

Behavioural responses in terms of feeding and reproduction in some grasshoppers (Orthoptera: Insecta)

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Abstract. Studies on the host preference in some acridids revealed sequentiality of feeding behaviour aided by various sensillae, the suitability of the host plant greatly depending upon the physical and chemical factors. Studies on acridids and pyrgomorphid species indicated that *Truxalis indica* feed exclusively on grasses, *Orthacris maindroni* only on dicot plants and *Atractomorpha crenulata* on both monocot and dicot plants. Significant variations in the quantitative food intake on diverse host plants during post-embryonic development were also evident. Distribution and density of diverse sensillae on the antennae, labrum, maxillary and labial palps as well as their role in food selection are documented. The impact of antennal and palpal ablation on host selection, the quantity of food intake as well as the influence of diverse host plants on fecundity are discussed.

Keywords. Quantitative food utilization; sensillae; degree of preference; post embryonic development; fecundity; grasshoppers.

1. Introduction

Food selection in polyphagous insects is known to involve the cumulative effects of physical, chemical and sensory factors which act independently or simultaneously. Short-term feeding behavioural effects on host selection appears to be influenced by the secondary plant chemicals acting as phagostimulants and/or deterrents and long-term physiological effects are known to involve nutrition and antibiosis (Chapman and Bernays 1977). The role of sensillae in the maxillary and labial palps in food selection was suggested by Blaney and Chapman (1969) and Bernays and Chapman (1970, 1973), their numerical variations among acridids feeding on graminaceous and broad-leaved plants reflecting their role in food selection (Chapman and Thomas 1978). Available information on feeding and food selection of essentially graminivorous acridids relates to specific aspects concerning short term behavioural effects pertaining to quantitative food intake and utilization. Long term physiological effects involving growth and reproduction on diverse host plants as well as the role of sensillae in food discrimination/avoidance, especially in dicot feeding grasshoppers, appear meagre. For a further understanding of the food selection of grasshoppers, an attempt has been made to study the feeding and behavioural dynamics involving feeding and reproduction of the polyphagous pest species, *Atractomorpha crenulata* (Fabricius), *Orthacris maindroni* Boliver (Pyrgomorphidae) and *Truxalis indica* Boliver (Acrididae).

2. Materials and methods

A. crenulata, *O. maindroni* and *T. indica* were collected from the fields in and around Madras, reared in cages and provided with their respective host plants for

feeding. Nymphal stages were isolated and reared individually in separate cages as well as in glass chimneys. In order to find out the exact day of moulting, the pterothorax of the nymphs was marked with cutex. Mating pairs were isolated from the cages and provided with transparent plastic vials (8 × 12 cm) filled with loose wet soil for oviposition. The number of egg pods laid in the vials could be easily counted through the transparent wall of the vials. The plastic vials containing egg pods were covered with thin muslin to prevent the escape of the emerging nymphs. The emerging nymphs were counted and reared individually in different host plants. Increase in the weight of the nymphal stages while feeding on different host plants was recorded through the use of a monopan balance.

To calculate the quantitative food intake and food utilization, fresh host plants were weighed initially and kept in a flask containing water and 15 adults/nymphs were allowed to feed for 24 hr, another set of host plants of similar weight were kept as control simultaneously to find out the quantitative food intake by the insects. After 24 hr, both the experimental as well as the control host plants were weighed. In order to assess the loss of weight in experimental leaves due to the feeding damage, both the control and experimental leaves were desiccated for 7 days. The difference in the dry weight between the control and experimental plants indicated the quantity of food intake/number of insects. Excreta of the experimental insects were collected in polyethylene papers during 24 hr of experimental period and weighed immediately as well as after complete desiccation for 7 days. The difference in the quantity of food intake and the quantity of excreta indicated the quantitative food utilization for specific host plants.

For light microscopic observations, the labrum, labium, maxillae and antennae of the grasshoppers were dissected in insect ringer, washed with distilled water, incubated in 1% boiling KOH for 5 min, washed well in distilled water and mounted in glycerine. For obtaining scanning electron microscope pictures, the labrum, labium, maxilla and antenna were washed well in 80% ethanol, dried and fixed on aluminium stubs using a double adhesive tape and coated with gold using an ion coater. The coated materials were examined in a Hitachi SEM and photographed using an attached Mamia camera.

For quantitative estimations of proteins, carbohydrates, total lipids and phenols, the standard methods of Lowry *et al* (1951), Dubois *et al* (1956), Kok (1971) and Bray and Thorpe (1954) respectively were followed.

3. Results

3.1 Role of sensillae in feeding behaviour

3.1a *Sensillae of the inner side of the labrum:* Studies by Chapman and Thomas (1978) on the distribution of sensillae on the inner side of labrum indicated the occurrence of diverse sensillae arranged in the 'alpha' and 'beta' tract in addition to the A-1 to A-3 sensillae. Further studies on the distribution of sensillae of *A. crenulata*, a dicot feeder and the *T. indica*, a monocot feeder indicated further variation in the distribution and the nature of sensillae. Hence as a convenient measure the sensillae of the innerside of the clypeo-labrum was further differentiated as S1 and S2 of the inner side of the distal margin of clypeus. In addition to the alpha and beta tracts of the labrum another tract was also distinguished, referred to here as gamma tract, with a

higher number of sensillae. All the sensillae of the gamma tract appeared to be of the campaniform type arranged in a 'V' shaped fashion. A-1 sensillae were not noticed both in light microscopic as well as in SEM studies. Further recognition of the sensillae of the alpha tract was made into the campaniform alpha-B sensillae (S-4a) and (S-4b) sensillae. In the beta tract all the sensillae appeared large, consisting of campaniform sensillae (S-5) and trichoid sensillae (S-6). In the free distal margins, another group of sensillae designated as S-7 was also recognised. In the inner side of the labrum, A-2 and A-3 sensillae alone were noticed (figure 8).

In *T. indica*, a similar distribution of sensillae was evident with the wide beta tract covering the entire distal margin of the labrum. The type S-7 sensillae were unrecognisable and numerical differences in the sensillae were also evident as compared to that of the other species studied (figure 8).

3.1b Sensillae of maxillary and labial palps: Studies by Haskell and Schoonhoven (1969) and Blaney (1974, 1975) indicated the presence of trichoid sensillae which are mechanical receptors as well as another group of chemosensory trichoid sensillae.

During the post-embryonic development of *A. crenulata* from the nymphs to the adults, a gradual increase in the number of sensillae at the palpal apices as well as on the surfaces of both maxillary and labial palps was observed (figures 1 and 2). A bottom collar is characteristic of the short trichoid apical sensillae, occurring at the apices of both maxillary and labial palps, the entire surface of the maxillary and labial palps bearing a number of trichoid and campaniform sensillae (figure 7).

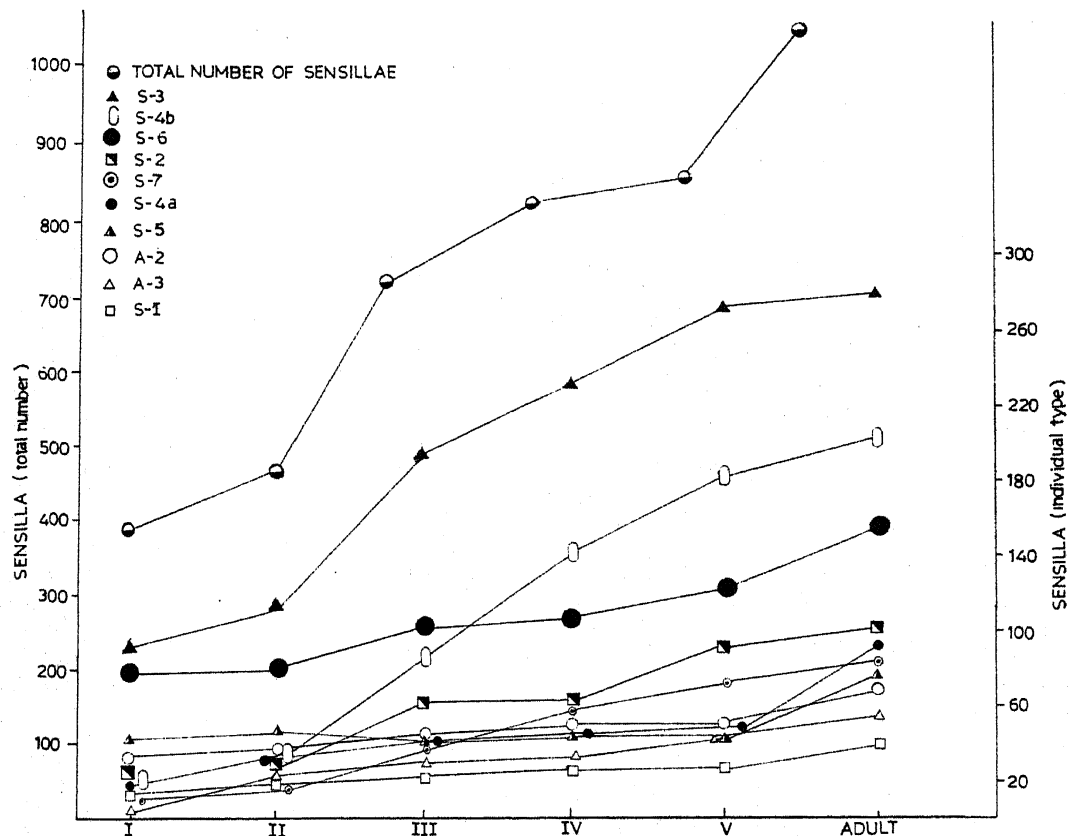


Figure 1. Numerical increase of sensillae on the inner side of the labrum of *A. crenulata* during post-embryonic development.

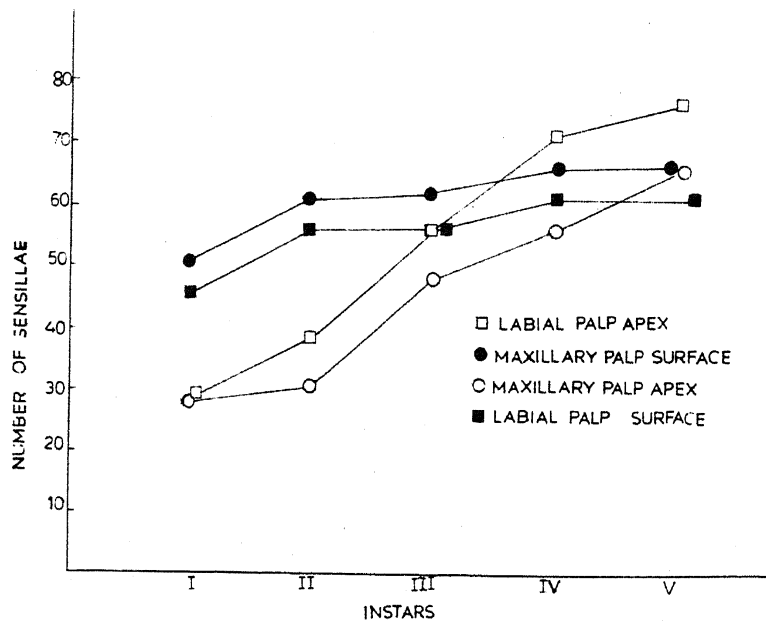


Figure 2. Numerical increase of sensillae on the maxillary and labial palps of *A. crenulata* during post-embryonic development.

3.1c *Numerical increase of sensillae during post-embryonic development:* A consistent increase in the total number of sensillae of the labrum was evident during post-embryonic development of *A. crenulata* (figure 2), the rate of increase of each type of sensillae varying considerably. A significant increase in the sensillae types S-4b, S-6 and S-3 to the extent of about 3–4 times was observed, while others like S-2, S-4a, S-7, S-5, A-2; A-3 and S-1 showed a gradual increase as they reached the adult stage. S-2 sensillae appeared to be numerically identical being constant during the first and second nymphal stages, increasing in numbers during the third, retaining the same number in the fourth and increasing again in the fifth stage nymphs.

Similarly the number of sensillae at the apices of the maxillary and labial palps also increased during post-embryonic development, with the trichoid sensillae on both palps being 22–27 and 24–30 in the first nymphs and 34 and 38 in the second nymphs respectively. Further increase in the number of sensillae was evident in the other stage also bearing 47 and 55, 57 and 72, 67 and 77 respectively in the maxillary and labial palps of 3rd, 4th and 5th instar nymphs (figure 2).

3.1d *Influence of sensory structures in the discrimination of host plants:* The antennae, maxillary and labial palps, labrum and hypopharynx are known to play a key role in food selection, aided by visual host location. To the control individuals, when nine host plants were offered simultaneously, the quantitative food intake in terms of dry weight consumed was found to be more in *Ricinus communis* L. and *Dolichos lablab* L. and, *Prosopis spicigera* L and *Calotropis gigantea* R. Br were not consumed. One side antennectomised individuals showed a similar feeding range, but with a substantial reduction in the quantity of food intake. Total antennectomy resulted in the quantitative food intake becoming very much reduced. Palpectomy involving labial and maxillary palps individually or together reduced the feeding range to three plants

when nine plants were offered simultaneously, with the quantity of food intake being reduced. Labrectomy had no influence on the feeding range, except for a substantial decrease in food intake.

3.2 Host range

Atractomorpha crenulata is a recognised cosmopolitan polyphagous pest species feeding on diverse crop plants. Both the adults and nymphs feed on a variety of crop as well as weed plants belonging to both dicot and monocot plants. Screening of diverse host plants in and around the habitat of *A. crenulata* showed their ability to feed on the members of family Euphorbiaceae, Solanaceae, Fabaceae, Poaceae, Amarantaceae and Asclepidaceae, their incidence being very high (more frequent) on the dicot plants especially by the nymphal stages. Screening of these host plants for various nymphal instars showed that they preferred Euphorbiaceae, Fabaceae, Amarantaceae and other dicot plants like *Clerodendrum* sp. However their incidence was low on monocots especially on the members of the family Poaceae. Though *A. crenulata* is on record as occurring on the members of the families Asclepiadaceae, Cucurbitaceae, Verbanaceae they avoided these plants for feeding. The present observations indicate that crop plants like *Ricinus communis* L., *Solanum melongena* L., *S. torvum* Sw., *Dolichos lablab* L., *Panicum maximum* Jacq., *Clerodendrum* sp., and *Achyranthes aspera* L., form the major food plants for the growth of *A. crenulata*. Though the nymphs have a wide host range, *R. communis*, *D. lablab* and *A. hypogaea* appear to be the preferred host plants.

The pyrgomorphid, *Orthacris maindroni*, in particular their nymphs fed exclusively on dicot plants like *R. communis*, *D. lablab*, *S. melongena*, *S. trilobatum*, *C. gigantea*, *Clerodendrum* sp. and *P. spicigera* exhibiting a preference within their range of host plants, to *R. communis* and weeds like *Clerodendrum* sp. They are polyphagous, feeding on the members of the families of Euphorbiaceae, Fabaceae, Solanaceae, Asclepidaceae, Vernoniaceae, Bignoniaceae and Mimoseae and their occurrence on *C. gigantea* appeared only more casual.

Truxalis indica feeds exclusively on monocots especially on *Cynodon dactylon* Pers. (Poaceae), *Cyperus rotundus* L. (Cyperaceae), *Carex* sp.

3.3 Host preference and food plant selection

Host preference of *A. crenulata* on the basis of quantitative food intake indicated that when seven preferred host plants viz *R. communis*, *S. melongena*, *D. lablab*, *P. maximum*, *S. trilobatum* and *Clerodendrum* sp were provided, quantitative food intake was more in *R. communis*, *D. lablab* and *S. melongena*. When the same host plants were offered individually, quantitative food intake was high among *R. communis*, *S. melongena* and *D. lablab*, and comparatively low in the other food plants. Simultaneous offering of the three host plants showed increased preference to *R. communis* and *D. lablab*, the former being more preferred than the latter.

Similar variation in the quantitative food intake of different nymphs on either host plants was also evident, with the first instar nymphs tending to feed on six out of eight host plants offered, indicating a distinct preference towards *R. communis* than to *D. lablab*. But the second stage nymphs showed a preference for all the six hosts offered

with a higher quantitative food intake in respect of *R. communis* and *S. melongena*. The third instar nymphs showed an increase in the host range, feeding on seven of eight hosts offered with a higher, but equal amount of food utilization on both *S. melongena* and *R. communis*, but lesser in *D. lablab*. Both fourth and fifth instar nymphs fed on all the eight host plants provided, a higher quantity of food intake being evident on *R. communis*, and very much less on *S. trilobatum* and *Oryza sativa* L (figure 3).

Individuals of *Orthacris maindroni* feed on a wide spectrum of dicot plants, exhibiting specific preference towards *R. communis* and to a lesser extent on *D. lablab* than the other host plants. Though they feed only on dicot plants, under experimental conditions it was possible to make them feed on monocot plants like *P. maximum*. *T. indica*, a monocot feeder showed a specific preference to *C. dactylon* and to lesser extent to other grasses and never fed on dicot plants. Though the adults of *O. maindroni* preferred *R. communis*, all the nymphal stages preferred to feed more on *Clerodendrum* sp, the adult showing a reduced preference.

3.4 Quantitative food utilization

In addition to the amount of food intake, the quantity of food utilized and the quantity of water excreted varied considerably while feeding on different host plants. When eight host plants were offered to *A. crenulata* individually, the amount of food consumed by 15 adults, as expressed in the form of dry weight was very high in *R. communis* (1,240 mg/15 adults), comparatively lower in *D. lablab* (780 mg/15 adults) and very low

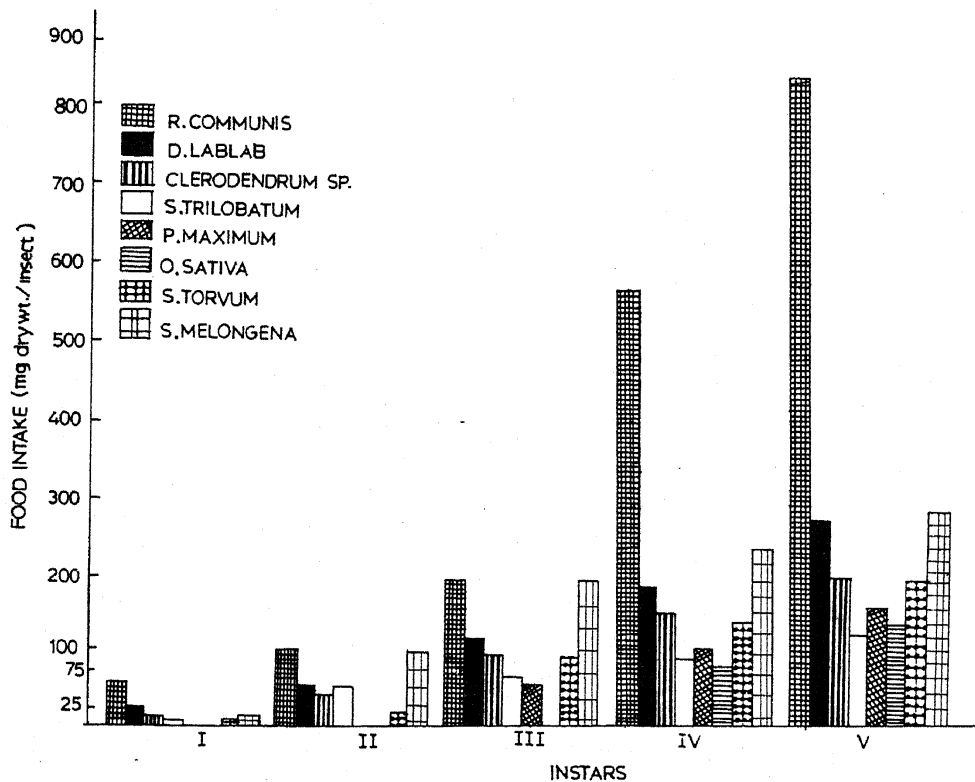


Figure 3. Quantitative food utilization by nymphal stages of *A. crenulata*.

in the case of *S. melongena*, *S. trilobatum*, *Clerodendrum* sp. and *P. maximum* (170–300 mg/15 adults). However the dry weight of food excreted was very high when fed on *R. communis* (430 mg/15 adults), as compared to (100–135 mg/15 adults) on other host plants. The amount of water consumed was also high (3,140 mg/15 adults) on *R. communis*, comparatively lower in *D. lablab* (1,040 mg/15 adults), and very low (286.1–664.6 mg/15 adults) in other host plants. Similarly water assimilation was also high for both *R. communis* (3.12 mg/15 adults) and *D. lablab* (1.01 mg/15 adults) than on other host plants (table 1).

Similar variations in the quantity of food utilization of diverse host plants were also noticed in *O. maindroni*, where the quantity of food consumed was high for *R. communis* (190 mg/15 adults) than on other host plants. When the same host plants were offered individually to *O. maindroni*, intake was very high in *D. lablab* (550 mg/15 adults) and comparatively lower (80–330 mg/15 adults) on other host plants like *S. melongena*, *S. trilobatum*, *P. maximum*, *C. gigantea*, *Clerodendrum* sp and *Bougainvillea* sp. The dry weight of excreta was very high (160–175 mg/15 adults) when fed on *D. lablab*, *P. maximum* and *C. gigantea*, and comparatively lower (60–135 mg/15 adults) on *S. melongena*, *S. trilobatum*, *R. communis*, *Clerodendrum* sp and *Bougainvillea* sp. Highest dry weight was assimilated when fed on *D. lablab* (375 mg/15 adults), comparatively lower on *Clerodendrum* sp and *R. communis* with 195 and 138 mg/15 adults respectively. In the other host plants it was considerably lower. Correspondingly the amount of water assimilated was equally high in *C. gigantea* (1,441 mg/15 adults), *D. lablab* (1,310 mg/15 adults) and *R. communis* (1,010 mg/15 adults) and in other plants it was considerably lower (table 2).

When a wide range of host plants were offered simultaneously to *Truxalis indica* there was a specific preference towards *Carex* sp (360 mg/5 adults), *Commelina* sp (200 mg/5 adults). However under continuous starvation they tend to feed on other dicot plants like *R. communis*.

3.5 Life cycle

A. crenulata being a polyphagous species, the different host plants seem to influence fecundity and the rate of post-embryonic development. Of the seven preferred host plants provided as nymphal diet, the development was quicker on both *R. communis* and *A. hypogaea*. On *Clerodendrum* sp, *S. torvum* and on *P. maximum* the duration of development was comparatively longer, whereas no development was observed when reared on *O. sativa* (Var. I.R. 50) (figure 4, table 3).

The rate of mortality of different nymphal instars as well as the number of nymphs attaining adult stage differ considerably on various host plants. Nymphal mortality in all host plants tested was very high in the first nymphal stage and was lower in the second with no mortality in the other stages. A very low nymphal mortality and a higher rate of adult emergence were evident in *R. communis* and *A. hypogaea*, whereas a very high nymphal mortality and low adult emergence were observed when reared on *Clerodendrum* sp and *P. maximum*. Interestingly mortality was 100% even in the first instar itself when reared on *O. sativa* (figure 5).

Table 1. Quantitative food utilization of *Atractomorpha crenulata* (adult)

	Host Plants						
	<i>Ricinus communis</i>	<i>Solanum melongena</i>	<i>Dolichos lablab</i>	<i>Panicum maximum</i>	<i>Solanum trilobatum</i>	<i>Clerodendrum</i> sp.	<i>Calotropis gigantea</i>
Dry weight fed (mg)	1240	300	780	170	200	208	—
Dry weight excreted (mg)	430	110	135	100	115	105	—
Dry weight assimilated (mg)	305	109	645	70	85	103	—
Moisture content of leaf (%)	71.51	68.90	57.07	63.95	58.37	67.34	79.4
Amount of water consumed (mg)	3140	664.6	1040	301.6	286.1	438.7	—
Water excreted (mg)	31.4	270	25.1	10.6	30.0	12.0	—
Water assimilated (mg)	3.12	637.6	1.01	290.9	256.1	426.7	—

Table 2. Quantitative food utilization of *Orthacris maindroni*

	Host plants							
	<i>Ricinus communis</i>	<i>Dolichos lablab</i>	<i>Solanum melongena</i>	<i>Solanum trilobatum</i>	<i>Panicum maximum</i>	<i>Calotropis gigantea</i>	<i>Clerodendrum</i> sp.	<i>Bougainvillea</i> sp.
Choice of 8 sp (dry wt. fed) (mg)	190	110	28	24	59	72	75	5
Dry wt. excreted when offered separately, dry wt. fed (mg)	300	550	175	130	270	300	230	80
Dry wt. excreted (mg)	112	175	90	80	170	160	135	60
Dry wt. assimilated (mg)	138	375	85	50	100	140	95	20
Moisture content of the leaf (%)	72.52	58.79	74.83	50.57	76.84	79.4	76.78	60.88
Amount of water consumed (mg)	1090	1330	695.2	262.9	1170	1460	990	205
Amount of water excreted (mg)	81.2	25	20	40.45	15	15	27	15
Water assimilated (mg)	1010	1310	675.2	222.5	1150	1,441	963	190

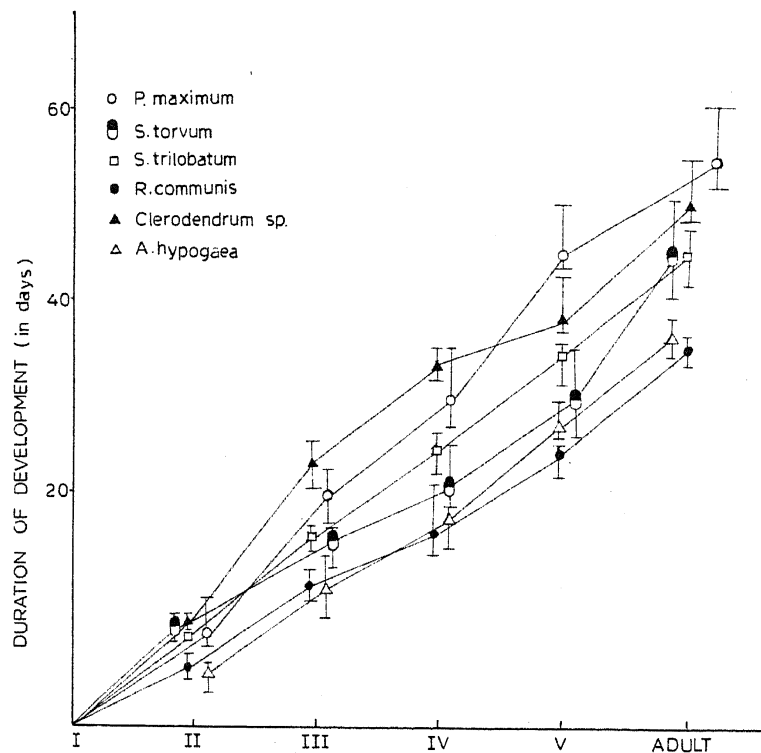


Figure 4. Developmental duration of *A. crenulata* when fed on different hosts.

3.6 Weight increase during the post-embryonic development

In addition to normal variations in the developmental rates as well as percentage of mortality of the nymphs when reared on different host plants there were considerable variations in the increase in the weight of the nymphs when reared on different hosts. The first instar nymphs when developed on *R. communis* showed a higher weight increase than on other hosts. From third instar nymphs onwards the weight increase became more pronounced in female nymphs than in male nymphs. Adults emerging from those nymphs fed on *R. communis* showed an increase in weight ranging from 75–90 mg in males and 220–250 mg in females, and a similar but comparatively lower weight increase was noticed on *A. hypogaea* with the weight increase of 168–260 mg in females and 65–70 mg in males respectively. Weight increase during the post-embryonic development was very low when reared on *P. maximum* where the emerging adults showed a very low weight, ranging from 60–65 mg and 110–115 mg in males and females respectively. On the other host plants the weight increase was moderate, ranging from 60–85 mg in males and 120–210 mg in the females (figure 6).

The first nymphal stage also differed considerably when developed on different host plants. Weight increase on both *R. communis* and *S. trilobatum* was higher (20–25 mg), and comparatively lower on *A. hypogaea* (15–20 mg). When developed on other host plants like *P. maximum*, *Clerodendrum sp.* and *S. torvum* the weight increase was very low, ranging from 12–20 mg. Similarly the second stage nymphs also showed a higher weight increase when reared on *R. communis* and *A. hypogaea* (30–55 mg). A very low weight increase was observed on *S. torvum* (20–30 mg). In other host plants like *P. maximum*, *S. trilobatum* and *Clerodendrum sp.* the weight increase was intermediate

Table 3. Impact of host plants on the life cycle and fecundity of *Atractomorpha crenulata* and *Orthacris maindroni*

Host plants	Incuba- tion period	No. of egg pods laid	No. of nymphs emerged from each pod	Total no. of nymphs emerged	Nymphal duration					Total duration
					I	II	III	IV	V	
<i>Atractomorpha crenulata</i>										
<i>Ricinus communis</i>	35.4±2.5* (33-38)	6.34±0.6 (6-7)	56.7±30.6 (30-90)	198.4±12.6 (185-210)	5.7±1.2 (5-7)	9.0±1.0 (8-10)	6.7±1.5 (5-8)	7.0±1.0 (6-8)	8.0±1.0 (7-9)	37.7±5.9 (31-42)
<i>Panicum maximum</i>	49.4±1.5 (48-51)	2.70±0.6 (2-3)	36.7±15.3 (20-50)	94.0±3.5 (90-96)	11.4±2.0 (9-13)	12.7±2.0 (11-15)	10.7±1.5 (9-12)	14.7±1.5 (13-16)	12.0±2.0 (10-14)	63.4±9.9 (52-70)
<i>Solanum trilobatum</i>	43.4±2.3 (42-46)	4.70±0.6 (4-5)	40.4±28.0 (12-68)	134.7±4.0 (130-137)	8.7±0.6 (8-9)	11.0±1.0 (10-12)	8.7±1.5 (7-10)	10.4±1.5 (9-12)	10.0±1.0 (9-11)	50.4±6.4 (43-54)
<i>Solanum torvum</i>	41.7±9.7 (31-50)	3.70±0.6 (3-4)	37.0±22.5 (14-59)	120.4±1.2 (119-121)	9.0±1.7 (7-10)	9.0±2.0 (7-11)	14.0±2.7 (11-16)	11.0±1.0 (10-12)	9.4±2.5 (7-12)	99.4±10.7 (37-56)
<i>Arachis hypogaea</i>	38.7±2.5 (36-41)	5.40±0.6 (5-6)	53.0±25.0 (27-77)	179.0±3.6 (175-182)	7.0±1.0 (6-8)	9.0±2.0 (7-11)	7.7±2.3 (5-9)	6.7±1.4 (5-8)	9.4±2.0 (7-11)	40.7±9.3 (30-47)
<i>Orthacris maindroni</i>										
<i>Clerodendrum</i> sp.	39.7±1.2 (39-41)	2.70±0.6 (2-3)	22.7±3.0 (20-26)	51.7±2.0 (51-54)	9.4±0.6 (9-10)	10.0±2.0 (8-12)	4.0±1.0 (3-5)	5.4±1.5 (4-7)	11.4±2.0 (9-13)	41.7±7.6 (33-47)
<i>Ricinus communis</i>	42.0±1.7 (40-43)	2.00±0.0 (2-2)	23.0±4.0 (19-27)	41.4±1.5 (40-43)	6.0±1.0 (5-7)	9.0±1.0 (8-10)	6.7±0.6 (6-7)	7.0±1.0 (6-8)	10.4±2.5 (8-13)	40.1±6.3 (33-45)
<i>Dolichos lablab</i>	36.4±1.5 (35-37)	1.00±0.0 (1-1)	22.4±1.2 (21-23)	40.7±0.6 (40-41)	5.4±1.2 (4-6)	7.4±0.6 (7-8)	5.7±0.6 (5-6)	6.0±0.0 (6-6)	7.0±2.0 (5-9)	26.7±1.5 (25-28)
<i>Solanum trilobatum</i>	40.0±1.0 (39-41)	1.70±0.6 (1-2)	25.4±2.5 (23-38)	50.4±1.2 (49-51)	6.4±1.2 (5-7)	8.7±1.2 (8-10)	6.0±1.7 (4-7)	6.7±2.0 (5-9)	9.7±2.5 (7-12)	40.4±9.0 (30-46)

*Standard deviation; figures in parenthesis indicate range.

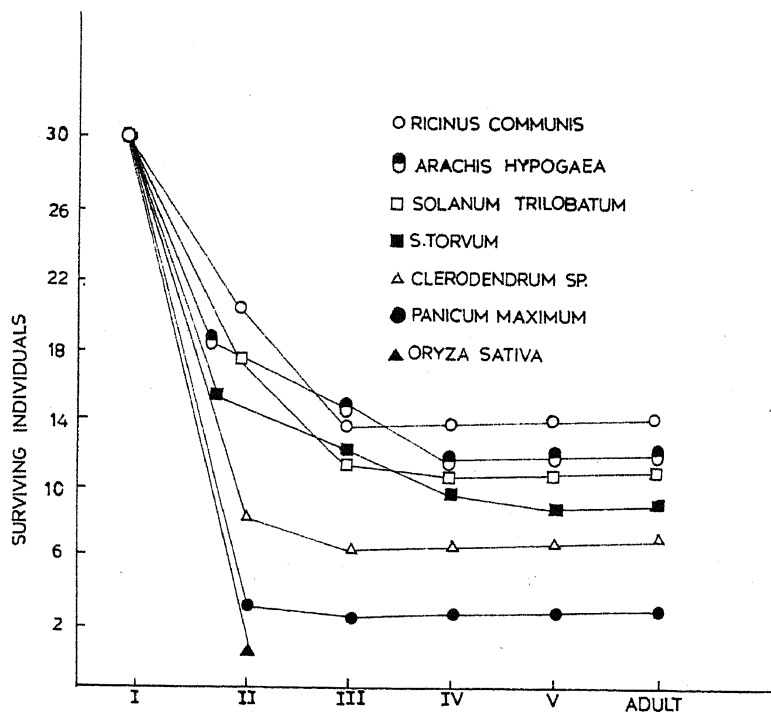


Figure 5. Survival rate of *A. crenulata* on different host plants.

ranging from 30–50 mg. The third instar nymphs reared on hosts like *R. communis* and *A. hypogaea* showed a higher rate of weight increase with 25–40 mg/nymphs (figure 6).

3.7 Impact of diverse host plants on fecundity

In many of the phytophagous insects, it is well known that the quality of food has a great impact on their fecundity and fertility. Many of the acridids, though polyphagous without showing any discrimination towards specific host plant, also indicated a significant variation in the number of egg pods laid as well as in the total number of nymphs that emerged. The present observations based on laboratory studies showed that the nature of host plants greatly influenced the fecundity and fertility. The number of pods laid was easily recognizable as they were laid close to the wall of the transparent plastic vial. Since it was not possible to count the number of eggs in each pod, the number of young ones emerging from each pod was taken into account. The highest number of egg pods (6/female) was laid when fed on *R. communis* and *A. hypogaea*, whereas the lowest number of egg pods (3/female) was laid when fed on *P. maximum*. Similarly the total number of nymphs emerging from all the pods was high (182–210/female) on *R. communis* and *A. hypogaea*, whereas it was low (96/female) on *P. maximum*. A moderate fecundity (120–137/female) was evident on *S. trilobatum* and *S. torvum*.

In *Orthacris maindroni*, no significant variation was apparent in the incubation period of eggs when fed on different host plants indicating that they did not influence much on it. However the number of egg pods laid by each female in its life time varied significantly. The highest number of pods (3/female) was laid on *Clerodendrum* sp and a

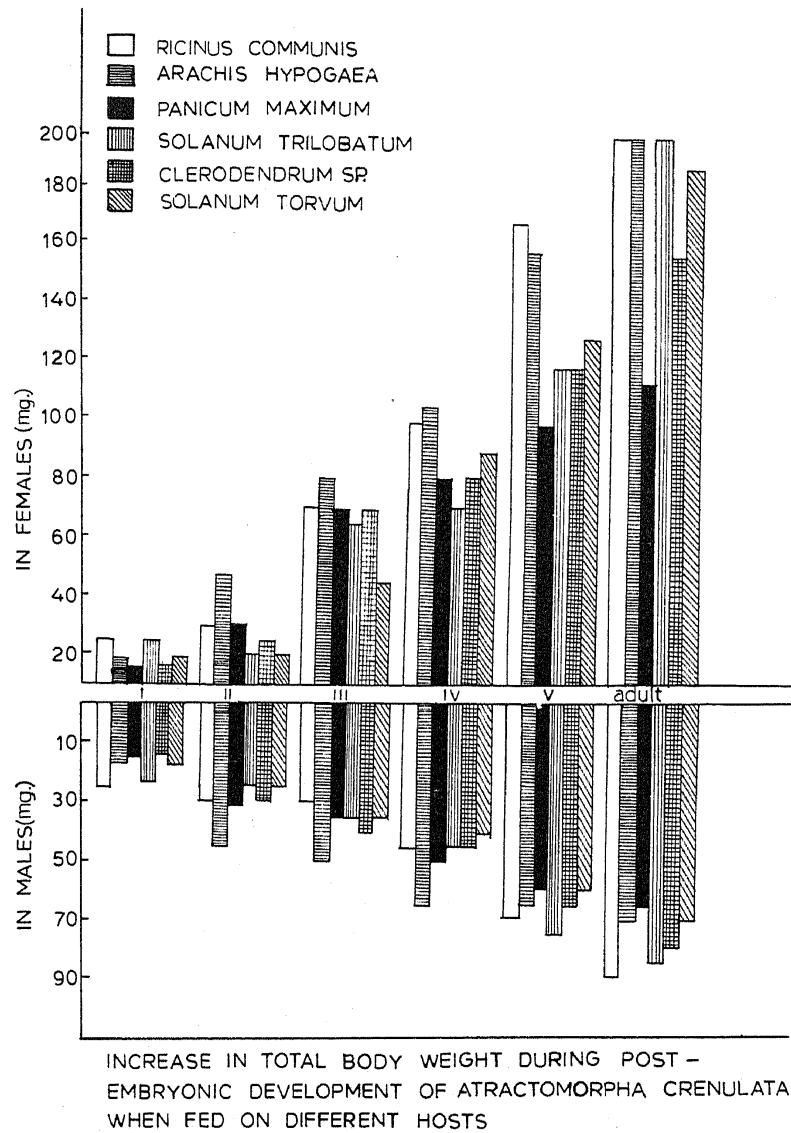


Figure 6. Increase in total body weight during post-embryonic development of *A. crenulata* when fed on different hosts.

lesser number of pods (2/female) on both *R. communis* and *S. trilobatum*, and only one pod was laid when fed on *D. lablab*. However no eggs were laid when fed with *P. maximum*. The total number of nymphs emerging was high and more or less equal (51–54/female) when fed on *Clerodendrum* sp and *S. trilobatum* and comparatively lesser (41–43/female) on *R. communis* and *D. lablab*.

3.8 Biochemical parameters of host plants

In order to assess the impact of various biochemical parameters of the host plants on the host preference of the grasshoppers, the following biochemical estimations were made (table 4).

Total phenols as expressed in mg/g dry weight (DW) of host tissue was very high (55 mg/g DW) in *D. lablab*, and comparatively low (12–3–40 mg/g DW) in other host plants. Total protein content was very high in *C. gigantea* (259.3 mg/g DW) and significantly lower in the rest of the host plants. *Clerodendrum* sp., showed a higher level of carbohydrates (425.9 mg/g DW), comparatively lower in *R. communis* and *S. trilobatum* (200–225 mg/g DW) and very low in the other host plants. A very high lipid content was recorded in *R. communis* (53 mg/g DW) and lower amounts in the other host plants ranging from 10.0–51.5 mg/g DW. Carbohydrate/protein ratio was greater in *C. gigantea* (1:20.75), comparatively lesser in *A. hypogaea*, *D. lablab*, *P. maximum*, *P. spicigera* and *S. torvum* (1:2.65–1:6.06) and very low in *Clerodendrum* sp., *R. communis* and *S. trilobatum* (1:0.19–1:0.57) (table 4).

4. Discussion

Studies on the distribution and abundance of diverse sensillae on the labrum, maxillary and labial palps, in *A. crenulata* (dicot-feeder), *O. maindroni* (feeding on both dicot and monocot plants) and *T. indica* (monocot feeder) indicated significant numerical and distributional variations, besides recognition of further types of sensillae in the inner side of the labrum. In all the three species discussed, A-1 sensillae were not evident, but with the 'beta' tract further divisible into the 'beta' and 'gamma' tracts. In each tract further sub-types were recognised. As many as seven types (S-1 to S-7) were evident in labrum itself. Such a recognition of sensillae was based only on their morphology, size and distribution and no functional significance is evident so far. Haskell and Schoonhoven (1969), Cook (1972), Chapman and Thomas (1978) and Chapman (1982) however showed the chemoreceptory nature of the A-1, A-2 and A-3 sensillae and suggested others probably as mechanoreceptors.

The recognition of two types of sensillae, type-A and type-B, on the surface of the maxillary and labial palps follows similar report by Abushama (1968) in *Poeciloceris hieroglyphicus* (Klug). But later studies by Blaney (1974, 1975) and Haskell and Schoonhoven (1969) suggested the mechanical and chemosensory nature of these sensillae, which are known to increase as they grow into adults. Chapman and Thomas (1978) noted that the total number of sensillae increased by 250% for a 10-fold increase in the surface area of the labrum. In addition to S-1 to S-7 sensillae all the other A-2 and A-3 sensillae also increased in number during post-embryonic development, a fact not reported earlier. As no prior report exists regarding the increase of sensillae in the maxillary and labial palps, the present observation showed an increase in the number of sensillae during post-embryonic development varying for each type of sensillae. Trends of an increase in sensilla number were recognised only from 3rd nymphs onwards; such an increase can be correlated with the increase in the quantitative food intake as well as the range of preference for their host plants. However, the role of various sensillae located at various regions of the mouth parts in host plant selection still remains unclear. Though Blaney and Chapman (1969) and Bernays and Chapman (1970) indicated the role of various sensillae in food plant selection, the removal of labrum, maxillary palps and labial palps individually or in combination did not narrow down the host plant spectrum. However there appears to be a definite role by these organs on the quantitative food intake, since their removal significantly reduced the food intake. Such a reduction in the food intake is also possibly due to the stress caused

Table 4. Percentage water content, dry weight (DW) and quantitative profile of phenol, protein, carbohydrates and lipids in host plants of some acridids*

	Water content (%)	% dry wt. of leaf over fresh wt.	Total phenol (mg/g DW)	Total protein (mg/g DW)	Total carbohydrate (mg/g DW)	Total lipids (mg/g DW)	Carbo-hydrate/Protein ratio
<i>Arachis hypogaea</i>	72	28	24	92.39	17	20	1:5.43
<i>Calotropis gigantea</i>	88	12	22	259.33	12.5	20	1:20.75
<i>Clerodendrum</i> sp	80	20	35	80.00	425.0	51.5	1:0.19
<i>Dolichos lablab</i>	83	17	55	198.53	75	20	1:2.65
<i>Panicum maximum</i>	85	15	40	66.66	11	47.5	1:6.06
<i>Prosopis spicigera</i>	73	27	40	109.70	40	25	1:2.74
<i>Ricinus communis</i>	75	25	38	68.00	200	53	1:0.34
<i>Solanum trilobatum</i>	82	18	12.3	129.17	225	15	1:0.57
<i>Solanum toruam</i>	77	23	20.5	163.04	44	10	1:3.70

* Mean of 3 replications

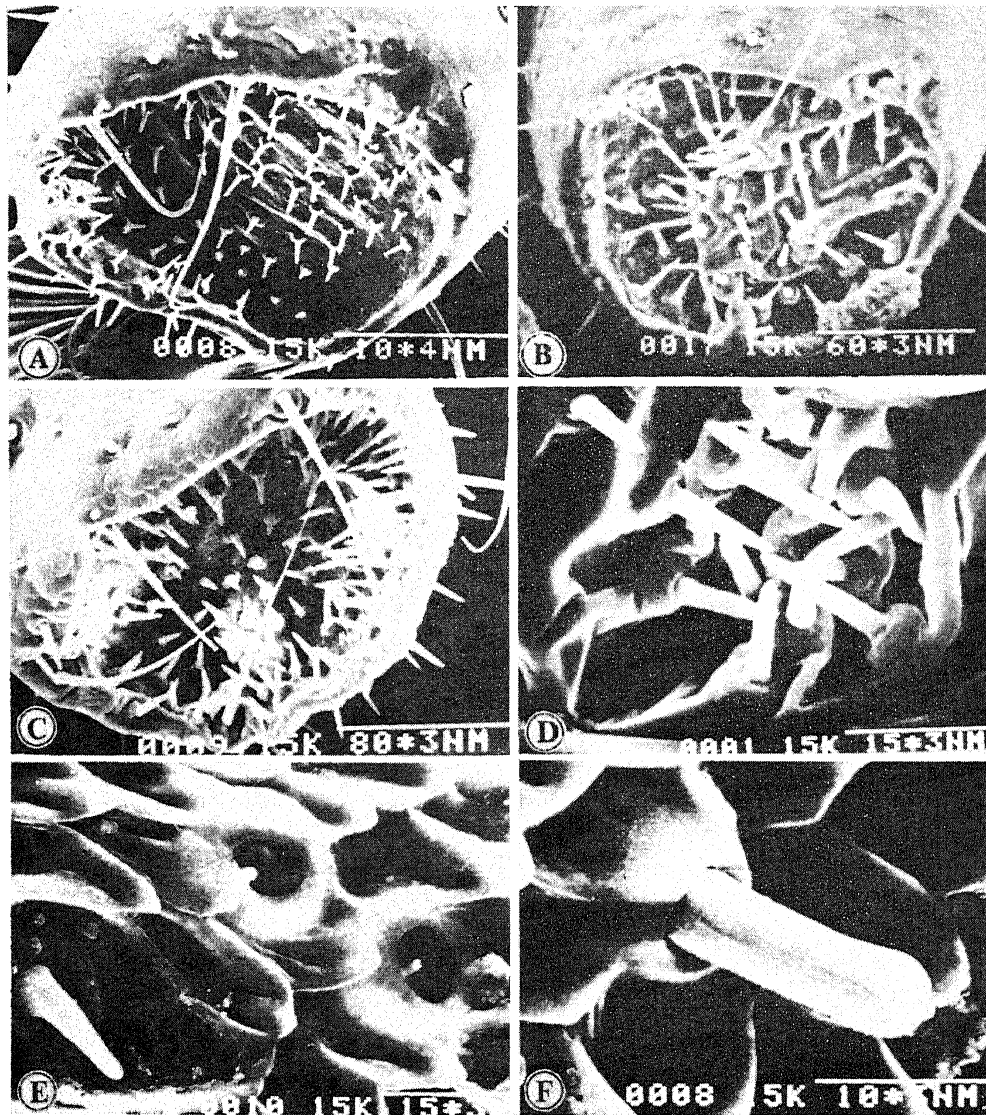


Figure 7. A-D. Sensillae at the palpal apices of late instars (D) portion of (B) enlarged; E, F. collared sensillae.

by their removal of various organs like maxillary and labial palps, labrum, antennae etc. To avoid such stress by mechanical injury, such ablated individuals were allowed for one to two days till they are normal in their feeding behaviour. Though in the present observations, ablations of sensillae in both maxillary and labial palps did not interfere with the host selection, earlier studies on *Locusta* (Blaney and Chapman 1969; Bernays and Chapman 1970) indicated the role of various sensillae at each palpal tip in food selection. The 'dome-shaped sensillae' alone appear to be chemosensory, functioning as feeding sensory structures. Though the host range or the host preference of acridids as in *Paulinea acuminata* does not depend upon the relative numbers of sensillae (Bennett 1970), the number of sensillae appears considerably small in acridids with a narrow host range than in those with a higher food range (Abushama 1968; Hummelen and Gillon

1968; Bennett 1970; Gillon 1972; Perkins 1973). Present investigations showed that the sensillae were larger in number in dicot feeders, lesser in mixed feeders and still lesser in monocot feeders supporting the observations by Chapman and Thomas (1978).

Detailed analysis of the host range of the three species of grasshoppers revealed their highly polyphagous nature, thereby exhibiting certain preference towards specific host plants. Both *A. crenulata* and *O. maindroni* preferred *R. communis* and *Clerodendrum* sp., respectively, whereas the monocot feeder *T. indica* preferred *C. dactylon*. Though the adults of both species can effectively survive on monocot plants, nymphal stages especially the first and second stage nymphs did not feed on the monocot plants like *P. maximum* and *O. sativa*, which is mainly due to the higher silica content of the leaves. Similar avoidance of nymphs of *Oxya nitidula* towards *P. maximum* due to the higher silica content was also reported by Meera (1982). In the present observations, food preferences were estimated on the following basis:

- (i) Short term feeding behavioural effects including
 - (a) frequent visit to specific host plants in the fields,
 - (b) orientation towards the preferred plants in the cages,
 - (c) higher quantitative food intake, and
 - (d) higher food utilization ability.
- (ii) Long term physiological effects involving
 - (a) duration of post-embryonic development,
 - (b) weight increase of the developing nymphs on diverse host plants, and
 - (c) fecundity and fertility.

On the basis of the all the above parameters, *R. communis* appeared to be the best suited and preferred host plant for both *A. crenulata* and *O. maindroni* and *C. dactylon* for *T. indica*. In addition the range of host plants of the above grasshoppers can be successfully correlated with their relative number of sensillae at various mouthparts like labrum, maxillary and labial palps etc. For example, *O. maindroni* and *A. crenulata* showing higher number of sensillae, fed on plants representing as many as 10 families, whereas the *T. indica* with a comparatively lower number of sensillae fed exclusively on members of Poaceae.

In addition the preference towards the specific host plants also varied between nymphs and adults. The nymphs preferred leaves of *R. communis* as they are thin, succulent without any trichomes or any other physical barriers. But it is well known that the host preference of grasshoppers is influenced by physical and chemical characteristics like nutrition or secondary chemicals (Gangwere 1972; Otte and Joern 1975, 1977; Chapman and Bernays 1977; Bernays and Chapman 1977). The quantitative food intake and utilization were also equally high when fed on *R. communis* than on other hosts. The nymphal diet also had a significant influence on the adult preference. However the adults showed a wide spectrum of host plants than that of the nymphs, their restriction is based upon the physical characters of the host plants.

Though the nymphs of *A. crenulata* were found to feed and develop well on a wide range of plants, the development was quicker with a lesser percentage of mortality on *R. communis* and *A. hypogaea*. Simultaneously the nymphs developing on *R. communis* and *A. hypogaea* showed a higher weight increase than on other plants. In addition, the fecundity and fertility were also equally high on the above host plants indicating that they are the most preferred hosts. Though there appears to be no positive correlation

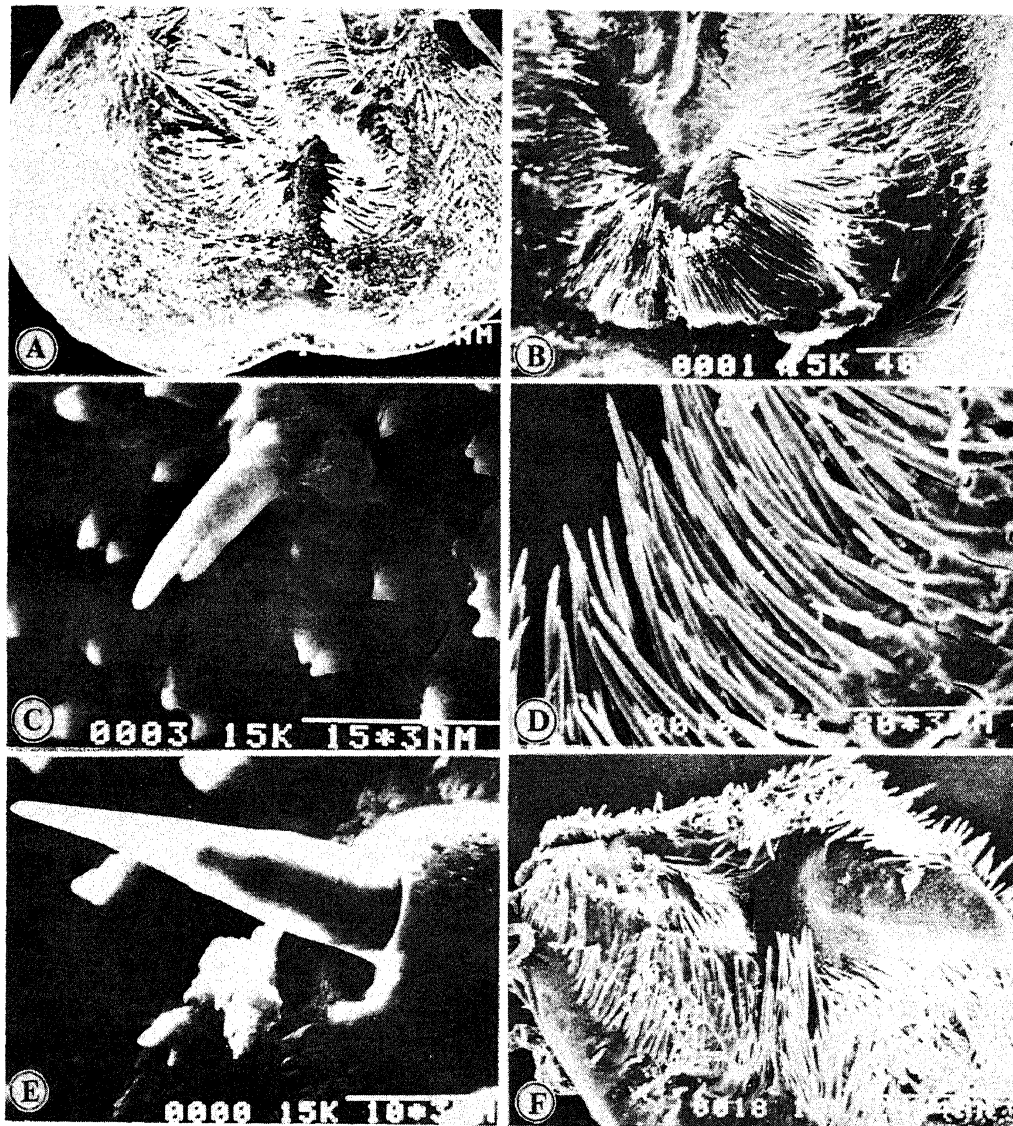


Figure 8. (A) Inner side of the labrum of *Atractomorpha crenulata*; (B) Inner side of the labrum of *Truxalis indica*; (C) Bifid sensilla in the labrum of *T. indica*; (D) Sensillae of the 'Beta' tract in the labrum of *T. indica*; (E) Sensillum with a bottom collar in the labrum of *T. indica*; (F) Hypopharynx of *A. crenulata*.

between biochemical parameters and host suitability or between incidence of higher lipid content and higher carbohydrate, protein ratios among these preferred hosts appear to be an effective factor for the higher developmental rates and increased fecundity of grasshoppers. Though the protein content of the hosts was known to increase the fecundity, present observations indicate that other nutrients like lipids, carbohydrates and carbohydrate:protein ratio may also influence the fecundity.

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