta indica* and tannic acid have been shown to deter feeding and decrease the *Cr* and *C* of many lepidopteran (Senthamizhselvan 1987) and coleopteran insects (Chandrakantha 1985). *R. communis* leaf treated with 0.5% ether extract of neem kernel decreased the *Cr* of *E. merione* to 0.9 kJ/g/day from 2.5 kJ/g/day of the larva feeding 0.1% extract treated leaf (table 2). Such plant chemicals seem to have a promising future as potential and safe pesticides.

Restricted availability of the preferred host plant due to over population of the pest and extensive defoliation elicits partial compensation by acceleration of *Cr* (Mathavan and Muthukrishnan 1976; Muthukrishnan *et al* 1978). For instance *Cr* of *Achaea janata* fed on 200 mg *R. communis* leaf/day was (3.98 kJ/g/day)

Table 1. Nitrogen, water and energy contents of the leaf of *R. communis* fertilized with different doses of nitrogen (urea).

Fertilizer (g/m ²)	Nitrogen (% dry wt.)	Water (% wet wt.)	Energy (J/mg)
75	1.235 ± 0.05	72.1 ± 3.40	18.568 ± 1.32
150	1.758 ± 0.06	74.8 ± 3.60	19.145 ± 1.40
300	2.322 ± 0.07	76.4 ± 3.9	22.122 ± 1.30
400	2.662 ± 0.06	80.7 ± 4.1	22.926 ± 1.32

Table 2. Bioenergetics of final instar *E. merione* fed *ad libitum* on *R. communis* leaf treated with different concentrations of ether extract of *A. indica* seed.

	<i>A. indica</i> seed extract concentration		
	0.1%	0.3%	0.5%
<i>D</i>	3.0	3.5	4.5
<i>C</i>	1834	1379	1021
<i>FU</i>	1054	845	686
<i>A</i>	780	534	335
<i>P</i>	339	183	109
<i>R</i>	441	351	175
<i>Cr</i>	2.5	1.1	0.9
<i>Ar</i>	1.1	0.4	0.3
<i>Pr</i>	0.5	0.1	0.1
<i>Mr</i>	0.6	0.3	0.2
<i>Ae</i> (%)	42.5	38.7	32.8
<i>Pe</i> ₁ (%)	18.5	13.2	10.7
<i>Pe</i> ₂ (%)	43.5	34.2	32.6

C, *FU*, *A*, *P* and *R* in J/insect.

Cr, *Ar*, *Pr* and *Mr* in kJ/g/day.

proportionately 22% higher than that (5.52 kJ/g/day) fed on two times more food (400 mg/day) (Muthukrishnan and Pandian 1984). Fed on restricted ration (25% of *ad libitum* level), the grasshopper *Poecilocus pictus* extended the nymphal duration and undertook an additional moult in order to acquire as much food energy as possible (Muthukrishnan and Delvi 1974). It may be interesting to note that insects feeding on same host plant display significantly different *Cr*. For instance fed on *C. gigantea*, *P. pictus* ingested it at the rate of 2.2–2.3 kJ/g/day compared with 17.7–18.1 kJ/g/day of *D. chrysippus* (table 3). Such differences may be explained by the life style of the insects. To compensate the non-feeding pupal and adult stages, the holometabolous *D. chrysippus* feeds at a faster rate than the hemimetabolous *P. pictus* which feeds throughout life (see Pandian 1973). Among the lepidopteran larvae moths are reported to feed at a faster rate than butterflies (table 3). It may be concluded that besides host plant characteristics, availability of the host plant, life stage and style of the insect determine the *Cr*.

4. Assimilation

Assimilation (*A*) and the rate of assimilation (*Ar*) are (i) directly influenced by the spectrum of digestive enzymes secreted, their rate of secretion and activity and (ii) indirectly influenced by *Cr*. Host plant characteristics such as N, water and allelochemic contents also influence assimilation indirectly through *Cr*. Allelochemics also exert a direct influence on assimilation efficiency by their effect on digestive enzymes. As the size of the meal passing through the foregut triggers secretion of digestive enzymes and determines their activity, a constant fraction of the ingested food is assimilated (Muthukrishnan and Pandian 1987).

Pandian and Marian (1986) related the *Ae* of over 60 species of lepidopteran larvae ranging from 19–81% with the N and water content of host plants and

Table 3. Inter specific differences in the utilization of *C. gigantea* leaf by the grasshopper *P. pictus* and the butterfly *D. chrysippus* and *R. communis* leaf by the butterfly *E. merione* and the moth *S. exigua*.

	<i>P. pictus</i> ^a		<i>D. chrysippus</i> ^b		<i>E. merione</i>	<i>S. exigua</i>
	0	0	0	0		
<i>D</i>	150.0	147.0	9.0	9.0	9.0	7.5
<i>C</i>	621.18	276.78	11.74	11.34	11.91	12.88
<i>FU</i>	282.91	120.40	5.53	4.86	5.72	6.88
<i>A</i>	338.27	156.38	6.21	6.48	6.19	6.00
<i>P</i>	171.84*	17.46	2.63	2.39	2.14	1.76
<i>R</i>	166.43	138.92	3.58	4.09	4.05	4.24
<i>Cr</i>	2.30	2.20	17.69	18.11	14.82	18.75
<i>Ar</i>	1.35	1.24	10.62	11.77	8.54	9.85
<i>Pr</i>	0.64	0.14	4.88	4.71	1.19	1.97
<i>Ae</i> (%)	54.5	56.5	52.9	57.1	52.07	46.6
<i>Pe</i> ₁ (%)	27.6	6.3	22.4	21.1	18.0	13.7
<i>Pe</i> ₂ (%)	50.8	11.2	42.4	36.9	34.6	25.6

^aRecalculated from Delvi (1972); rearing temperature 36°C.

^bRecalculated from Mathavan and Bhaskaran (1975); rearing temperature 32°C.

*Includes egg production of 46.93 kJ.

D, Feeding duration; *C*, consumption; *FU*, faeces and urine; *A*, assimilation;

P: production; *R*, metabolism (in kJ/insect) *Cr*, *Ar*, *Pr* rates of *C*, *A*, and *P* in kJ/g insect/day.

obtained a highly significant positive correlation between food N and *Ae* ($r=0.704$). The relationship was more significant ($r=0.868$) when water content of the host plants was considered as a second predictor variable. However, increase in N and water contents of *R. communis* leaf due to increased fertilizer application decreased the *Ae* of *E. merione* and *P. scintillans* (Senthamizhselvan and Muthukrishnan 1990).

Digestibility reducing quantitative chemicals such as tannins, lignins and fibres increase in concentration with age of the host plant. Therefore, earlier instars which prefer to feed on tender leaf with more N and water and less concentration of digestibility-reducing chemicals assimilate the food more efficiently than the later instars which feed tough senescent leaf (Senthamizhselvan and Muthukrishnan 1989). Some of the chemicals like tannin bind with leaf protein and render the plant tissue only partly digestible (Denno and Donnelly 1981). A few of them like soyabean trypsin inhibitor bind with proteases and render them inactive (Applebaum and Brick 1972). Effect of digestibility-reducing chemicals of the host plant varies between species. Grasshoppers and beetles display high tolerance to lignin and tannin compared with lepidopteran larvae (Bernays 1978). Effect of qualitative chemicals such as gallic acid, flavonoids, terpenoids etc. is mostly concentration-dependent and varies also with age of the insect. For instance, with increasing gallic acid concentration from 0.01–0.05 and 0.1 M in the leaf, *Ae* of *Spodoptera littoralis* decreased from 52–38 and 33%, respectively (Mansour 1981). *Ae* of *E. merione* fed on 0.5% neem extract treated leaf was (32.8%) significantly less than that (42.5%) fed on 0.1% extract treated leaf (table 4). Whereas the efficiency of final instar *Spodoptera eridania* decreased with the concentration of DIMBOA in the maize that of the penultimate instar increased (table 4). On the other hand caffeine (0.5%) increased the *Ae* of *D. chrysippus* (Muthukrishnan *et al* 1979).

Table 4. Effect of plant allelochemicals on assimilation efficiency ($X \pm SD$) of Lepidopterous larvae (from Muthukrishnan and Pandian 1987).

Chemical and its concentration	Assimilation efficiency (%)	Reference
<i>A. ipsilon</i> (V instar)		
Control	34 ± 1.1	
<i>p</i> -Benzoquinone, 3.75 × 10 ⁻² M	26 ± 2.2	
Control	31 ± 0.7	
Duroquinone, 3.75 × 10 ⁻² M	28 ± 0.9	
Control	41 ± 1.6	Reese and Beck (1976)
Resorcinol, 3.75 × 10 ⁻² M	45 ± 3.4	
Control	32 ± 0.5	
Phloroglucinol, 3.75 × 10 ⁻² M	30 ± 0.5	
Control	38 ± 1.5	
Gallic acid, 3.75 × 10 ⁻² M	29 ± 1.7	
<i>S. littoralis</i> (V instar)		
Control	51	
Gallic acid, 1 × 10 ⁻² M	52 ± 1.2	
5 × 10 ⁻² M	38 ± 0.8	
10 ⁻¹ M	33 ± 1.9	Mansour (1981)
Coumarin, 1 × 10 ⁻¹ M	Refused to feed	
1 × 10 ⁻² M	56 ± 0.7	
5 × 10 ⁻² M	44 ± 0.5	
<i>S. eridania</i> (V instar)		
B-49 corn DIMBOA, 5.5 mg g ⁻¹	81 ± 0.7	
San Juan corn DIMBOA, 3.59 mg g ⁻¹	79 ± 2.8	Manwoto and Scriber (1981)
DIMBOA-free corn	68 ± 2.5	
DIMBOA 2.4 mg g ⁻¹		
<i>S. eridania</i> (VI instar)		
DIMBOA, 5.5 mg g ⁻¹	58 ± 5.0	
3.59 mg g ⁻¹	61 ± 3.8	Manwoto and Scriber (1981)
2.45 mg g ⁻¹	64 ± 2.8	
<i>D. chrysippus</i> (V instar)		
Control	58 ± 3.0	
0.5% caffeine	70 ± 1.0	Muthukrishnan <i>et al</i> (1979)

It is generally believed that *Ae* is negatively correlated to *Cr*. A faster *Cr* results in rapid passage of food through the gut and provides less time for digestive enzymes to act on the substrate. Increase in *Cr* of *E. merione* and *P. scintillans* feeding N and water-rich leaf account for the decrease in *Ae* (Muthukrishnan and Senthamizhselvan 1990). Decreased consumption of the less preferred host plant was compensated by increased assimilation efficiency *S. eridania* (Soo Hoo and Fraenkel 1966). The relationship between *Cr* and *Ae* is a complex one. A low *Cr* may increase the *Ae* because of prolonged retention of food in the gut and a highly digestible food may lower the *Cr*. Therefore, it is difficult to evaluate the cause and effect relationship between them.

5. Metabolism

Part of the assimilated energy is allocated to metabolism. It depends on that quantum of ingested energy available for assimilation and required for growth to the critical minimum weight. In addition to maintenance of vital activities, the very act of feeding involves expenditure of energy. Foraging insects like bees spend 3.7–8.2% of the energy of the pollen and nectar collected by them as energy cost of foraging (Pandian 1985). Energy allocated to metabolism bears a significant positive linear relationship with Cr in several insects (Pandian *et al* 1978; see also Muthukrishnan and Pandian 1987). Increase in Cr over this minimal level involves further expenditure of energy. To enhance the Cr by 1 J/g/day above the maintenance level, *A. janata* reared at 27°C has to spend 0.225 J/g/day on metabolism (Muthukrishnan and Pandian 1984).

Low water content and high concentrations of allelochemicals in the food result in enhanced metabolic rate. Insects feeding on wilting senescent leaves (Marian and Pandian 1980) and those feeding tree leaves (Scriber 1978) with low water content suffer considerable metabolic strain on account of producing metabolic water. Detoxification of toxic chemicals in the host plants also imposes a heavy metabolic cost. Phytophagous insects employ mixed function oxidases (MFO) for this purpose. Unfortunately the metabolic cost of secreting and operating MFO has not been worked out so far. However it can be inferred from the data on net conversion efficiency (Pe_2) of insects reared on host plants with different concentrations of toxins (table 5). Detoxification of 0.5% nicotine or 0.1% atropine in the host plant cost 8 or 3% of assimilated energy for the final instar *Manduca sexta* larvae. Ingestion of 0.5% caffeine treated leaf doubled the metabolic cost of *D. chrysippus* larva (Muthukrishnan *et al* 1979). However, Mr of *E. merione* feeding 0.5% neem extract treated leaf was 3 times less than that feeding 0.1% extract treated leaf (table 2). Manuwoto and Scriber (1981) have shown that previous experience with the plant toxin would help the insect to considerably minimise the energy expenditure on detoxification. Exposure to unusual toxins as experienced by the insects while switching over to unusual host plants enhances the cost of detoxification, as the insect has to secrete an appropriate enzyme for the purpose.

6. Conversion

Percentage of assimilated energy allocated to tissue growth (Pe_2) varies widely among phytophagous insects. For instance, it varies from 2–87% in the forb-chewing Lepidoptera, 8–72% in the tree foliage feeding Coleoptera and 8–54% in the grass feeding Orthoptera (Slansky and Scriber 1982). Host plant quality especially N, water and allelochemical concentrations account for such variations in Pe_2 . Depending on host plant quality polyphagous insects adjust the rate of food consumption (Cr) and efficiencies of assimilation (Ae) and growth (Pe_2). For instance, the final instar *P. rapae* adjusts the high N content (6.9%) of *Brassica oleracea* and the consequent increase in Cr to 4.232 kJ/g/day by maintaining the Ae (28%) and Pe_2 (41.9%) at low levels; on the other hand, feeding N-poor (3.83%) *Cleome spinosa*, the larva maintains a low Cr (3.136 kJ/g/day) but assimilates ($Ae=33%$) and converts ($Pe_2=54.5%$) with greater efficiency (Slansky and Feeny 1979). Finke (1977) has also reported a positive relation between food N and gross

Table 5. Effect of plant toxins on the net conversion efficiency (Pe_2) of final instar lepidopterous larvae as an indication of the cost of neutralization of toxins (from Muthukrishnan and Pandian 1987).

Species	Test food	Pe_2 (%)	Reference
<i>M. sexta</i>	Diet	48.5	Schoonhoven and Meerman (1978)
	Diet + 0.5% nicotine	40.3	
	Diet + 0.1% atropine	45.5	
<i>D. chrysippus</i>	<i>C. gigantea</i>	48.7	Muthukrishnan <i>et al</i> (1979)
	+ 0.1% caffeine	42.6	
	+ 0.2% caffeine	35.3	
	+ 0.3% caffeine	32.0	
	+ 0.4% caffeine	27.9	
	+ 0.5% caffeine	18.0	
	+ 0.1% theophylline	43.6	
	+ 0.2% theophylline	44.5	
	+ 0.3% theophylline	39.7	
	+ 0.4% theophylline	35.0	
<i>S. littoralis</i>	Semisynthetic diet	44.2	Mansour (1981)
	+ 10^{-2} M gallic acid	39.5	
	+ 10^{-1} M gallic acid	38.3	
	+ 10^{-2} M coumarin	18.0	
<i>S. eridania</i> ^a	Low DIMBOA corn ^b (0.05 mg DIMBOA day ⁻¹)	53.6	Manuwoto and Scriber (1981)
<i>S. eridania</i>	San Juan corn (0.1 mg DIMBOA day ⁻¹)	17.3	
	B49 corn (0.23 mg DIMBOA day ⁻¹)	12.4	

^aPenultimate instar. ^b2,4-Dihydroxy-7-methoxy-1,4-benzoxazine.

conversion efficiency (Pe_1) of *Papilio polyxenes* larva. A direct linear relationship between leaf water content and conversion efficiency (Pe_1 and Pe_2) has been reported for the polyphagous *S. eridania* by Soo Hoo and Fraenkel (1966) and *H. cecropia* by Scriber (1977). An increase in leaf water content from 52–90% resulted in an increase in the Pe_2 of lepidopteran larva from 8–50% (Scriber 1979). As stated already energy cost of production of metabolic water or detoxification of defense chemicals results in low Pe_2 . Any factor which decreases energy expenditure on metabolism would help the insect to enhance the production efficiency. The sawfly *Neodiprion sertifer* larva restricts its active metabolism to a low level by avoiding movement in search of feeding sites and manages to realise a Pe_2 as high as 81%.

References

- Applebaum S W and Brick Y 1972 Natural mechanisms of resistance to insects in legume seeds; in *Insects and mite nutrition* (ed.) J G Rodriguez (Amsterdam: North Holland Publishing Co.) pp 629–636
- Bernays E A 1978 Tannins: An alternative view point; *Entomol. Exp. Appl.* **24** 244–253
- Brattsten L 1979 Biochemical defense mechanisms in herbivores against plant allelochemicals; in *Herbivores: Their interaction with secondary plant metabolites* (eds) G A Rosenthal and D H Janzen (New York: Academic Press) pp 199–270

- Chandrankantha J 1985 *Insect-seed interactions—Bioenergetics of Callosobruchus maculatus*, Ph. D. thesis, Madurai Kamaraj University, Madurai
- Delvi M R 1972 *Ecophysiological studies on the grasshopper Poeciloceris pictus*, Ph. D. thesis, Bangalore University, Bangalore
- Denno F and Donnelly M A 1981 Patterns of herbivory on passiflora leaf tissues and species by specialised and generalised insects; *Ecol. Entomol.* **6** 11–16
- Edney E B 1957 *The water relations of terrestrial arthropods* (Cambridge: Cambridge University Press)
- Feeny P P 1976 Plant apparency and chemical defense: Biochemical interactions between plants and insects; in *Recent advances in phytochemistry* (eds) J Wallace and R Mansell (New York: Plenum) pp 1–40
- Finke M D 1977 *Factors controlling the seasonal food plant utilization by larvae of the specialised herbivore Papilio polyxenes (Lepidoptera)*, M. S. thesis, Wright State University, Dayton, Ohio, USA
- Krishnan M 1984 *Studies on the bioenergetics of a chosen insect pest (Pericallia ricini Fab.)*, Ph. D. thesis, Madurai Kamaraj University, Madurai
- Mansour M H 1981 Efficiency of two allelochemicals on the conversion of ingested and digested food into the body tissues of *Spodoptera littoralis* (Biosd.) (Lepidoptera: Noctuidae); *Z. Angew. Entomol.* **92** 493–499
- Manuwoto S and Scriber J M 1981 Consumption and utilization of three maize genotypes by the Southern armyworm *Spodoptera eridania* (Cram.); *J. Econ. Entomol.* **7** 163–167
- Marian M P and Pandian T J 1980 Effects of feeding senescent leaf of *Calotropis gigantea* on food utilization in the monarch butterfly *Danaus chrysippus*; *Entomology* **5** 257–264
- Mathavan S and Bhaskaran R 1975 Food selection and utilization in a damid butterfly; *Oecologia* **18** 55–62
- Mathavan S and Muthukrishnan J 1976 Effects of ration levels and restriction of feeding duration on food utilization in *Danaus chrysippus* (Lepidoptera: Danaidae); *Entomol. Exp. Appl.* **19** 155–162
- Mattson W J 1980 Herbivory in relation to plant nitrogen content; *Annu. Rev. Ecol. Syst.* **11** 119–161
- Muthukrishnan J and Delvi M R 1974 Effect of ration levels on food utilization in the grasshopper *Poeciloceris pictus*; *Oecologia (Berlin)* **16** 227–236
- Muthukrishnan J, Mathavan S and Navarathina Jothi V 1978 Effect of the restriction of feeding duration on food utilization, emergence and silk production in *Bombyx mori* L. (Lepidoptera: Bombycidae); *Monit. Zool. Ital.* **12** 87–94
- Muthukrishnan J, Mathavan S and Venkatasubbu K 1979 Effects of caffeine and theophylline on food utilization and emergence in *Danaus chrysippus* L. (Lepidoptera: Danaidae); *Entomon* **4** 307–312
- Muthukrishnan J and Pandian T J 1984 Effects of interaction of ration and temperature on growth and bioenergetics of *Achaea janata* Linnaeus (Lepidoptera: Noctuidae); *Oecologia (Berlin)* **62** 272–278
- Muthukrishnan J and Pandian T J 1987 Insecta; in *Animal Energetics* (eds) T J Pandian and F J Vernberg (New York: Academic Press) Vol. 1, pp 373–511
- Pandian T J 1973 Food intake and energy expenditure pattern in two insect primary consumers; *Curr. Sci.* **42** 423–425
- Pandian T J 1985 Behavioural energetics; *Proc. Indian Acad. Sci. (Anim. Sci.)* **94** 219–224
- Pandian T J, Pitchairaj R, Mathavan S and Palanichamy R 1978 Effect of temperature and leaf ration on the water budget of the final instar larva of *Danaus chrysippus* L. (Lepidoptera: Danaidae); *Monit. Zool. Ital.* **12** 17–28
- Pandian T J and Marian 1986 Prediction of assimilation efficiency of lepidopterans; *Proc. Indian Acad. Sci. (Anim. Sci.)* **95** 641–665
- Petrusewicz K and MacFayden A 1970 Productivity of terrestrial animals: Principles and Methods; *IBP Hand Book* No 13 (Oxford: Blackwell)
- Reese J C and Beck S D 1976 Effect of allelochemicals on the black cutworm *Agrotis ipsilon*: Effects of p-benzoquinone, hydroquinone and quoninone on larval growth, development and utilization of food; *Ann. Entomol. Soc. Am.* **69** 59–67
- Rosenthal G A, Hughes C G and Janzen D H 1982 *L. canavanine*, a dietary nitrogen source for the seed predator *Caryedes brasiliensis* (Bruchidae); *Science* **217** 353–355
- Rosenthal G A and Janzen D H 1979 *Herbivores: Their interaction with secondary plant metabolites* (New York: Academic Press)
- Russell F C 1947 The chemical composition and digestibility of fodder shrubs and tree; *St. Publ. Commonw. Agric. Bur.* **10** 185–231
- Schoonhoven L M 1981 Chemical mediators between plants and phytophagous insects; in *Semiochemical: their role in pest control* (eds) D A Nordlud, R L Jones and W J Lewis (New York: Wiley) pp 31–50

- Schoonhoven L M and Meerman J 1978 Metabolic cost of changes in diet and neutralization of allelochemicals; *Entomol. Exp. Appl.* **24** 689–693
- Scriber J M 1977 Limiting effects of low leaf water content on nitrogen utilization, energy budget and larval growth of *Hyalophora cecropia* (Lepidoptera: Saturniidae); *Oecologia (Berlin)* **28** 269–287
- Scriber J M 1978 The effects of larval feeding specialization and plant growth form upon the consumption and utilization of plant biomass and nitrogen: an ecological consideration; *Entomol. Exp. Appl.* **24** 694–710
- Scriber J M 1979 Effect of leaf water supplementation upon post-ingestive nutritional indices of forb-, shrub-vine-, and tree-feeding lepidoptera; *Entomol. Exp. Appl.* **25** 240–252
- Scriber J M 1983 Feeding specialization, physiological efficiency and host plant races in Lepidoptera; in *Temporal and spatial variation in host plant quality: Responses of herbivorous insects* (eds) R F Denno and M S McClure (New York: Academic Press) pp 373–412
- Scriber J M and Feeny P P 1979 Growth of herbivorous caterpillars in relation to feeding specialization and growth form of their food plants; *Ecology* **60** 829–850
- Scriber J M and Slansky F Jr 1981 The nutritional ecology of immature insects; *Annu. Rev. Entomol.* **26** 183–211
- Senthamizhselvan M 1987 *Physiological studies on chosen insect pests, predators and parasites*, Ph.D. thesis, Madurai Kamaraj University, Madurai
- Senthamizhselvan M and Muthukrishnan J 1989 Effect of feeding tender and senescent leaf by *Eupterote mollifera* and tender leaf and flower by *Spodoptera litura* on food utilization; *Proc. Indian Acad. Sci. (Anim. Sci.)* **98** 77–84
- Senthamizhselvan M and Muthukrishnan J 1990 Effect of application of nitrogen fertilizer to soil on host plant utilization by lepidopteran larvae; *Oecologia (Berlin)* (in press)
- Slansky F Jr and Feeny P P 1977 Stabilization on the rate of nitrogen accumulation by larvae of the cabbage butterfly on wild and cultivated food plants; *Ecol. Monogr.* **47** 209–228
- Slansky F Jr and Scriber J M 1982 Selected bibliography and summary of quantitative food utilization by immature insects; *Entomol. Soc. Am. Bull.* **28** 43–55
- Soo Hoo C F and Fraenkel G 1966 The consumption, digestion and utilization of food plants by a polyphagous insect, *Prodenia eridonia* Cramer; *J. Insect Physiol.* **12** 711–730
- Southwood T R E 1972 The insect-plant relationship an evolutionary perspective; in *Insect/plant relationships*, (ed.) F Van Emden (London: Blackwell) pp 3–30
- Taylor W E and Bardner R 1968 Leaf injury and food consumption by larvae of phaedon cochleariae (Coleoptera: Chrysomelidod) and *Plutella maculipennins* (Lepidoptera: Plutellidae) feeding on turnip and radish; *Entomol. Exp. Appl.* **11** 177–184
- Waldbauer G P 1968 The consumption and utilization of food by insects; *Adv. Insect Physiol.* **5** 229–288