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Effect of feeding tender and senescent leaf by *Eupterote mollifera* and tender leaf and flower by *Spodoptera exigua* on food utilization

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Abstract. Food consumption and utilization efficiencies of *Eupterote mollifera* fed on tender leaf were higher than those of counterparts ingesting senescent leaf, while in *Spodoptera litura* individuals fed on flower showed higher values in comparison to those that consumed tender leaf. Food utilization parameters of these insects depend upon the nutritional quality of the food.

1. Introduction

Reviews of Slansky and Scriber (1985) and Muthukrishnan and Pandian (1987) show food quality and availability remarkably influence rates and efficiencies of food utilization in herbivorous insects. Russel (1947) and Mattson (1980) demonstrated that nitrogen content of plants varies widely not only between different species but also between the different parts of the same plant. Herbivores feeding nutrient rich seed, pollen or nectar display higher efficiencies of assimilation and production than others feeding on leaf or flower (e.g. *Megachile pacifica* feeding on pollen and nectar: $Ase = 88\%$; $Pe_2 = 66\%$: Wightman and Rogers 1978; *Callosobruchus analis* fed on seeds: $Ase = 85\%$, $Pe_2 = 59\%$: Wightman 1978). Senthamizhselvan and Murugan (1988) demonstrated that different levels of nutrients in the host plant leaves not only influence ingestion and transformation of food in *Atractomorpha crenulata* but also its fecundity. Barring the publication of Marian and Pandian (1980) very little is known on the effect of age-dependent changes in nutritional quality of the host plant leaf and food utilization by lepidopterous larvae. The present paper reports food utilization of *Spodoptera litura* fed *ad libitum* on tender leaf and flower of *Brassica oleracea* and of *Eupterote mollifera* fed on tender leaf and senescent leaf of *Moringa olifera*.

2. Materials and methods

Newly hatched larvae of *Spodoptera exigua* and *E. mollifera* were collected from their host plants (*B. oleracea* and *M. olifera*). As soon as the larvae moulted into penultimate instar, they were divided into two groups each. One group of *E. mollifera* was fed on tender leaf and the other on senescent leaf. *S. litura* larvae were fed on flower or tender leaf of *B. oleracea*. As lepidopterous larvae ingest more than 80% of their total food consumption during the penultimate and final instar larval stages (Waldbauer 1968), the present experiment was restricted to these instars only. The fourth leaf from the terminal bud was considered as tender leaf and the wilted, less chlorophyll containing yellowish leaf at the bottom-most part of the stem

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or branch of the plant as the senescent leaf. The larvae were fed *ad libitum* on tender leaf or senescent leaf or flower twice a day. Food consumption (C), assimilation (A), production (P) and metabolism (M) of the larvae were estimated following the gravimetric method of Waldbauer (1968) and the scheme of energy balance followed in the present study is the IBP formula of Petrusewicz and Macfadyen (1970) represented as

$$C = P + R + FU$$

and described in detail elsewhere (Senthamizhselvan and Muthukrishnan 1988). Energy content of the samples of leaf or flower, feces and insect was estimated in a 1421 semimicro bomb calorimeter. Nitrogen content of the sample was estimated in microkjeldahl apparatus following the method of Umbreit *et al* (1974). Considering the energy and nitrogen content of appropriate samples, C, FU and P of the larvae, energy and nitrogen budgets were calculated. Rates of food energy or nitrogen ingestion (Cr) or (NCr), assimilation (Ar) or (NAr), production (Pr) or (NPr) and metabolism (Mr) or residual were calculated following the method described by Muthukrishnan and Pandian (1987). Energy budget for the non-feeding pupal period was prepared following the formulae given below:

$$TL = Ex + Pu + R1$$
$$Pu = Pc + A + R2$$
$$A = E + Ad + R3$$

TL, Pu, A and Ad represent the energy contents of terminal larva, pupa, freshly emerged adult and adult at death respectively. Ex, Pc and E represent the energy allocated to exuvia (final instar), pupal case and egg respectively. $R1$, $R2$ and $R3$ represent energy expended on metabolism by pharate pupa, pharate adult and adult respectively. Metabolic rate of the pharate pupa and pharate adult as well as the adult was calculated by dividing the energy expended on metabolism during the respective stages by the product of mid-body weight (g) and duration (day) (see also Muthukrishnan and Pandian 1984).

3. Results

Table 1 provides data on nitrogen, water and energy contents of the food. Tender leaf of *M. olifera* contained more nitrogen (4·83%) and water (74·71%) than the senescent leaf (2·08%; 50·04%). Nitrogen content of the flower of *B. oleracea* (6·35%) was twice more than that (3·15%) of the tender leaf. Energy content of the insects at the commencement of V instar varied between 391 and 648 J. Despite commencing with low energy content *E. mollifera* accumulated more energy (3431 J) than *S. litura* by extending the duration of the larval period to 10 days; the duration for *S. litura* feeding on flower was 6–6·5 days. Ingestion of senescent leaf resulted in a less significant prolongation of the larval duration and a very highly significant decrease in the energy contents of the terminal larva, pupa and adult. For instance, energy content of terminal larva, pupa and adult of *E. mollifera* in the senescent leaf schedule was 1572, 1336 and 624 J, respectively against 3431, 3088 and 1814 J for those in the tender leaf schedule (figure 1). In about 6·5 days female *S. litura* feeding on flower accumulated 5816 J at the time of completion of larval development, while male completed larval development in 5·9 days and contained 4149 J. Female or

Table 1. Nitrogen, water and energy content of the host plants.

Host plant	Nitrogen (% dry wt)	Water (%)	Energy (J/mg)
M. olifera			
Tender leaf	4·83 ± 0·26	74·71 ± 4·07	20·06 ± 0·80
Senescent leaf	2·08 ± 0·17	50·04 ± 3·30	14·95 ± 0·52
B. oleracea			
Flower	6·35 ± 0·26	80·46 ± 4·10	21·55 ± 0·82
Tender leaf	3·15 ± 0·17	76·31 ± 3·82	18·33 ± 0·59

Each value (X ± SD) represents the average of 4 estimations.

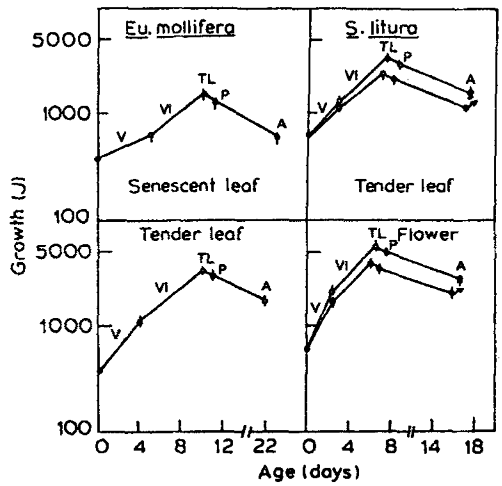

Figure 1. Growth of *E. mollifera* and *S. litura* fed *ad libitum* on tender or senescent leaf or flower of their respective host plant. Roman numerals and vertical lines indicates larval instars and SD respectively.

male *S. litura* feeding on tender leaf for about 7·5 or 7 days accumulated 3475 or 2536 J. At the time of emergence, *S. litura* female or male in the flower feeding schedule contained 2992 or 2097 J; corresponding energy content of the adult in the tender leaf feeding schedule was 1702 or 1170 J.

E. mollifera ingested (16331 J) 44% more food than larva feeding on senescent leaf (8740 J) (table 2). A 2-fold increase in the N content of *B. oleracea* flower over that of tender leaf resulted in about 35% increase in the ingestion of flower by female *S. litura* (table 2). A comparison of feeding rates of these two species indicated that the *Cr* of the larva feeding on tender leaf or flower increased from that feeding on senescent leaf. For instance, *Cr* of *E. mollifera* feeding on tender leaf increased to 5·57 kJ/g/day from 2·758 kJ/g/day of the larvae feeding senescent leaf. However, the increase in *Cr* of *S. litura* male or female feeding on flower over that feeding on tender leaf was only marginal (table 2).

Corresponding to the increase in *C* of the larvae feeding tender leaf, energy loss through *FU* also increased. During the last two instars, *E. mollifera* in the tender leaf schedule lost 7431 J equivalent *FU* compared with 4391 J in the senescent leaf

Table. 2 Overall energy budget for the penultimate and final instar larval stages of the pests fed *ad libitum* on their host plant.

	E. mollifera		*S. litura*			
			Female		Male	
Parameter	Tender leaf	Senescent leaf	Flower	Tender leaf	Flower	Tender leaf
D	10·0	11·0	6·5	7·5	5·9	7·0
*C**	16330·8	8740·1	23968·0	15515·8	17756·4	11662·0
*FU**	7430·8	4391·0	10511·7	7431·4	8103·5	5720·1
*A**	8900·0	4351·0	13456·3	8084·4	9652·9	5941·9
*P**	3041·5	1179·9	5164·0	2795·4	3516·3	1906·9
*R**	5858·5	3171·1	8292·3	5289·4	6136·6	4035·0
*Cr***	5·570	2·758	8·239	5·519	7·720	4·729
*Ar***	3·056	1·378	4·659	2·897	4·243	2·419
*Pr***	0·991	0·357	1·720	0·995	1·491	0·759
*Mr***	2·066	1·021	2·939	1·882	2·752	1·660
Ase(%)	54·5	49·8	56·1	52·1	54·4	51·0
Pe_1(%)	18·6	13·5	21·5	18·0	19·8	16·4
Pe_2(%)	34·2	27·1	38·2	34·6	36·4	32·1

Each value represents the average performance of 10–13 larvae.
D, Day; C, consumption; FU, faeces; A, assimilation; P, production; R, metabolism; Cr, consumption rate; Ar, assimilation rate; Pr, production rate; Mr, metabolic rate; Ase, Assimilation efficiency; Pe_1, Gross production efficiency; Pe_2, Net production efficiency.
*J/larvae; **kJ/g/day.

schedule (table 2). Briefly, feeding water and N rich host plant resulted in the loss of lesser fraction of the ingested energy through *FU*.

During the last two instars, *E. mollifera* feeding on tender leaf assimilated 8900 J compared with 4351 J feeding on senescent leaf. Remarkable differences were observed between energy assimilated by *S. litura* males and females feeding on flower and tender leaf of *B. oleracea* (table 2). Similar trends were observed for *Ar* like that of consumption rate. For instance, *Ar* of *E. mollifera* feeding on tender leaf was 3·387 kJ/g/day compared with 1·260 kJ/g/day for that feeding senescent leaf (table 2). Assimilation efficiency of the larva feeding on tender leaf was significantly higher than that of feeding on senescent leaf. For example, the efficiency of *S. litura* larva feeding on *B. oleracea* flower was significantly higher than that of the larva feeding on tender leaf (table 2). Larvae feeding on tender leaf displayed higher metabolic rate than those feeding on senescent leaf. At an overall rate of 2·066 kJ/g/day *E. mollifera*, feeding on tender leaf metabolised 5859 J of assimilated energy. On the other hand, larvae feeding on senescent leaf metabolised 3171 J at the rate of 1·02 kJ/g/day (table 2). Briefly, irrespective of the life stage or food quality, the larvae expended over 60% of the assimilated energy on metabolism. Larvae feeding on tender leaf registered more than 2-fold increase in production over those feeding on senescent leaf. For instance, *E. mollifera* feeding on tender leaf produced larval matter equivalent to 3042 J compared with 1180 J for those feeding on senescent leaf. Briefly, increase in consumption or assimilation owing to the better quality of the food resulted in an increase in production. Net production efficiency of the larvae feeding on flower was 3% more than that feeding tender leaf. Similar trends were observed for the *S. litura* larvae feeding on tender or senescent leaf.

Irrespective of food quality or species, the pharate pupal period lasted for 1 day.

E. mollifera expended about 25 J of the energy accumulated in the terminal larva (*TL*) to exuvia (*Ex*) and about 50 J to silk production and cocoon formation (*Pc*). Briefly, energy loss on final instar *Ex*, and *Pc* appears to be determined by the size of the *TL*. After incurring a loss of 343 and 236 J on structural and functional components, *TL* of *E. mollifera* belonging to the tender and senescent leaf schedules metamorphosed into pupa with 3088 and 1336 J. Energy content of female *S. litura* pupa in the flower or tender leaf schedule was 5234 or 2996 J, while corresponding value for the male was 3692 or 2155 J (table 3). In the process of transformation of pupa into adult, more than 40% of the energy was lost on *Pc* and maintenance metabolism. The efficiency with which pupal matter was transformed into adult (pupal efficiency) was higher in the tender leaf feeding schedule than in the senescent leaf schedule. A critical analysis of the metabolic rates of pharate pupa and pharate adult of these pests revealed that the rates were higher in the tender leaf schedule and flower schedule and the rate for the male *S. litura* was higher than that of the female in both the schedules. The energy cost of metamorphosis ranged from 184 J/g/day to 514 J/g/day. *S. litura* feeding on flower or tender leaf expended 557·3 J (453 egg) or 259·3 J (211 egg) on egg production. Egg production efficiency of *S. litura* ranged between 15·2 and 18·6% (table 3).

Trends obtained for nitrogen ingestion by the larvae were similar to those

Table 3. Energy budget of pharate pupa and pharate adult of *E. mollifera* and *S. exiqua.*

	E. mollifera		*S. litura*			
			Female		Male	
Parameter	Tender leaf	Senescent leaf	Flower	Tender leaf	Flower	Tender leaf
*TL**	3430·7 ± 183·4	1572·0 ± 84·3	5816·0 ± 288·6	3475·4 ± 182·3	4148·7 ± 207·3	2535·5 ± 140·8
PPD	1·0 ± 0·0	1·0 ± 0·0	1·0 ± 0·0	1·0 ± 0·0	1·0 ± 0·0	1·0 ± 0·0
Exuvia*	26·4 ± 1·3	24·8 ± 1·2	23·7 ± 1·1	22·0 ± 0·9	22·0 ± 0·9	20·4 ± 0·8
Silk*	52·5 ± 2·8	48·3 ± 3·6	—	—	—	—
Pupa*	3087·6 ± 169·6	1336·2 ± 72·3	5234·4 ± 280·5	2994·8 ± 162·4	3692·3 ± 199·8	2155·2 ± 166·8
R1*	264·2 ± 15·8	162·7 ± 9·8	558·6 ± 32·3	438·6 ± 24·6	434·3 ± 22·1	359·9 ± 19·4
PAD	9·0 ± 0·5	9·0 ± 0·5	9·0 ± 0·5	9·0 ± 0·5	9·0 ± 0·5	9·0 ± 0·5
Adult*	1813·9 ± 98·7	624·0 ± 34·8	2991·5 ± 171·4	1701·6 ± 91·9	2097·2 ± 114·5	1170·3 ± 64·2
*Pc**	43·4 ± 2·6	40·1 ± 2·2	53·6 ± 2·9	44·3 ± 2·0	51·4 ± 2·8	43·8 ± 2·2
*R2**	1230·3 ± 67·5	672·1 ± 37·4	2189·3 ± 130·4	1249·9 ± 67·3	1543·7 ± 82·9	941·1 ± 51·6
PE(%)	58·7 ± 3·1	46·7 ± 2·4	57·2 ± 3·0	56·8 ± 2·8	56·8 ± 2·8	54·3 ± 2·4
Egg*	—	—	557·3 ± 32·1	259·3 ± 14·9	—	—
EPE(%)	—	—	18·6 ± 1·0	15·2 ± 1·0	—	—
*AD**	808·6 ± 44·7	312·4 ± 17·8	885·6 ± 47·7	507·1 ± 27·9	199·2 ± 56·4	555·9 ± 30·4
ADU	3·5 ± 0·5	3·5 ± 0·5	3·5 ± 0·5	3·5 ± 0·5	3·0 ± 0·5	3·0 ± 0·5
*R3**	961·9 ± 52·7	271·5 ± 14·7	1495·0 ± 84·0	890·9 ± 49·4	1026·6 ± 56·8	570·6 ± 31·1
*PPMr***	370·0 ± 20·2	312·4 ± 18·4	724·5 ± 39·6	695·5 ± 39·4	779·6 ± 42·4	767·3 ± 42·1
*PAMr***	264·4 ± 16·8	209·9 ± 12·7	499·0 ± 27·4	335·5 ± 20·1	513·5 ± 28·6	394·9 ± 22·4
*AMr***	1876·0 ± 101·6	852·2 ± 48·1	2366·4 ± 132·1	1858·0 ± 99·8	2061·7 ± 111·0	1811·4 ± 97·4
*MMr***	244·7 ± 14·2	184·1 ± 12·9	455·2 ± 25·2	350·8 ± 20·1	483·4 ± 26·1	367·7 ± 19·8

Each value (X ± SD) represents the average performance of 10–13 insects.

TL, Terminal larva; PPD, pharate pupal duration (day); R1, pharate pupal metabolism; R2, pharate adult metabolism; R3, adult metabolism; PAD, pharate adult duration (day); Pc; pupal case; PE, pupal efficiency; EPE, egg production efficiency; Ad, adult at death; ADU, adult duration (day); PPMr, pharate pupal metabolic rate; PAMr, pharate adult metabolic rate; AMr, adult metabolic rate; MMr, metamorphic metabolic rate. *J/insect; **J/g live insect/day.

reported for the ingestion of food energy. At an overall rate of 13·423 and 11·691 or 8·888 mg/g/day, *E. mollifera* and *S. litura* female or male belonging to tender leaf feeding schedules ingested 39·339 and 28·451 or 21·443 mg nitrogen respectively (table 4). About 10–40% of the ingested nitrogen was lost through *FU* by the larvae in the different feeding schedules. The nitrogen assimilation rate (*NAr*) of *E. mollifera* feeding tender leaf (11·808 mg/g/d) was 6 times more than the corresponding rate of the larvae feeding on senescent leaf (2·011 mg/g/d). Nitrogen assimilation efficiency (*NAse*) depended on N content of the food. The efficiency ranged between 52·4 and 90·1%. At an overall rate of 9·64 and 6·279 or 4·847 mg/g/d, *E. mollifera* and *S. litura* female or male feeding on tender leaf accumulated 28·368 and 17·624 or 12·041 mg nitrogen respectively (table 4).

4. Discussion

Under conditions of extreme defoliation of host plant, lepidopterous larvae may be forced to consume leathery, nutritionally poor senescent leaf (Marian and Pandian 1980). A comparison of N, water and energy contents of tender and senescent leaf of *M. olifera* showed that the senescent leaf is nutritionally inadequate. Ingestion of nutritionally inadequate leaf produced several negative effects like decrease in the final body weight or energy content of the terminal larva and adult, larval and pupal mortality, and significant reduction in rates and efficiencies of food utilization in *E. mollifera*. Similar negative effects have been reported by Marian and Pandian (1980) for *Danaus chrysippus* fed on senescent leaf of *Calotropis gigantea*. *Cr* of *E. mollifera* fed on senescent leaf was about 50% of those fed on tender leaf. The reduction in *Cr* and *NCr* was apparently due to about 35% decrease in the water content and 40–57% decrease in the N content of the senescent leaf. However, the response of the chrysomelid beetle *Phaedon cochlearriae* feeding less N containing 8 week old turnip leaf was quite different. The beetle feeding 49% less

Table 4. Overall nitrogen budget for the penultimate and final instar larval stages of the pests fed *ad libitum* on their host plant.

	E. mollifera		*S. litura*			
			Female		Male	
Parameter	Tender leaf	Senescent leaf	Flower	Tender leaf	Flower	Tender leaf
D	10·0	11·0	6·5	7·5	5·9	7·0
*C**	39·339	12·183	70·578	28·451	52·287	21·443
*FU**	5·774	5·801	6·958	6·808	5·275	5·241
*A**	33·565	6·382	63·620	21·643	47·012	16·202
*P**	28·368	4·826	53·697	17·624	36·531	12·041
*r**	5·197	1·556	9·923	4·019	10·490	4·161
*NCr***	13·423	3·845	24·016	11·691	18·657	8·888
*NAr***	11·808	2·011	23·122	8·853	17·190	6·782
*NPr***	9·640	1·504	17·608	6·279	12·514	4·847
NAse(%)	85·32	452·38	90·1	76·1	89·9	75·6
NPe_1(%)	72·11	39·61	76·1	61·9	69·9	56·2
NPe_2(%)	84·52	75·62	84·4	81·4	77·7	74·3

Each value represents the average performance of 10–13 larvae.
See table 2 for abbreviations; r, residual.

N containing leaf displayed 28% increase in *Cr* over that feeding 4 week old leaf (Taylor and Bardner 1968). A comparison of Pe_2 of *D. chrysippus* feeding on senescent leaf (VI instar: 13·6%) with that of *E. mollifera* (VI instar: 28·7%) suggests that *E. mollifera* compensates the poor nutritional quality of the leaf by maintaining their Pe_2 at a level far higher than that of *D. chrysippus*. The decrease in the *Cr* of larvae feeding on senescent leaf points out the role of water and N contents of the food in eliciting positive feeding responses and regulation of food intake as in several other insects (Bernays and Simpson 1982). The finding that the *Cr* of *S. litura* feeding N and water rich flower (female: 8·239 kJ/g/d) is more than that of the larva feeding tender leaf (female: 5·519 kJ/g/d) substantiates the above conclusion. Higher nutritional quality of *B. oleracea* flower enabled *S. litura* not only to utilize the flower more efficiently but also to allocate more energy to egg production. The data obtained on ingestion of tender and senescent leaf or flower by the pests confirm the conclusion of Schoonhoven (1981) that plant chemicals like sugar, protein and water contents are responsible for feeding responses and regulation of food intake. The poor assimilation efficiency of the larvae in the senescent leaf schedule was due to low N and water and the presence of a greater proportion of indigestible matter like fibre. It is interesting to note that Pandian and Marian (1985) have obtained a significant positive correlation between N content of food and *Ase* of lepidopterous insects.

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