Biological Studies of Insects Feeding on the Kudzu Plant, *Pueraria lobata* (Leguminosae)

II. Seasonal Abundance, Habitat and Development

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Abstract

The seasonal abundance and habitat of 18 insect and 1 mite species from among the 62 Kudzu feeding species in the Kagoshima area and reported in Part I under the same title are described. They belong to 14 insect families of 4 orders and 1 mite family. Distribution within the plant of 4 leafminers and development and reproduction of 3 selected species are also mentioned, and the information is evaluated for possible biological control of the Kudzu plant.

Key words: Kudzu plant, feeding species, seasonal abundance, habitat, development

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Introduction

Pueraria lobata (WILLD.) Ohwi, called Kudzu or Kudzu plant and belonging to Leguminosae, is one of the most serious weeds in Japan and other countries (DICKENS, 1974; KASAHARA, 1982; KITAMURA and MURATA, 1979; SASEK and STRAIN, 1990) despite its use as a food, medicine, in textiles and as an anti-erosion plant (e.g., KUBO *et al.*, 1977; PATTERSON, 1976).

The Kudzu plant may also play an important role in crop insect pest management in the sense of the argument made by van EMDEN (1965, 1981) since many insects and mites associated with the plant feed on various crops in Japan.

A preliminary survey on these associated insects was carried out in Yamaguchi, Japan (KANEKO, 1986), primarily to determine species composition. Thereafter the first author began biological studies on the dominant phytophagous bugs of the plant in the same area in 1986–1987 and reported the biology of two species (TAYUTIVUTIKUL and YANO, 1989, 1990). She has continued this study in Kagoshima City for the past three years, and the first segment of the results appeared as Part I of this title (TAYUTIVUTIKUL and KUSIGEMATI, 1992).

Part I listed the feeding speices of the plant found by field surveys in the Kagoshima area as well as literature. A total of 109 species belonging to 46 families of 6 insect orders and 2 species of Acarina, both from published records and newly found species, was listed. In the Kagoshima area, 61 species of Insecta and one species of Acarina were observed feeding on the plant.

Among those found in the Kagoshima area, 18 insect species and 1 mite species were

studied for their seasonal abundance and habitat and the findings are presented here as the second part of this study. These insect species are: 5 species of Hemiptera, 5 species of Coleoptera, 3 species of Diptera and 5 species of Lepidoptera. Four leafminers among them *—Japanagromyza tristella, Liocrobyla lobata, Neolithocolletis hikomonticola* and *Spulerina dissotoma*—were studied for their distribution within the plant. The development and reproduction of three other species—Homoeocerus unipunctatus, Hedylepta misera and Matsumuraeses falcana—were studied since these were dominant in the area.

Together with Part I, the overall study covers: (1) composition of Kudzu-feeding species, (2) seasonal abundance and habitat of selected species, (3) biology and distribution within the plant of the four leafminers, and (4) developmental data of the three dominant species.

The data obtained allow evaluation of Kudzu-feeding species for future biological control programs since the species studied are expected to be candidates as biological control agents.

Materials and Methods

1. Sampling procedure

The sites of field studies and samplings of feeding species were referred to in Part I (TAYUTIVUTIKUL and KUSIGEMATI, 1992). Additional notes on the method of sampling for seasonal abundance are described here.

Newly developed branches were selected for this phenological study. Leaves of the top, middle and basal strata, classified based on the growing parts from a single main stem (Fig. 1), were sampled from twenty plants at Korimoto graveyard and ten plants at Toso. Thirty ternate compound leaves from each stratum were randamly selected at one week intervals, namely 90 compound leaves containing 270 leaflets from two sites were sampled. Number of individuals per 90 leaflets are generally illustrated in the figures.

Leaves with insects were put into plastic bags and brought back to the laboratory, and the total number of insects (eggs, larvae, adults and galls) and mites were recorded. Samplings were made throughout the growing period of the Kudzu plant. Flying insects such as *Japanagromyza tristella* were counted at sight before brunch samplings.

2. Number of Larval instars

The head capsule with of the four leafminer species mentioned was measured to find the number of larval stages. Ten to twenty larvae of each species collected from the Korimoto graveyard were studied once a week from April to September, 1990.

3. Distribution study

The distribution patterns of leafmining species on the plant were surveyed at the Korimoto graveyard from late March to early December in 1989. Whole leaves of ten randomly selected plants were surveyed each week. All mines containing larvae and pupae found on the leaves were recorded.

Branches of the Kudzu plant were classified based on their place of origin. The main stem



Fig. 1. Diagram of Kudzu branching structure.

branch was designated as the primary branches (1°) , branches originating from the 1° branch were secondary branches (2°) , branches from the 2° branch were the tertiary branches (3°) , and so on up to the hexanary branches (6°) (Fig. 1). The exact position of branches and the leaves on each branch were recorded in the distribution study.

4. Rearing and developmental study

Rearing of one phytophagous bug, *H. unipunctatus*, and two phytophagous moths, *H. misera* and *M. falcana*, was done in the spring of 1988 using field collected adults of the former and larvae of the latter two as initial materials. Rearing was carried by feeding Kudzu plants under four different temperature conditions $(15^{\circ}C, 20^{\circ}C, 25^{\circ}C \text{ and } 30^{\circ}C \pm 1^{\circ}C)$ with illumination by fluorescent light and a photoperiod of 14:10 (L:D). The population of *M. falcana* was successively used in the developmental study after identification, and was not mixed with *M. vicina* as in the phenological study.

For developmental studies at each constant temperature, newly laid eggs were removed daily from oviposition cases, which were glass cylinders $(15 \times 20 \text{ cm})$ the end of which was covered with a fine mesh cloth, set on Kudzu planted pots in the laboratory. Eggs were placed in petri dishes (9.5 cm diameter) lined with moist filter paper, and were checked daily for hatching.

First instar nymphs of *H. unipunctatus* were reared individually in cases similar to the oviposition cases described. Larvae of *H. misera* and *M. falcana* were placed individually in the petri dishes mentioned and fed on young fresh Kudzu leaves which were changed daily. The time required for complete development to the adult stage was determined. Because of larval mortality, however, the number of individuals used at each larval stadium differed slightly.

Developmental rates (1/number of days for development) were determined from the rearing data. Data for larval and pupal development at constant temperatures were obtained from individuals surviving to the adult stage.

Linear relationships were figured by regression of mean developmental rate on temperature, and linear equations were determined for each developmental stage. The total effective temperature and developmental zero (threshold temperature of development) of both sexes were calculated by each regression.

For the studies on fertility and longevity, all newly emerged adults were removed daily and paired, and each pair was placed in the same type of case used for nymphal rearings of H. *unipunctatus* at respective temperatures. Adults of H. *unipunctatus* were fed the same sort of food as the nymphs.

Adults of *H. misera* and *M. falcana* were fed on cotton swabs with a 10% honey solution. Insects were transferred daily to a cylinder case containing a Kudzu plant. Eggs laid on the plant were removed and counted daily, and the date of death was recorded for each adult. Whenever one of a pair died, the remaining individual was supplied with another partner of the other sex so that pairs were maintained as long as possible. The longevity of the adults and the period of preoviposition and oviposition were also observed.

The time required for development and data of fertility and longevity were analyzed by an analysis of variance with DUNCAN's new multiple range test for differences between the sexes at the same temperature and between temperatures in the same sex.

Results and Discussion

1. Seasonal abundance and habitat

Seasonal abundance and habitat on the plants of 19 feeding species observed in the two study sites are presented here. Species are: 2 species of Homoptera, 3 species of Heteroptera, 5 species of Coleoptera, 3 species of Diptera, 5 species of Lepidoptera and 1 species of Acarina.

Habitat of each species is described based on its stratum location, top, middle and basal. Each stratum of a main stem has branches with leaves growing at different degress. In the following pages, however, leaves of the top stratum are referred to as younger and those of the basal as older. This reflects a tendency, rather than absolute degrees of growth strictly speaking.

1.1 Geisha distinctissima (WALKER) (Hemiptera: Flatidae)

1.1.1 Seasonal abundance

Seasonal abundance of nymphs and adults on the plants is illustrated in Fig. 2. The nymphs appeared in April, increased rapidly in May and reached a peak in June and July, then collapsed in late July. Adult populations appeared from early June to October, and were abundant from July to September. These data clearly indicate one generation a year on the plant. ISHIHARA (1968) stated that overwintered eggs of this polyphagous species



Fig. 2. Seasonal abundance of Geisha distinctissima on Pueraria lobata. (O-O: nymph; O-O: adult)

hatch in early summer and adults emerge in late July, but no locality names were given. The present result shows an earlier occurrence of this species.

1.1.2 Habitat

The largest number of nymphs and adults was found on the middle stratum. Out of 137 nymphs, 48.9% (67 nymphs) were found on the middle stratum, 35.8% (49) on the basal stratum and 15.3% (21) on the top stratum. Out of 85 adults, 67.1% (57 adults) were found on the middle stratum, 17.6% (15) on the top stratum and 15.3% (13) on the basal stratum. Both stages usually feed on the petiole or the stem. This result suggests that both nymphs and adults feed mainly on the middle stratum rather than other strata.

1.2 Orosanga japonicus (MELICHAR) (Hemiptera: Ricaniidae)

1.2.1 Seasonal abundance

Seasonal abundance of nymphs and adults of *O. japonicus* on the plant is illustrated in Fig. 3. Nymph populations appeared from May to July and from August to October, though few nymphs were found after October in 1989. Adults were found from June to November, suggesting that this species probably occurs twice a year on Kudzu judging from the data obtained in 1988.

AVIDZBA and BOBOKHIDZE (1982) and DZHASHI et al. (1982) reported that this species feeding bay (*Laurus nobilis*), tea, grape vine and other crops overwinters in the egg stage and spends one generation a year in the southern USSR. The latter authors also mentioned that nymphs of this species hatch in mid April and adults occur in July-October. ISHIHARA (1968) stated that this species overwinters in the egg stage and adult emergence is late July in the western Japan. These published records as well as the present data indicate a rather fluctuating life cycle of this species.



Fig. 3. Seasonal abundance of Orosanga japonicus on Pueraria lobata. (O-O: adult)

1.2.2 Habitat

Out of 208 nymphs, 48.6% (101 nymphs) were found on the middle stratum and 47.1% (98) were found on the basal stratum. Only 4.3% (9) were found on the top stratum. Out of 91 adults, 62.6% (57 adults) were found on the middle stratum, 31.9% (29) on the basal stratum and 5.5% (5) on the top stratum. Nymphs thus feed mainly on middle and basal strata rather than on the top stratum, while adults prefer the middle stratum.

AVIDZBA and BOBOKHIDZE (1982) reported that adult damage was seen on all parts of bay showing rather similar tendency seen in the present data.

1.3 Homoeocerus unipunctatus (THUNBERG) (Hemiptera: Coreidae)

1.3.1 Seasonal abundance

Seasonal abundance of eggs, nymphs and adults on Kudzu is illustrated in Fig. 4. Adults were found throughout April to November, eggs from late April to October, and nymphs from late May to October with a marked peak in July, 1989. These data are not clear and it is difficult to determine the life cycle of this species on the plant. Laboratory studies on development described later, however, indicate two generations a year through the Kudzu growing season in the Kagoshima area. Overwintering in the adult stage is suspected in this area.

1.3.2 Habitat

Individuals of each developmental stage were found on different strata with the largest number of eggs found on the middle stratum. Out of 50 eggs, 56% (28 eggs) were found on the middle stratum, 36% (18) on the basal stratum and only 8% (4) on the top stratum. Nymph populations were highest on the middle stratum followed by top and basal strata. Out of 102 nymphs, 56.9% (58 nymphs) were found on the middle stratum, 25.5% (26) on



the top stratum and 17.6% (18) on the basal stratum. Adults were found mainly on the top and middle strata. Of 148 adults, 43.9% (65 adults) were found on the top stratum, 31.8% (47) on the middle stratum and 24.3% (36) on the basal stratum. Adults thus feed on all strata, but rather prefer younger leaves. They usually oviposit on the intermediate leaves.

Most eggs were found on the underside of the leaves: about 66%, 24% and 10% on the underside, petiole and upperside, respectively. About 74% of nymphs were found on the underside of the leaves and adults were found on all parts of the plant. TAKASU and HIROSE (1986) reported that the egg parasitoid *Ooencyrtus nezarae* produced a large number of progeny on eggs of this species on Kudzu, but no egg parasitoids were found during the present study.

1.4 Chauliops fallax Scott (Hemiptera: Lygaeidae)

1.4.1 Seasonal abundance

Seasonal abundance of eggs, nymphs and adults on Kudzu is illustrated in Fig. 5. Adults were found throughout the Kudzu growing season with 3 peaks in May to June, mid August and September to October, though the second peak in August was small. The egg occurrence pattern was similar to that of adults, though the peaks occurred earlier than those of adults in 1989. Nymphs were found from May to October with 2 peaks in June to July and August to September. The data suggest that this species may have two generations a year on the plant. Comparison of the seasonal abundance of this species in the Yamaguchi area reported earlier (TAYUTIVUTIKUL and YANO, 1989) shows patterns in the two areas to be similar, though the adult occurrence seen in 1989 in Kagoshima has more distinct peaks.



1.4.2 Habitat

Eggs, nymphs and adults were found mainly on the basal stratum. Out of 409 eggs, 85.8% (351 eggs) were found on the basal stratum and 14.2% (58) on the middle stratum. From 335 nymphs, 85.4% (286 nymphs) were found on the basal stratum and 14.6% (49) on the middle stratum. In the same way, out of 503 adults, 83.7% (421 adults) were found on the basal stratum and only 16.3% (82) on the middle. No individuals in any stages were found on the top stratum, This supports the results of TAYUTIVUTIKUL and YANO (1989) who observed the biology of this species in the Yamaguchi area.

These authors found three egg parasitoids, *Ooencyrtus nezarae* Ishii, and *Ooencyrtus* sp. of Encyrtidae, and *Telenomus* sp. of Scelionidae, but no egg parasitoids were observed during the present study. The leaves attacked by this species show numerous minute yellowish specks with a loss of chlorophyll content as reported by LAL (1975).

1.5 Megacopta punctatissima (MONTANDON) (Hemiptera: Plataspidae)

1.5.1 Seasonal abundance

Seasonal abundance of each stage on Kudzu is shown in Fig. 6. A rather large population of adults was found from April to mid June, early July to late August and September to October. A large number of eggs was found from April to June and late July to September. The first peak of nymphs was seen from May to July and the second one from late August to October. This species may thus have two generations a year as HIBINO and ITO (1983) observed in the Aichi Prefecture, though ISHIHARA (1968) mentioned one generation a year in the western Japan. These two published records also mentioned that this species overwinters in the adult stage which is also intimated by the present data.

In the Yamaguchi area, however, this species may have one generation a year on Kudzu,



based on field surveys and developmental studies in the laboratory (TAYUTIVUTIKUL and YANO, 1990). As mentioned above, data from Kagoshima area rather clearly show two generations a year, and two different peaks found in egg numbers strongly support two generations.

1.5.2 Habitat

Females laid eggs in egg-masses with an average of 31.7 eggs/egg-mass. Eggs were found abundantly in the top stratum. Out of 529 eggs, 62.6% (331 eggs) were found on the top stratum, 25.7% (136) on the middle stratum and 11.7% (62) on the basal stratum. Nymphs were found mainly on the middle and top strata. Of 507 nymphs, 50.1% (254 nymphs) were found on the top stratum, 49.1% (198) on the middle stratum and 10.8% (55) on the basal stratum. Adults were primarily on the top and middle strata like nymphs. Out of 584 adults, 39.9% (233 adults) were found on the top stratum, 40.2% (235) on the middle stratum and 19.9% (116) on the basal stratum. These orders of habitat preference in nymphs and adults are different from those observed in the Yamaguchi area (TAYUTIVUTIKUL and YANO, 1990). The general tendency, however, is the same, and the feeding habit of nymphs preferring young to old parts of the branches was seen in both areas. Adults of this species aggregate on Kudzu as reported by FUJISAKI (1977). HIBINO and ITO (1983) reported that the rate of sexual encounters between males and females is higher in larger aggregations, but no such behavior was observed in Kagoshima. TAKASU and HIROSE (1985), and TAYUTIVUTIKUL and YANO (1990) reported that eggs of this species were heavily parasitized by Overcyrtus nezarae, but no parasitization was found in the present study.

1.6 Anomala lucens BALLION (Coleoptera: Scarabaeidae)

1.6.1 Seasonal abundance

Few adults of this species were found on Kudzu throughout the field survey (Fig. 7). Adults were first found in mid May and appeared until mid September suggesting the species may have one generation a year like *A. cuprea* (HOPE).



Fig. 7. Seasonal abundance of adult Anomala lucens on Pueraria lobata.

1.6.2 Habitat

Almost all the adults were found on the middle stratum. Out of 31 adults, 93.5% (29 adults) were found on the middle stratum and only 6.5% (2) on the basal stratum; none was found on the top stratum. This suggests that adults feed mainly on leaves of intermediate growth rather than those in other growth stages.

1.7 Trachys auricollis E. SAUNDERS (Coleoptera: Buprestidae)

1.7.1 Seasonal abundance

Seasonal abundance of larvae, pupae and adults of this leafmining buprestid species on Kudzu is presented in Fig. 8. Adults were found for a long period from April until October without a remarkable peak in population. Larvae in mines appeared from June to September and pupae from July to October suggesting that adult oviposition occurs in late May and June. According to these data, one or two generations a year on the plant may be indicated (cf. following lines). Measurement of the head capsule width of larvae collected periodically from the field in 1990 shows that there are four larval stages (Fig. 9). Mean head capsule width and standard deviations are given in Table 1.

The seasonal changes in number of individuals of each immature stage shown in Fig. 10



Fig. 8. Seasonal abundance of *Trachys auricollis* on *Pueraria lobata*.
(●—●: larva; △···△: pupa; ○···○: adult)

Table 1. Measurements of larval head capsule width of *Trachys* auricollis.

| Instar | No larvae | Head capsule | width (mm) |
|--------|------------|------------------|------------|
| Instal | NO. Iaivae | Mean (±SD) | Range |
| 1 | 27 | 0.31 ± 0.018 | 0.29-0.35 |
| 2 | 38 | 0.41 ± 0.016 | 0.37-0.45 |
| 3 | 38 | 0.50 ± 0.018 | 0.47-0.55 |
| 4 | 35 | 0.61 ± 0.021 | 0.58-0.67 |



Fig. 9. Frequency distribution of larval head capsule width of Trachys auricollis.



Fig. 10. Seasonal changes in the number of each immature stage of Trachys auricollis.

and the data of seasonal abundance mentioned above suggest that this species may have two generations a year.

1.7.2 Habitat

Out of 29 larvae, 82.8% (24 larvae) were found on the middle stratum and 17.2% (5) were found on the basal stratum. Pupae were more numerous in the basal stratum. Out of 12 pupae, 83.3% (10) were found in the basal stratum and 16.7% (2) on the middle stratum. This tendency in pupae should be confirmed by further surveys since the number of individuals examined was small. Adults were found mainly on the middle stratum. Out of 49 adults, 65.3% (32 adults) were found on the middle stratum and 34.7% (17) on the basal stratum. Thus all stages of this species inhabit primarily the leaves intermediate in growth.

Adults feeding on the intermediate leaves chew from the leaf edge (Fig. 41). Females oviposited on the surface of the leaves. Larvae mined inside the leaves forming blotch mines, and fed on the palisade parenchyma from the beginning until pupation which took place in the same mines. Larvae were often found mining in the edge of the leaves and made mines across the veins. This behavior is similar to that of *Trachys* sp. (possibly *T. virescens* KERR.) the larvae of which are leafminers; adults usually feed on the margins of tender leaves of okra in India (RAWAT and JAKHMOLA, 1969).

1.8 Pagria signata (MOTSCHULSKY) (Coleoptera: Chrysomelidae)

1.8.1 Seasonal abundance

Seasonal abundance of adults of this chrysomelid species on Kudzu is illustrated in Fig. 11. Adults appeared from April to November until the time their population was seen on the plant. A clear difference is seen in the mode of seasonal abundance between 1988 and 1989, and the probable cause is assumed to be biological factors in addition to sampling errors, but, not climate factors. Though it is not possible to determine the number of generations from the present data, the overlapping of generations and/or long adult longevity are suspected.



Fig. 11. Seasonal abundance of adult Pagria signata on Pueraria lobata.

1.8.2 Habitat

The largest number of adults was found on the middle stratum. Out of 121 adults, 71.1% (86 adults) were found on the middle stratum, 28.1% (34) on the basal stratum and only 0.8% (1) on the top stratum. These figures indicate that adults feed on the intermediate leaves rather than on young or mature leaves.

1.9 Episomus turritus (GYLLENHAL) (Coleoptera: Curculionidae)

1.9.1 Seasonal abundance

Data on the collection of adults from Kudzu is presented in Fig. 12. Few adults were found from late April to September with a slight difference between the two years. It is difficult to estimate the number of generations from the available data.

1.9.2 Habitat

Out of 18 adults, 83.3% (15 adults) were found on the middle stratum and 16.7% (3) on the basal stratum. No adults were found on the top stratum. The activity site of adults on the plant is therefore usually intermediate branches rather than young or mature branches.

1.10 Eugnathus distinctus ROELOFS (Coleoptera: Curculionidae)

1.10.1 Seasonal abundance

Only 3 adults were found after August in 1988, and 2 adults in May and June in 1989 at the Toso field site (Fig. 13). No adults were found at the Korimoto graveyard suggesting that the occurrence of this species on Kudzu in the Kagoshima area is rare, though the species is known to be rather common in Japan. The number of generations was not estimated by these data.



Fig. 13. Seasonal abundance of adult Eugnathus distinctus on Pueraria lobata.

1.10.2 Habitat

All adults were found on the middle stratum indicating a preference for the intermediate leaves, though this requires further confirmation.

1.11 Pitydiplosis sp. (Diptera: Cecidomyiidae)

1.11.1 Seasonal abundance

Figure 14 shows seasonal changes in the number of galls produced by Pitydiplosis sp. on



Fig. 14. Seasonal abundance of galls produced by Pitydiplosis sp. on the leaves of Pueraria lobata.

the leaves of Kudzu (excluding fallen leaves). Midge-galls were most abundant in late May, reached a peak in early June, and gall populations remained on the plant until September. YUKAWA (1987), based on his observations on Kudzu, reported that this species is univoltine: adults emerge in April to June, larvae mature in summer and galls drop to the ground with the leaves during October to December. The present data on Kudzu also clearly show one generation a year.

1.11.2 Habitat

Midge-galls were found in the basal and middle strata. Out of 984 midge-galls, 56.7% (558 galls) were found on the basal stratum and 43.3% (426) on the middle stratum. None was found on the top stratum. The oviposition of this species thus seemed not to synchronize with the shooting period of the top stratum because, in general, the species lays its eggs on those parts of the plant, where cell division is actively observed, i.e., buds, shoots or flower bud.

The gall is concave on the upper surface and convex on the under surface of the leaf (Figs. 45 and 46) and has a disc-shaped larval chamber in its center. Only a single midge larva inhabits this chamber.

1.12 Genus sp. (Diptera: Cecidomyiidae)

1.12.1 Seasonal abundance

This species has not been identified, but is thought to be a new species of the supertribe Cecidomyiidi (YUKAWA and IKENAGA, unpublished).

Seasonal changes in the number of galls produced by this species on the leaves of Kudzu are shown in Fig. 15 and suggest the possibility of two generations a year. Finding of the galls on the plants continuously from May to early December with two rather distinct peaks



Fig. 15. Seasonal abundance of galls produced by a cecidomyiid sp. on the leaves of Pueraria lobata.

in 1989 may support this.

1.12.2 Habitat

A remarkable number of midge-galls was found on the basal stratum. Out of 369 midge-galls, 66.4% (245 galls) were found on the basal stratum and 33.6% (124) on the middle stratum. None was found on the top stratum. As with the preceding species, oviposition of this species also does not appear to synchronize with the growth of the top stratum. All galls were found on the underside of the leaves (Fig. 47).

1.13 Japanagromyza tristella (THOMSON) (Diptera: Agromyzidae)

1.13.1 Seasonal abundance

Seasonal abundance of larvae and adults on Kudzu in 1988 and 1989 is presented in Fig. 16. Four adult peaks were recognized in mid April, early June, late June to early August and late August to September. Larvae were found from April to November with several fluctuations. Since larval abundance was variable through the period surveyed, it is difficult to predict the number of generations of this species. The above data on adults, however, suggest that the species may have at least four generations a year on the plant.

1.13.2 Habitat

Larvae were found mostly on the middle stratum. Of 140 larvae, 88.6% (124 larvae) were found on the middle stratum, 6.4% (9) and 5.0% (7) were found on the basal and top strata, respectively. This result indicates that larvae feed mainly on intermediate leaves rather than on new or old leaves.

The larvae made blotch type mines on the surface of young leaves (Fig. 42). The mining of a larva proceeded directly into the chlorophyll containing parenchyma of the leaf and the miners were clearly visible when the leaves held up to the light. The mature larvae moved



Fig. 16. Seasonal abundance of Japanagromyza tristella on Pueraria lobata. (---O: adult)

to the outside of the mines for pupation. No larvae were found in mature or fallen leaves suggesting that mature larvae moved out of these leaves to pupate for overwintering on the ground. LABONTE and LIPOVSKY (1967) reported that Japanagromyza viridula (Cog.) larvae formed blotch type mines on red oak, Quercus rubra, and white oak, Q. alba, and that the adult ovipositor pierced the upper epidermis of young leaves for their feeding which was not observed in this species.

1.14 Hedylepta misera (BUTLER) (Lepidoptera: Pyralidae)

1.14.1 Seasonal abundance

Figure 17 shows the seasonal abundance of larvae on Kudzu and suggests that three generations a year may develop. The first generation began increasing in late April, reached a peak in late May and decreased towards late June. The second generation required about one month for development and the third generation began from August to October. Laboratory studies on the development, however, suggest that there could be four generations during the Kudzu growing season in the Kagoshima area based on the total effective temperature and developmental zero mentioned in later. The difference in the number of generations between the field and laboratory data is probably due to overlapping of the later generations in the field during August to November, and also to the low density of field populations.

1.14.2 Habitat

Larvae were found mainly on the middle stratum. Out of 118 larvae, 60.2% (71 larvae) were on the middle stratum and 39.8% (47) on the top stratum. None was found on the basal stratum. This result shows that larvae of this species feed on intermediate leaves rather than old or young leaves.



Fig. 17. Seasonal abundance of Hedylepta misera larvae on Pueraria lobata.

1.15 Matsumuraeses falcana (WALSINGHAM) and/or M. vicina KUZNETZOV (Lepidoptera: Tortricidae)

Two closely related tortricid species were found on Kudzu in this study, *Matsumuraeses falcana* (WALSINGHAM) and *M. vicina* KUZNETZOV. It was difficult to distinguish the larvae of these species in these phenological and habitat studies. The following data thus combines the two species.



Fig. 18. Seasonal abundance of Matsumuraeses falcana and/or M. vicina larvae on Pueraria lobata.

1.15.1 Seasonal abundance

Figure 18 illustrates the seasonal abundance of larvae on Kudzu in the field showing three generations a year on the plant. Three relatively large larval populations were found from April to June, June to August and August to September. However, the laboratory studies on the development of *M. falcana* suggest that there could be five generations through the Kudzu growing season in the Kagoshima area based on the total effective temperature and developmental zero. The difference in the number of generations between the field and laboratory data may be due to the overlapping of generations, to the low density of the later generations or to mixed populations of *M. vicina* and/or *M. falcana* in the field data. OKU *et al.* (1983) reported that two generations of *M. falcana* and *M. vicina* developed on the soybean after July in the Tohoku district of Japan. RAZOWSKY and YASUDA (1975) assumed that *M. falcana* may have three or four generations a year from early April to late November in Japan.

The present data obtained on Kudzu in southern Kyushu provide additional data on the life cycle of this species group.

1.15.2 Habitat

Larvae (Fig. 44) were found mostly on the top stratum. Out of 337 larvae, 90.2% (304 larvae) were found on the top stratum and 9.8% (33) on the middle stratum. None was found on the basal stratum. Larvae of this species thus feed mainly on young leaves and few feed on the intermediate leaves.

1.16 Liocrobyla lobata KUROKO (Lepidoptera: Gracillariidae)

1.16.1 Seasonal abundance

Seasonal abundance of larvae and pupae in mines on Kudzu leaves is illustrated in Fig. 19,



Fig. 19. Seasonal abundance of *Liocrobyla lobata* on *Pueraria lobata*. (●—●: larva; △…△: pupa)



Fig. 20. Seasonal changes in the number of each larval instar of Liocrobyla lobata.



Fig. 21. Frequency distribution of larval head capsule width of *Liocrobyla lobata*.

and seasonal changes in the individual numbers of each larval instar in Fig. 20 indicating that there are three or four generations a year. The first and second generations seem to occur between April and August and the following two generations between September and November. This species probably overwinters in the pupal stage since mature larvae were found in late November, and no immature individuals were found on fallen leaves. Measurements of the head capsule width of larvae collected periodically from the field indicate that there are five larval stadia (Fig. 21). The mean widths of the larval head capsule and standard deviations are given in Table 2.

1.16.2 Habitat

Larvae were found on the middle and basal strata. Out of 153 larvae, 54.9% (84 larvae) and 45.1% (69) were found on the basal and middle strata, respectively. Only 7 pupae were found on the basal stratum and 3 pupae on the middle stratum. Larvae therefore feed on

| Instar | No larvae | Head capsule width (mm) | |
|--------|-----------|-------------------------|-----------|
| | | Mean (±SD) | Range |
| 1 | 35 | 0.17 ± 0.011 | 0.15-0.18 |
| 2 | 23 | 0.24 ± 0.008 | 0.23-0.26 |
| 3 | 16 | 0.29 ± 0.009 | 0.28-0.31 |
| 4 | 21 | 0.34 ± 0.011 | 0.32-0.37 |
| 5 | 41 | 0.43 ± 0.024 | 0.38-0.47 |

 Table 2.
 Measurements of larval head capsule width of Liocrobyla lobata.

both intermediate and mature leaves, and only a few of them became pupae on a leaf. Most larvae might pupate on the ground or pupae might have fallen to the ground since mines contained no pupae as mentioned below.

This species makes mines between the epidermis of the leaf (Fig. 48). The early instar larvae first make a linear mine feeding on spongy parenchyma, then later instar larvae make a blotch mine under the upper surface of the leaf, probably because the palisade parenchyma provides them with more food than the spongy parenchyma does. Larvae feed inside the mines until they reach the pupal stage, although since no pupae were found inside the mines. Pupation may take place outside the mines. No larvae or pupae were found in the fallen leaves suggesting that this miner probably overwinters in the pupal stage.

1.17 Neolithocolletis hikomonticola KUMATA (Lepidoptera: Gracillariidae)

1.17.1 Seasonal abundance

This species may have four generations a year judging from the seasonal abundance of larvae and pupae in mines on Kudzu leaves (Figs. 22 and 23). Relatively large populations



Fig. 22. Seasonal abundance of *Neolithocolletis hikomonticola* on *Pueraria lobata*. (●—●: larva; △···△: pupa)



Fig. 23. Seasonal changes in the number of each immature stage of Neolithocolletis hikomonticola.



Head capsule width (mm)

Fig. 24. Frequency distribution of larval head capsule width of Neolithocolletis hikomonticola.

of larvae were found from late May to early June and also from late October to November. The last one (October–November) consisted of the fourth generation larvae for overwintering, and the first one (May–June) was apparently produced by adults derived from the overwintered larvae. Each of the summer generations (peaks in middle June and early September) required about one month to develope. The first generation in the spring required a slightly longer period than did the summer generations because of lower temperature, and the fourth generation in the fall required nearly six months including diapause during the winter. Frequency distribution of head capsule width of larvae collected from the field shown in Fig. 24 indicates that there are five or six larval stadia. Two larvae with the samllest head capsule width may represent the first stadium (six stadia in this case) or belong to the following population (five stadia in this case). The mean widths of the larval head

| Instar | No larvae | Head capsule width (mm) | | |
|--------|-----------|-------------------------|-------------|--|
| motar | | Mean (±SD) | Range | |
| 1-2 | 81 | 0.15 ± 0.012 | 0.10-0.16 | |
| 3 | 49 | 0.20 ± 0.011 | 0.17-0.21 | |
| 4 | 84 | 0.25 ± 0.014 | 0.22 - 0.27 | |
| 5 | 36 | 0.30 ± 0.012 | 0.28 - 0.32 | |
| 6 | 55 | 0.35 ± 0.011 | 0.33-0.38 | |

Table 3. Measurements of larval head capsule width of *Neolithocolle*tis hikomonticola.

capsule and standard deviations are given in Table 3 where the two larvae with the smallest head capsule width are represented as the first stadium.

1.17.2 Habitat

Larval and pupal populations were mostly found on the basal stratum throughout the survey period. Out of 2862 larvae, 62.6% (1792 larvae) were found on the basal stratum and 37.4% (1070) on the middle stratum. Similarly, out of 210 pupae, 71.0% (149) and 29.0% (61) were found on the basal and middle strata, respectively. No larvae were found on the top stratum, suggesting that larvae feed mainly on the mature leaves and develop inside leaves until pupation.

The larvae make short blotch type mines inside the undersurface of the leaf (Fig. 50), and live in the spongy parenchyma which contains primarily liquid substances. They cannot cross the mid or side veins of the leaves, and therefore form mines restricted to within veins. In late autumn, the larvae make flat cocoons inside the mine which serves solely for overwintering. A larva remains inside the mine even after the leaf has fallen, and after hibernation it pupates in the mine the following spring.

1.18 Spulerina dissotoma (MEYRICK) (Lepidoptera: Gracillariidae)

1.18.1 Seasonal abundance

Figures 25 and 26 illustrating the seasonal abundance of larvae on Kudzu and the seasonal changes in the number of individuals in the larval stage show that this species has at least four generations a year. The first population began increasing in May, reached a peak in early June and collapsed by the end of the month. Both the second and third generations in summer (July–September) each required only a month for development. The last generation seemed to start from the end of September, and required about six or seven months including the overwintering period of pupae. Measurement of the head capsule width of larvae collected from the field in 1990 indicates that there are five larval stadia (Fig. 27). The mean widths of the head capsule and standard deviations are given in Table 4.

1.18.2 Habitat

Out of 97 larvae, 45.4% (44 larvae) and 54.6% (53) were found on the middle and basal strata, respectively. None was found on the top stratum and no pupae were found on any strata throughout the survey period. This suggests that larvae of this species feed on the intermediate and mature leaves, and do not pupate on or in the leaf.

The larvae make mines just under the upper surface of the leaf (Fig. 49), and live singly in



Fig. 26. Seasonal changes in the number of each larval instar of Spulerina dissotoma.

| Inctor | Head ca | | sule width (mm) | |
|--------|------------|------------------|-----------------|--|
| mstar | NO. Idivae | Mean (±SD) | Range | |
| 1 | 35 | 0.20 ± 0.007 | 0.18-0.20 | |
| 2 | 41 | 0.24 ± 0.014 | 0.21-0.25 | |
| 3 | 38 | 0.29 ± 0.013 | 0.26-0.31 | |
| 4 | 31 | 0.34 ± 0.012 | 0.32-0.36 | |
| 5 | 48 | 0.40 ± 0.013 | 0.37-0.43 | |

Table 4. Measurements of larval head capsule width of Spulerina dissotoma.

blotch mines within the palisade parenchyma. They are able to cross the secondary and tertiary veins of the leaf. Pupation takes place outside of the mines. No larvae or pupae



were found in the fallen leaves in autumn.

Fig. 27. Frequency distribution of larval head capsule width of Spulerina dissotoma.

1.19 Tetranychus kanzawai KISHIDA (Acarina: Tetranychidae)

1.19.1 Seasonal abundance

Figure 28 presents the seasonal abundance of adults on Kudzu. They appeared from April to July and from September to early December, and the population density was low during summer. The overlapping development makes it difficult to determine the number of generations on the plant.



Fig. 28. Seasonal abundance of adult Tetranychus kanzawai on Pueraria lobata.

1.19.2 Habitat

Out of 2974 adults, 65.0% (1934 adults) were found on the basal stratum and 35.0% (1040) on the middle stratum. No adults were found on the top stratum. Individuals were found on the underside of the leaves (Fig. 43). This species appears to feed mainly on mature leaves.

1.20 Summary

1.20.1 Seasonal occurrence

The number of generations of the Kudzu feeding species shows a tendency according to the taxa to which they belong, especially the orders. Species belonging to Hemiptera, Coleoptera and Cecidomiidae of Diptera have one or two generations a year, while species belonging to Lepidoptera and Agromyzidae of Diptera have several generations and most of the latter group are leafminers. Seasonal abundance of some species was not clearly determined due to the low density or assumed overlapping of generations.

The period of occurrence of the species feeding on Kudzu described in the preceding pages is illustrated in Fig. 29, and reveals that all the developmental stages of the species occur on the plant during its growing period. Many species are found throughout the Kudzu growing period, while others appear only during part of it. This is probably because of the successive growth pattern of the Kudzu plant mentioned.



Fig. 29. Seasonal occurrence of selected feeding species on *Pueraria lobata* in Kagoshima City (1988–1989) (for details, see text).

Figure 29 does not explain the microhabitat of these species such as the different strata of branches and different plant parts affected, but it does show a superficially uniform temporal pattern on Kudzu.

1.20.2 Habitat

Habitat preference in the different strata of branches was clearly identified in the species

studied. Nine species, half of the total surveyéd, were predominant on the middle stratum. The remaining species were largely on the basal stratum (7 species) or top stratum (2 species). The middle stratum was selected as the second preference by 9 species. Thus may species prefer leaves from Kudzu branches in the intermediate growth stage for thier food and/or resting place.

Only 2 species were found most numerous on the top stratum, and this was the second preference of only 1 species. This is rather unexpected but the reason could be that Kudzu is a vine plant and grows too rapidly for the insects to follow its growth.

Feeding species are grouped here according to the plant part affected.

Leaf, petiole and stem feeding species:

Homoeocerus unipunctatus, Episomus turritus, Eugnathus distinctus Leaf and flowerhead feeding speices:

Chauliops fallax, Anomala lucens

Leaf and young stem feeding species:

Matsumuraeses falcana, M. vicina

Leaf feeding species:

Pagria signata, Hedylepta misera, Tetranychus kanzawai

Leafmining species:

Trachys auricollis, Japanagromyza tristella, Liocrobyla lobata, Neolithocolletis hikomonticola, Spulerina dissotoma

Gall-making speices:

Pitydiplosis sp., Genus sp. (Cecidomyiidae)

Petiole and stem feeding species:

Geisha distinctissima, Orosanga japonicus

Flowerhead, petiole and stem feeding species:

Megacopta punctatissima

Next, they are grouped according to habitat preference or stratum of the branch with which they are mainly associated. The stratum on which about 70% of total individuals are found is designated as the affected part here.

Species found mainly on the top stratum:

Megacopta punctatissima, Matsumuraeses falcana, M. vicina

Species found mainly on the middle stratum:

Geisha distinctissima, Orosanga japonicus, Homoeocerus unipunctatus, Anomala lucens, Trachys auricollis, Pagria signata, Episomus turritus, Eugnathus distinctus, Japanagromyza tristella, Hedylepta misera, Liocrobyla lobata

Species found mainly on the basal stratum:

Chauliops fallax, Pitydiplosis sp., Genus sp. (Cecidomyiidae), Neolithocolletis hikomonticola, Spulerina dissotoma, Tetranychus kanzawai

The above grouping shows that many species feed on the same stratum of the branch. Considering their different developmental time and microhabitat on the plant, however, even those species in the same group seem to have a different ecological niche within the plant.

2. Distribution of leafminers within the plant

Among the feeding species mentioned in the preceding pages, five leafminer species were surveyed for their detailed distribution within the Kudzu leaves.

Before describing the leafminer distribution, seasonal changes in the Kudzu leaves are reviewed.

Seasonal changes in the number of Kudzu leaves attached to different branches $(1^{\circ}-6^{\circ})$ branches) on 10 plants during the growing season in 1989 are shown in Fig. 30 on the 1° branch, Kudzu leaves first appeared in late March. The number increased gradually in May, and reached a peak of 388.8 leaves that month when the 2° branch started developing. The number of leaves on the 2° branch reached a maximum in June and thereafter declined gradually until December. The 3°, 4°, 5° and 6° branches were first found in June, July, August and September, respectively. The number of total leaves decreased slightly in August because of a typhoon. The maximum number of leaves was 1407 per 10 plants in July. All the leaves were dead or had fallen by late December.

The distribution pattern of five leafminer species—*Neolithocolletis hikomonticola, Liocrobyla lobata, Spulerina dissotoma* (Lepidoptera, Gracillariidae); *Japanagromyza tristella* (Diptera, Agromyzidae); *Trachys auricollis* (Coleoptera, Buprestidae)—was studied by counting the number of mines containing larvae on the leaves of different branches. No leafminers of *T. auricollis* were found throughout the field survey in this distribution study. Results of the four remaining species are presented as follows:



Fig. 30. Seasonal changes in the number of Kudzu leaves attached to different branches on 10 plants.

2.1 Japanagromyza tristella (THOMSON)

Seasonal changes in the mean number of larvae per leaflet on the different branches are presented in Fig. 31. This species was found only in younger leaves 2 to 5 weeks after the sprouting of Kudzu. The first leafminer was found in the first week of April. The date of the first distinct peak in the mean number was April 10 on the 1° branch. A few larvae then appeared from May to July on the 2° branch, from June to August on the 3° branch, and from July to August on the 4° branch. The leafminers of this speices were not seen on the 5° or 6° branches and after September. The result shows that the miners attack the newly growing branches as the season progresses.



Fig. 31. Seasonal changes in the mean number of larvae of *Japanagromyza tristella* per leaflet on different aged branches of *Pueraria lobata*.

| $/ \bullet - \bullet : 1^{\circ}$ | branch; | 00: | 2° | branch |
|-----------------------------------|---------|--------------------------------|----|----------|
| (▲—▲: 3° | branch; | $\triangle \cdots \triangle$: | 4° | branch) |
| \ _ _ : 5° | branch; | □…□: | 6° | branch/ |

As mentioned with regard to seasonal abundance (p. 53), the larval mines of this species were seen from April to November. The reason no larvae were found after September may be that the samll sampling numbers and/or the survey site in this study.

2.2 Liocrobyla lobata KUROKO

Seasonal changes in the mean number of larvae per leaflet are shown in Fig. 32. The larvae were found mainly in May and June on the 1° branch with a peak on June 12. On the 2° branch, they were found from early June until early August with a peak on July 11, and on the 3° branch from middle July until early September. They increased in number again on the 5° branch in October and November. No larvae were found on the 4° or 6° branches.

The first generation was abundant on leaves of the 1° branch and the second generation was found on the 2° and 3° branches. A small number of third generation larvae developed on the 3° branch also, and the fourth generation was found only on the 5° branch. Because



Fig. 32. Seasonal changes in the mean number of larvae of *Liocrobyla lobata* per leaflet on different aged branches of *Pueraria lobata* (for symbols, see Fig. 31).

of the low population density, no damage by this miner was found on the 4° or 6° branches throughout the survey period.

2.3 Neolithocolletis hikomonticola KUMATA

Seasonal changes in the mean number of larvae and pupae per leaflet are illustrated in Fig. 33. The leafminer's activity on the 1° branch, as indicated by the presence of the mines, was first noticed on May 1 six weeks after observation began. The population increased in May and June with a peak on May 29. A second peak was found on the 2° and 3° branches on



Fig. 33. Seasonal changes in the mean number of larvae and pupae of *Neolithocolletis hikomonticola* per leaflet on different aged branches of *Pueraria lobata* (for symbols, see Fig. 31).

July 17, a third on the 3° branch again on August 28, and a fourth between October and November on the 5° branch when lesser peaks also occurred on the 3°, 4°, 6° and 2° branches. These results coincide with the phenological data obtained from the field surveys at Toso and Korimoto (Fig. 22).

As can be noted in Fig. 33, this species in the fourth generation attacks most branches except the 1° branch, though in differing intensities. This differs from the two preceding species, and this behavior creates a large population after October.

The small population in the third generation was due to a strong typhoon that caused defoliation of the Kudzu leaves.

2.4 Spulerina dissotoma (MEYRICK)

Seasonal changes in the mean number of larvae per leaflet on different branches are shown in Fig. 34. Only a few larvae were found from May to early September, but from the middle of September to the middle of November the population increased rapidly. The first larva was found on May 15 on the 1° branch, and a few larvae appeared in June and July. They were found on the 2° and 3° branches from July until early December. On the 4° and 5° branches, larvae were found from August to December and on the 6° branch they appeared one month later than on the 4° and 5° branches.

The tendency to attack all branches except 1° after September as shown in Fig. 34 is similar to that of *N*. *hikomonticola* where, however, the first generation was also abundant on the 1° branch.



Fig. 34. Seasonal changes in the mean number of larvae of *Spulerina dissotoma* per leaflet on the different aged branches of *Pueraria lobata* (for symbols, see Fig. 31).

The reason few miners of this species were seen on the 1° branch is unknown, but may be due to the site characteristics in the Korimoto graveyard.

2.5 Summary

Distribution of the four leafminers on branches in different growing stages changed successively from spring to autumn. Mines of all four species were found on the 1° branch in spring with the exception of *S. dissotoma* of which the first generation on the 1° branch was very low in density. In later seasons, mines were found on branches that developed subsequent to the 1° branch.

This indicates that these species first make their mines on newly developed leaves, namely in their first generation, and then make them on successive branches according to the progress of the season in following generations.

This tendency is complemented by the results obtained in habitat studies. Mines were mostly found on the basal stratum and then on the middle stratum except those of *Japanagromyza tristella*.

The mines of *J. tristella* were primarily on the middle stratum, and a few on the basal stratum. This does not correlate well with the results of the distribution studies where mines were found on the 1° branch in spring. The reason for this contradiction is unknown, but may have to do with the different number of sites used in the two studies.

3. Development and reproduction

Development and reproduction data of the following three species are described here. Those of two other species, *Chauliops fallax* and *Megacopta punctatissima*, reported earlier (TAYUTIVUTIKUL and YANO, 1989, 1990) are also pertinent.

3.1 Homoeocerus unipunctatus (THUNBERG)

3.1.1 Development

The survival of eggs and nymphs at four constant temperatures is shown in Table 5. Percentage of egg hatching at 15°C was only 36%, significantly lower than those at 20°C, 25°C and 30°C. Percentage of nymphal survival was the greatest at 25°C (67.12%) followed by those at 20°C and 30°C. No nymphs survived to adults at 15°C. Percentage of egg hatching was greater than that of nymphal survival at all temperatures.

Table 5. Percentage survival of eggs and nymphs of *Homoeocerus unipunctatus* at 4 constant temperatures.*

| Temp. (°C) | No. eggs | % hatched | No. first instars | No. nymphs surviving to adult | % survival |
|---------------|----------|--------------|----------------------|----------------------------------|------------|
| 15 | 100** | 36.00a | 36 | | _ |
| 20 | 93 | 88.17b | 82 | 46 | 56.10a |
| 25 | 77 | 94.80b | 73 | 49 | 67.12ab |
| 30 | 102 | 90.20b | 92 | 47 | 51.09ac |

* Figures followed by the same letter are not significantly different at the 5% level of Chi-Square test.

** Eggs deposited at 20°C.

Table 6 summarizes the developmental data at constant temperatures. There was no significant difference between sexes in the duration of each nymphal stage or of total nymphal stage at any temperature except the first stage at 20°C.

| Temp. | Sex | No. | Mean | duration in days Instar | ±SD* |
|------------------------|------------------------------|-------------------------------------|--|---|---|
| (\mathbf{C}) | | individuals | 1 | 2 | 3 |
| 20 | М | 22 | $5.90 \pm 0.29a$ | 7.73±0.46a | $11.36 \pm 0.66a$ |
| | F | 24 | $6.46 \pm 0.59b$ | $7.62 \pm 0.49a$ | $11.25 \pm 0.79a$ |
| 25 | М | 23 | $3.65 \pm 0.71c$ | 5.91 ± 0.67 b | $7.96 \pm 0.64 b$ |
| | F | 26 | $4.04\pm0.82c$ | $5.92 \pm 0.56b$ | $8.08 \pm 0.74b$ |
| 30 | М | 25 | 2.48 ± 0.51 d | $4.16 \pm 0.37c$ | $5.40 \pm 0.50c$ |
| | F | 22 | $2.64 \pm 0.66d$ | $4.27 \pm 0.46c$ | $5.41 \pm 0.50c$ |
| | | | | | |
| Temp. | 0 | No | Mean | duration in days; | ±SD* |
| /° / \ | Sex | INO. | | Instar | |
| (°C) | Sex | individuals | 4 | 5 | 1-5 |
| (°C) | Sex M | individuals 22 | $\frac{4}{15.32\pm0.48a}$ | 18.32±0.72a | 1-5 58.64 ± 1.14a |
| (°C) | Sex M F | individuals 22 24 | $\begin{array}{r} 4 \\ 15.32 \pm 0.48a \\ 15.42 \pm 0.65a \end{array}$ | | 1-5 58.64 ± 1.14a 59.12 ± 1.62a |
| (°C) 20 25 | Sex M F M | individuals 22 24 23 | $\begin{array}{r} 4 \\ 15.32 \pm 0.48a \\ 15.42 \pm 0.65a \\ 8.78 \pm 0.60b \end{array}$ | | $ \begin{array}{r} 1-5 \\ 58.64 \pm 1.14a \\ 59.12 \pm 1.62a \\ 38.30 \pm 1.02b \end{array} $ |
| (°C) 20 25 | Sex M F M F | individuals 22 24 23 26 | $\begin{array}{c} 4 \\ 15.32 \pm 0.48a \\ 15.42 \pm 0.65a \\ 8.78 \pm 0.60b \\ 8.92 \pm 0.63b \end{array}$ | 5 18.32 ± 0.72a 18.85 ± 1.01a 11.96 ± 0.64b 11.88 ± 0.71b | $ \begin{array}{r} 1-5 \\ 58.64 \pm 1.14a \\ 59.12 \pm 1.62a \\ 38.30 \pm 1.02b \\ 38.85 \pm 1.01b \\ \end{array} $ |
| (°C) 20 25 30 | Sex M F M F M | 22 24 23 26 25 | $\begin{array}{c} 4\\ 15.32 \pm 0.48a\\ 15.42 \pm 0.65a\\ 8.78 \pm 0.60b\\ 8.92 \pm 0.63b\\ 7.40 \pm 0.51c\end{array}$ | $\frac{5}{18.32 \pm 0.72a}$ $18.32 \pm 0.72a$ $18.85 \pm 1.01a$ $11.96 \pm 0.64b$ $11.88 \pm 0.71b$ $10.00 \pm 0.64c$ | 1-5 58.64 ± 1.14a 59.12 ± 1.62a 38.30 ± 1.02b 38.85 ± 1.01b 29.48 ± 1.12c |

 Table 6.
 Duration of nymphal stages of Homoeocerus unipunctatus at 3 constant temperatures.

* Figures followed by the same letter are not significantly different at the 5% level (DUNCAN's new multiple range test).

Developmental zero and total effective temperature are shown in Table 7 and Fig. 35 and reveal highly positive r^2 values. This analysis demonstrates that the developmental zero for eggs is 13.55°C, and those for nymphs varied from 7.51°C to 12.95°C for males and from 7.68°C to 13.40°C for females. The developmental zero for development during the preoviposition period is 10.49°C.

Development from egg of one generation to egg of the following generation required 884.44 day-degrees in females. Egg development required an average of 108.22 day-degrees, which was about 12% of the total effective temperature. The nymphal period of both sexes required 591.72 day-degrees which was 67% of the total effective temperature. The preoviposition period required 184.50 day-degrees which was 21% of the total effective temperature.

The first and second nymphal instars completed their development faster than other nymphal instars and required only 42.74 and 90.09 day-degrees for males and 44.54 and 97.28 day-degrees for females, respectively, about 5% and 10% of the total effective temperature for nymphal development. The fifth instar required the largest amount of total effective temperature, followed by fourth and third instars. The effective temperatures required for the development of third, fourth and fifth instars was about 12%, 16% and 24% of total effective temperature for nymphal stage, respectively.

| Stage | | Regression equation | r | r ² | Developmental zero (°C) | Effective temperature (day-degrees) |
|--------|---------|-----------------------|-------|----------------|-------------------------------|---|
| Egg (M | +F) | Y = -0.1234 + 0.0092X | 0.998 | 0.997 | 13.35 | 108.225 |
| | 1st | Y = -0.3029 + 0.0234X | 0.998 | 0.996 | 12.95 | 42.735 |
| | 2nd | Y = -0.0979 + 0.0111X | 0.987 | 0.974 | 8.82 | 90.094 |
| Nymph | 3rd | Y = -0.1100 + 0.0097X | 0.992 | 0.984 | 11.32 | 102.881 |
| 5 1 | 4th | Y = -0.0682 + 0.0069X | 0.974 | 0.948 | 9.87 | 144.718 |
| | 5th | Y = -0.0341 + 0.0045X | 0.987 | 0.975 | 7.51 | 220.264 |
| | 1st-5th | Y = -0.0166 + 0.0017X | 0.999 | 0.998 | 9.81 | 591.716 |

 Table 7. Developmental zero and effective temperatures for development of *Homoeocerus unipunctatus*.

 A. Male

B. Female

| Stage | | Regression equation | r | r ² | Developmental zero (°C) | Effective temperature (day-degrees) |
|----------|---------|-----------------------|-------|----------------|-------------------------------|---|
| | 1st | Y = -0.3007 + 0.0224X | 0.995 | 0.990 | 13.40 | 44.543 |
| | 2nd | Y = -0.0790 + 0.0103X | 0.988 | 0.976 | 7.68 | 97.276 |
| Nymph | 3rd | Y = -0.1075 + 0.0096X | 0.988 | 0.976 | 11.19 | 104.167 |
| | 4th | Y = -0.0712 + 0.0070X | 0.981 | 0.962 | 10.16 | 142.653 |
| | 5th | Y = -0.0378 + 0.0047X | 0.989 | 0.978 | 8.02 | 212.314 |
| | 1st-5th | Y = -0.0378 + 0.0047X | 0.999 | 0.999 | 9.93 | 591.716 |
| Preovipo | osition | Y = -0.0569 + 0.0054X | 0.984 | 0.968 | 10.49 | 184.502 |



3.1.2 Fertility

Fertility of this species reared at three constant temperatures is shown in Table 8. The difference in the number of eggs per mated female was significant between 20°C and higher temperatures. The daily number of eggs laid per female is shown in Fig. 36. Preoviposi-

| Temperature | No females | No. eggs laid p | er female |
|-------------|--------------|------------------|-----------|
| (°C) | ito: iemaies | Mean (±SD)* | Range |
| 20 | 11 | 4.45±2.11a | 2- 7 |
| 25 | 14 | $9.79 \pm 5.55b$ | 3-22 |
| 30 | 14 | $8.86 \pm 4.47b$ | 3-14 |

Table 8. Fertility of Homoeocerus unipunctatus.

* Figures followed by the same letter are not significantly different at the 5% level (DUNCAN's new multiple range test).



Fig. 36. Daily fertility and survival of adult female of *Homoeocerus unipunctatus*. (.....: eggs laid;: adult survival)

tion period was 20.54 days at 20°C, 11.86 days at 25°C and 9.71 days at 30°C. The mean oviposition periods per female were slightly different between the constant temperatures, 15, 17 and 12 days at 20°C, 25°C and 30°C, respectively. The mean number of eggs laid per day per female was very low at any constant temperature, but this may be due to the small number of individuals observed.

3.1.3 Longevity

Adult longevity in pair rearing is shown in Table 9. There was a significant difference among temperatures observed in females but no significant difference was seen for males. The female longevity was slightly longer than the male and there was a negative relationship between the temperature and the longevity.

| | Temperature | No. adults | Longevity (d | lays) |
|--------|-------------|------------|----------------------|-------|
| Sex | (°C) | reared | Mean $(\pm SD)^{**}$ | Range |
| Male | 20 | 11 | $22.00\pm7.00a$ | 9-36 |
| | 25 | 14 | $22.35 \pm 4.16a$ | 16-30 |
| | 30 | 14 | $18.64 \pm 4.55a$ | 10-25 |
| Female | 20 | 11 | $29.45 \pm 6.77b$ | 22-42 |
| | 25 | 14 | 23.85 ± 3.72 ac | 18-29 |
| | 30 | 14 | $19.43 \pm 3.90 ad$ | 12-24 |

Table 9. Adult longevity of Homoeocerus unipunctatus.*

* Reared in pairs.

** Figures followed by the same letter are not significantly different at the 5% level (DUNCAN's new multiple range test).

3.2 Hedylepta misera (BUTLER)

3.2.1 Development

Percentage survival of eggs, larvae and pupae at each constant temperature is shown in Table 10. Percentage of egg hatching at 25°C (78.25%) was significantly higher than at 20°C and 30°C. No eggs hatched at 15°C. Larval survival followed the same pattern as the eggs, being highest at 25°C and lowest at 30°C. Pupal survival was lowest at 20°C which was greater than both larval survival and egg hatching, though not statistically different in either larvae or pupae.

Mean duration of larval and pupal stages at three constant temperatures is shown in Table 11. The developmental period at each temperature of both sexes showed a highly negative

Table 10. Percentage survival for the immature stages of Hedylepta misera at 4 constant temperatures.*

| | | ~ | | No. larvae | No. pupae | % su | rvival |
|---------------|-------------|--------------|----------------------|-----------------------|-----------------------|--------|--------|
| Temp. (°C) | No. eggs | % hatched | No. first instars | surviving to adult | surviving to adult | Larvae | Pupae |
| 15 | 175** | 0 | | | | | |
| 20 | 390 | 62.82a | 81 | 46 | 38 | 56.79 | 82.61 |
| 25 | 515 | 78.25b | 103 | 66 | 57 | 64.08 | 86.36 |
| 30 | 473 | 57.93a | 95 | 52 | 47 | 54.74 | 90.38 |

* Figures followed by the same letter are not significantly different at the 5% level of Chi-Square test.

** Eggs deposited at 20°C.

| Temp. (°C) | Sex | No. individuals | | Mean duration Inst | in days±SD* tar | |
|----------------|-----------------------|----------------------------|---|---|--|-------------------|
| <u> </u> | | | 1 | 2 | 3 | 4 |
| 20 | Μ | 21 | $5.24 \pm 0.44a$ | $7.29 \pm 0.46a$ | 6.86±0.36a | $6.33 \pm 0.48a$ |
| | F | 18 | $5.56 \pm 0.51b$ | $7.39 \pm 0.50a$ | $6.89 \pm 0.32a$ | $6.67 \pm 0.48b$ |
| 25 | Μ | 27 | $3.15 \pm 0.36c$ | $4.85 \pm 0.36b$ | $4.70 \pm 0.54b$ | $3.78 \pm 0.58c$ |
| | F | 30 | $3.13 \pm 0.35c$ | $4.83 \pm 0.46b$ | 4.70 ± 0.60 b | $3.83 \pm 0.53c$ |
| 30 | Μ | 23 | $2.39\pm0.50d$ | $3.57 \pm 0.51c$ | $3.17 \pm 0.49c$ | $3.09 \pm 0.29 d$ |
| | F | 24 | 2.50 ± 0.51 d | $3.79 \pm 0.42c$ | $3.21 \pm 0.42c$ | $3.12 \pm 0.34d$ |
| | | | | | | |
| Temp. (°C) | Sex | No. individuals | Mean | duration in days Instar | ±SD* | |
| | | | | | | |
| | _ | | 5 | 1-5 | Pupa | |
| 20 | М | 21 | $\frac{5}{7.24\pm0.44a}$ | $\frac{1-5}{32.95 \pm 1.02a}$ | Pupa 14.05±0.59a | |
| 20 | M F | 21 18 | $5 \\ 7.24 \pm 0.44a \\ 7.39 \pm 0.50a$ | $\frac{1-5}{32.95 \pm 1.02a} \\ 33.89 \pm 1.02b$ | Pupa $14.05 \pm 0.59a$ $14.22 \pm 0.65a$ | |
| 20 25 | M F M | 21 18 27 | $5 \\ 7.24 \pm 0.44a \\ 7.39 \pm 0.50a \\ 4.82 \pm 0.40b \\$ | $ \begin{array}{r} 1-5 \\ 32.95 \pm 1.02a \\ 33.89 \pm 1.02b \\ 21.30 \pm 0.67c \\ \end{array} $ | Pupa $14.05 \pm 0.59a$ $14.22 \pm 0.65a$ $9.67 \pm 0.68b$ | |
| 20 25 | M F M F | 21 18 27 30 | $5 \\7.24 \pm 0.44a \\7.39 \pm 0.50a \\4.82 \pm 0.40b \\4.73 \pm 0.45b \\$ | $\frac{1-5}{32.95 \pm 1.02a} \\ 33.89 \pm 1.02b} \\ 21.30 \pm 0.67c \\ 21.23 \pm 1.10c \\ \end{array}$ | $\begin{array}{c} Pupa \\ \hline 14.05 \pm 0.59a \\ 14.22 \pm 0.65a \\ 9.67 \pm 0.68b \\ 9.83 \pm 0.53b \end{array}$ | |
| 20 25 30 | M F M F M | 21 18 27 30 23 | $5 \\7.24 \pm 0.44a \\7.39 \pm 0.50a \\4.82 \pm 0.40b \\4.73 \pm 0.45b \\3.83 \pm 0.39c \\$ | $\begin{array}{c} 1-5\\ \hline 32.95 \pm 1.02a\\ 33.89 \pm 1.02b\\ 21.30 \pm 0.67c\\ 21.23 \pm 1.10c\\ 16.04 \pm 0.64d \end{array}$ | Pupa $14.05 \pm 0.59a$ $14.22 \pm 0.65a$ $9.67 \pm 0.68b$ $9.83 \pm 0.53b$ $6.65 \pm 0.49c$ | |

Table 11. Duration of larval and pupal stages of Hedylepta misera at 3 constant temperatures.

* Figures followed by the same letter are not significantly different at the 5% level (DUNCAN's new multiple range test).

| Stag | e | Regression equation | r | r ² | Developmental zero (°C) | Effective temperature (day-degrees) |
|-------|---------|-----------------------|-------|----------------|-------------------------------|---|
| Egg(M | (+F) | Y = -0.1390 + 0.0097X | 0.980 | 0.960 | 14.32 | 102.987 |
| | 1st | Y = -0.2594 + 0.0227X | 0.998 | 0.996 | 11.41 | 43.995 |
| | 2nd | Y = -0.1503 + 0.0143X | 0.999 | 0.999 | 10.49 | 69.784 |
| Larva | 3rd | Y = -0.1988 + 0.0169X | 0.993 | 0.985 | 11.74 | 59.067 |
| | 4th | Y = -0.1662 + 0.0166X | 0.987 | 0.973 | 10.01 | 60.241 |
| | 5th | Y = -0.1056 + 0.0123X | 0.997 | 0.994 | 8.57 | 81.169 |
| | 1st-5th | Y = -0.0332 + 0.0032X | 0.999 | 0.999 | 10.40 | 313.480 |
| Pupa | | Y = -0.0894 + 0.0079X | 0.994 | 0.989 | 11.31 | 126.422 |

Table 12. Developmental zero and effective temperatures for development *Hedylepta misera*. A. Male

B. Female

| Stag | e | Regression equation | r | r ² | Developmental zero (°C) | Effective temperature (day-degrees) |
|--------|----------|-----------------------|-------|----------------|-------------------------------|---|
| | 1st | Y = -0.2503 + 0.0220X | 0.988 | 0.977 | 11.38 | 45.455 |
| | 2nd | Y = -0.1190 + 0.0128X | 0.998 | 0.995 | 9.27 | 77.882 |
| Larva | 3rd | Y = -0.1930 + 0.0166X | 0.994 | 0.988 | 11.59 | 60.060 |
| | 4th | Y = -0.1814 + 0.0170X | 0.985 | 0.970 | 10.67 | 58.824 |
| | 5th | Y = -0.1115 + 0.0261X | 0.993 | 0.986 | 8.88 | 79.618 |
| | 1st-5th | Y = -0.0324 + 0.0031X | 0.997 | 0.995 | 10.37 | 319.489 |
| Pupa | | Y = -0.0746 + 0.0072X | 0.997 | 0.995 | 10.40 | 139.470 |
| Preovi | oosition | Y = -0.1041 + 0.0127X | 0.976 | 0.952 | 8.19 | 78.616 |

relationship. The difference of developmental time of larval stage between sexes was significant only at 20°C. The first and fourth larval instars reared at 20°C had a significantly different developmental time between sexes, 5.24 and 6.33 days for males and 5.56 and 6.67 days for females, respectively. The pupal stage was significantly different in both sexes at 30° C.

The developmental zero and total effective temperature are shown in Table 12 and Fig. 37. Linear models for each stage fit the developmental rate data well as shown by the high r^2 values. The developmental zero for eggs was 14.32°C which required the highest temperature of all stages. Male larvae in the first, second, and third instars and pupae requied slightly higher developmental zero than females. The developmental zero which was 10.40°C for the entire larval period was calculated in both sexes and was lowest (8.19°C) for the preoviposition period.

Development from egg of one generation to egg of the following generation required 640.56 and 621.50 day-degrees for males and females, respectively. Egg development required an average of 102.99 day-degrees accounting for about 16% of the total effective temperature. The larval period required 313.48 and 319.49 day-degrees accounting for 50.47% and 49.84% of the total effective temperature for males and females, respectively. The female pupae required a substantially longer period for development than male pupae. Preoviposition period required 78.62 day-degrees accounting for about 12% of the total effective temperature.

The first larval instar required the lowest total effective temperature to complete its development accounting for about 7% of the total effective temperature of the larval period.



The fifth instar of both sexes required the highest level followed by the second, fourth and third instars for males, and followed by the second, third and fourth instars for females, respectively.

| Temperature | No females | No. eggs laid per female | | |
|-------------|--------------|--------------------------|--------|--|
| (°C) | ivo. remaies | Mean (±SD) | Range | |
| 20 | 22 | 105.54 ± 44.69 | 22-165 | |
| 25 | 25 | 118.87 ± 43.34 | 44-202 | |
| 30 | 30 | 108.58 ± 33.66 | 34-164 | |

Table 13. Fertility of Hedylepta misera.

Not significantly different at the 5% level (DUNCAN's new multiple range test).



Fig. 38. Daily fertility and survival of adult females of *Hedylepta misera*. (.....: eggs laid; ——: adult survival)

3.2.2 Fertility

The average number of eggs per mated female reared at three constant temperatures is shown in Table 13. No significant differences were observed between temperatures.

Daily oviposition rates are shown in Fig. 38. Both preoviposition and oviposition periods were shortened as the temperature increased with an average of 6.08, 5.53 and 3.92 days for preoviposition and 5.23, 5.40 and 3.92 days for oviposition at 20°C, 25°C and 30°C, respectively.

3.2.3 Longevity

Adult longevity in isolated rearing is shown in Table 14. There was a significant difference among the temperatures studied and a negative relationship was observed between temperature and longevity of both sexes. The mean adult longevity days decreased as the temperature increased. Those of males and females were significantly different at 25° C. The greatest longevity was 21 days at 20° C for both sexes and the shortest was 2 and 4 days at 30° C for males and females.

| ~ | Temperature | No. adults | Longevity (d | ays) |
|--------|-------------|------------|-------------------|-------|
| Sex | (°C) | reared | Mean (±SD)** | Range |
| Male | 20 | 21 | $16.62 \pm 3.28a$ | 7-21 |
| | 25 | 27 | $10.81 \pm 1.92b$ | 6-15 |
| | 30 | 23 | $8.39 \pm 2.15c$ | 2-11 |
| Female | 20 | 18 | $16.50 \pm 4.13a$ | 5-21 |
| | 25 | 30 | $12.07 \pm 2.35d$ | 7-15 |
| | 30 | 24 | $8.71 \pm 1.94c$ | 4-12 |

Table 14. Adult longevity of Hedylepta misera.*

* Isolated rearing.

** Figures followed by the same letter are not significantly different at the 5% level (DUNCAN's new multiple range test).

3.3 Matsumuraeses falcana (WALSIGHAM)

3.3.1 Development

Percentage survival for the immature stages of this species at constant temperature is shown in Table 15. Percentage of egg hatching at 25° C (28.84%) was significantly higher than at 20° C and 30° C. There was no egg hatching at 15° C as it was almost the same

Table 15. Percentage survival for the immature stages of *Matsumuraeses falcana* at 4 constant temperatures.*

| Temn | No | 0% | No first | No. larvae | No. pupae | % su | rvival |
|------|-------|---------|----------|-----------------------|-----------------------|--------|--------|
| (°C) | eggs | hatched | instars | surviving to adult | surviving to adult | Larvae | Pupae |
| 15 | 240** | 0 | | | | | |
| 20 | 425 | 76.71a | 100 | 71 | 48 | 71.00 | 67.60 |
| 25 | 577 | 82.84b | 87 | 62 | 45 | 71.26 | 72.58 |
| 30 | 401 | 63.34c | 135 | 80 | 49 | 59.26 | 61.25 |

* Figures followed by the same letter are not significantly different at the 5% level of Chi-Square test.

** Eggs deposited at 20°C.

temperature as the developmental zero mentioned below. Larval and pupal survival were not significantly different. These data are similar to the results reported by FUJIYOSHI *et al.* (1981) in which the rate of pupation and adult emergence were above 55% and 50%, respectively, when rearing took place at 23°C with a LD 16:8 photoperiod.

The developmental time of larvae and pupae at each constant temperature is summarized in Table 16. The developmental time decreased as the temperature increased showing significant negative relationship. The total larval period between the sexes was significantly different at 25°C, while at 20°C the duration of the second and fourth larval stages was significantly different, and at 25°C, only the second larval instar showed significant difference in duration between sexes. FUJIYOSHI *et al.* (1981) reported that the duration from egg to adult emergence was 30–40 days when reared at 23°C with a LD 16:8 photoperiod on an artificial diet.

| Temp. | Sex | No. | | Mean duration Ins | in days±SD* tar | |
|-------|-----|-------------|------------------|----------------------------|--------------------|-------------------|
| (°C) | | individuals | 1 | 2 | 3 | 4 |
| 20 | М | 26 | $2.77 \pm 0.43a$ | $3.19 \pm 0.40a$ | $4.08 \pm 0.48a$ | $4.65 \pm 0.48a$ |
| | F | 22 | $2.77\pm0.43a$ | $2.77 \pm 0.43b$ | $4.32 \pm 0.48a$ | $4.36 \pm 0.49b$ |
| 25 | М | 20 | $1.95 \pm 0.22b$ | $2.85 \pm 0.40c$ | $2.90 \pm 0.48b$ | $3.55 \pm 0.85c$ |
| | F | 25 | $1.88\pm0.33b$ | $2.56\pm0.51d$ | $2.84 \pm 0.37b$ | $3.40 \pm 0.50c$ |
| 30 | Μ | 23 | $1.43 \pm 0.51c$ | $1.87 \pm 0.34e$ | $2.13 \pm 0.34c$ | 2.39 ± 0.50 d |
| | F | 26 | $1.38\pm0.50c$ | $1.92 \pm 0.27e$ | $2.15 \pm 0.37c$ | $2.42 \pm 0.58d$ |
| Temp. | Sex | No. | Mean | duration in days Instar | ±SD* | |
| (°C) | | individuals | 5 | 1-5 | Pupa | |
| 20 | М | 26 | $7.31 \pm 0.47a$ | $22.00 \pm 0.98a$ | $12.38 \pm 0.80a$ | |
| | F | 22 | $7.46 \pm 0.60a$ | $22.18 \pm 0.91a$ | $12.40 \pm 0.67a$ | |

 $16.50 \pm 0.83b$

 $15.60 \pm 0.87c$

 $11.91 \pm 1.24d$

 $11.88 \pm 0.99d$

 $9.60 \pm 0.50b$

 $9.48 \pm 0.51b$

 $7.13 \pm 0.34c$

 $7.27 \pm 0.45c$

Table 16. Duration of larval and pupal stages of *Matsumuraeses falcana* at 3 constant temperature.

* Figures followed by the same letter are not significantly different at the 5% level (DUNCAN's new multiple range test).

 $5.25 \pm 0.55b$

 $4.92 \pm 0.57b$

 $4.09\pm0.60c$

 $4.00 \pm 0.63c$

Table 17 and Fig. 39 present the developmental zero and total effective temperature for all stages of both sexes. Linear models for all stages fit well the developmental rate data as shown by the high r^2 values. Egg stage had the highest developmental zero, 15.43°C. The developmental zero of total larval period for males and females was 8.56°C and 8.46°C, respectively. The second and fourth larval stages of males required a slightly higher developmental zero (6.97°C and 10.00°C) than those of females (6.16°C and 8.00°C). The developmental zero of pupal stage was similar to those of the second larval stadia in both sexes.

25

30

Μ

F

Μ

F

20

25

23

26

| Stag | je | Regression equation | r | r ² | Developmental zero (°C) | Effective temperature (day-degrees) |
|-------|---------|--|-------|----------------|-------------------------------|---|
| Egg(N | (+F) | Y = -0.4527 + 0.0293X | 0.999 | 0.998 | 15.43 | 34.083 |
| | 1st | Y = -0.3211 + 0.0338X | 0.998 | 0.997 | 9.49 | 29.568 |
| | 2nd | Y = -0.1546 + 0.0222X | 0.934 | 0.873 | 6.97 | 45.106 |
| Larva | 3rd | Y = -0.2073 + 0.0224X | 0.998 | 0.996 | 9.25 | 44.603 |
| | 4th | $\mathbf{Y} = -0.2033 + 0.0203 \mathbf{X}$ | 0.981 | 0.962 | 10.00 | 49.189 |
| | 5th | Y = -0.0786 + 0.0108X | 0.999 | 0.999 | 7.31 | 92.850 |
| | 1st-5th | Y = -0.0330 + 0.0038X | 0.993 | 0.986 | 8.56 | 259.740 |
| Pupa | | Y = -0.0404 + 0.0060X | 0.993 | 0.986 | 6.79 | 168.067 |

 Table 17.
 Developmental zero and effective temperatures for development of Matsumuraeses falcana.

 A.
 Male

B. Female

| Stag | e | Regression equation | r | r ² | Developmental zero (°C) | Effective temperature (day-degrees) |
|--------|----------|--|-------|----------------|-------------------------------|---|
| | 1st | Y = -0.3655 + 0.0362X | 0.999 | 0.999 | 10.11 | 27.662 |
| | 2nd | Y = -0.1321 + 0.0214X | 0.990 | 0.980 | 6.16 | 46.642 |
| Larva | 3rd | Y = -0.2324 + 0.0233X | 0.999 | 0.999 | 9.99 | 42.974 |
| | 4th | Y = -0.1468 + 0.0184X | 0.986 | 0.972 | 8.00 | 54.500 |
| | 5th | Y = -0.0937 + 0.0116X | 0.994 | 0.988 | 8.48 | 86.356 |
| | 1st-5th | $\mathbf{Y} = -0.0331 + 0.0039 \mathbf{X}$ | 0.999 | 0.999 | 8.48 | 256.410 |
| Pupa | | Y = -0.0354 + 0.0057X | 0.998 | 0.995 | 6.19 | 174.520 |
| Preovi | position | Y = -0.1680 + 0.0145X | 0.988 | 0.976 | 11.57 | 68.870 |



Total effective temperature from egg of one generation to egg of the following generation was 530.76 day-degrees for males and 533.88 day-degrees for females. Egg development required an average of 34.08 day-degrees accounting for only 6% of the total effective temperature. The larval period required 259.74 and 256.41 day-degrees, accounting for 48.83% and 47.95% of the total effective temperature for males and females, respectively. The pupal period needed 168.07 day-degrees for males and 174.52 day-degrees for females, and accounted for 31.60% and 32.64% of the total effective temperature. The preoviposition period required 68.87 day-degrees accounting for about 13% of the total effective temperature.

The first larval instar completed its development faster than other instars and required only 29.57 day-degrees for males and 27.66 day-degrees for females, about 6% and 5% of the total larval period. The fifth instar required the highest total effective temperature with an average of 92.85 and 86.36 day-degrees for males and females, respectively. The second, third and fourth instars required an average of 45.11, 44.60 and 49.19 day-degrees, about 9%, 8% and 9% of the total effective temperature for males, and 46.64, 42.97 and 54.50 day-degrees, about 9%, 8% and 10% of the total larval effective temperature for females, respectively.

3.3.2 Fertility

The average number of eggs per mated female reared under constant temperatures is shown in Table 18. No significant differences were observed between fertility at the three rearing temperatures. The highest mean number of eggs laid per female was at 25° C and the lowest was at 30° C. The maximum number of eggs laid was 186 at 25° C, and the minimum was 12 at 30° C.

| Temperature | No females | No. eggs laid p | per female | |
|-------------|-------------|--------------------|------------|--|
| (°C) | NO. Temates | Mean (±SD) | Range | |
| 20 | 12 | 100.83 ± 45.05 | 23-163 | |
| 25 | 18 | 120.56 ± 57.69 | 16-186 | |
| 30 | 17 | 97.76 ± 41.02 | 12-151 | |

Table 18. Fertility of Matsumuraeses falcana.

Not significantly different at the 5% level (DUNCAN's new multiple range test).

Daily oviposition rates are shown in Fig. 40. The average during the preoviposition period was 12.38, 9.60 and 7.13 days at 20°C, 25°C and 30°C, respectively. Oviposition period decreased as temperature increased. The average daily number of eggs per female from the average preoviposition period for those tested was high and an oviposition period was extended at 20° C and 25° C.

3.3.3 Longevity

Adult longevity in isolated rearing shown in Table 19 was significantly different between 20°C and 30°C for males. There was no significant difference between 20°C and 25°C, but at 30°C female longevity differed significantly. The mean adult longevity between the sexes at the same temperature, however, was not significantly different, the longest being 22 and 20



Fig. 40. Daily fertility and survival of adult females of *Matsumuraeses falcana*. (.....: eggs laid; ——: adult survival)

| Table 19. | Adult | longevity | of | Matsumuraeses | falcana.* |
|-----------|-------|-----------|----|---------------|-----------|
|-----------|-------|-----------|----|---------------|-----------|

| Sex | Temperature (°C) | No. adults reared | Longevity (days) | |
|--------|---------------------|-------------------|---------------------|-------|
| | | | Mean (±SD)** | Range |
| Male | 20 | 26 | $14.23 \pm 3.96a$ | 6-22 |
| | 25 | 20 | $12.20 \pm 2.17 ab$ | 8-16 |
| | 30 | 23 | $11.30 \pm 2.38b$ | 6-15 |
| Female | 20 | 22 | $14.55 \pm 3.67a$ | 5-20 |
| | 25 | 25 | $12.76 \pm 3.00a$ | 6-17 |
| | 30 | 26 | $10.50 \pm 2.50 b$ | 4-14 |

* Isolated rearing.

** Figures followed by the same letter are not significantly different at the 5% level (DUNCAN's new multiple range test).

for males and females at 20°C.

3.4 Summary

3.4.1 Development

No egg hatching was seen at 15°C for any of the three species, indicating their adaptation to the growth of Kudzu plant. Percentage survival of larvae was generally high at 25°C for all species.

Effective temperature for egg development of *M. falcana* was small than those of other two species, though developmental zero was almost the same for all three. Effective temperature of the coreid bug *H. unipunctatus* was much greater than those of the two lepidopterous species.

3.4.2 Reproduction

Fertility data in *M. falcana*, especially the range in number of eggs laid per female, was rather variable. Daily fertility and survivorship of adults of all species were quite similar.

Adult longevity of the coreid bug *H. unipunctatus* was somewhat shorter than the lygaeid bug *Chauliops fallax* reported by TAYUTIVUTIKUL and YANO (1989).

4. Evaluation of feeding species for possible use in a biological control program

Based on these fundamental studies of Kudzu feeding species, some notes and discussions are made here to evaluate them for future biological control of the Kudzu plant.

4.1 Species composition

As listed in Table 1 of Part I (TAYUTIVUTIKUL and KUSIGEMATI, 1992), a total of 109 Kudzu feeding species of insects and 2 mites is known to date, which include 61 insect species and 1 mite species found by the present survey in the Kagoshima area. The species composition found is diverse, and more feeding species are expected to be found when surveys are made in other areas.

The number of insects and mites associated with Kudzu is comparable to that of quickweeds, *Galinsoga* species in the United States which includes 122 insects and mites (BATRA, 1979) and to the 35 insects species used in an attempt to control *Lantana* (WATERHOUSE and NORRIS, 1987). Though data on insect species composition associated with weeds are rare, these cases mentioned might be among the most diverse.

Judging from the rich insect fauna associated with the plant, Kudzu might have been introduced to Japan in older times, and could thus be ecologically referred to as a native plant. However, even though Kudzu is not a weed which has recently invaded, its biological control is not hopeless as ANDRES and GOEDEN (1971) and other authors have stated that biological control against native weeds can also be achieved.

Among the insects found, the families Coreidae (Hemiptera), Buprestidae, Cerambycidae, Chrysomelidae and Curculionidae (Coleoptera), Agromyzidae (Diptera), and Tortricidae (Lepidoptera) are recognized as having been used successfully in the biological control of other weeds in the past (HUFFAKER, 1964). This can be viewed fundamentally encouraging.

Several insect species including a brupestid are expected to be advantageous biological control agents owing to their monophagous and other habits, and they are discussed below.

Three species of Cecidomyiidae may arouse an argument in future as HARRIS (1991) mentioned the impact of gall-inducers.

Two spider mites, *Panonychus citri* and *Tetranychus kanzawai*, attack Kudzu. History shows that the spider mite, *Tetranychus desertorum* BANKS, which was accidentally introduced into Australia from Texas proved useful for prickly pear control before the success of the pyralid moth *Cactoblastis cactorum* (BERGROTH) (DODD, 1940). The present two species, however, are well-known crop pests, and therefore are not being considered for utilization in the control of Kudzu.

Each phytophagous species on Kudzu has a particular ecological niche including its own life cycle, microhabitat and feeding habit as mentioned, and each is able to coexist with other species on the same host plant (Fig. 29). This is one of the reasons for Kudzu's rich fauna, and it also means that niches are already occupied by these native insects. This creates the biggest challenge for future biological control program of the plant in Japan.

4.2 Food and feeding habits

Host plants, especially the economically important ones, of Kudzu feeding species were listed in Table 1 of Part I and, as stated in that publication, only 14 of these species are monophagous to Kudzu. Judging from their feeding habits, species of Buprestidae, Agromyzidae and four lepidopterous families may be more advantageous as biological control agents than other monophagous species of Miridae, Thripidae, Curculionidae and Cecidomyiidae. Leafmining species among the first mentioned group should be espescially given attention for this purpose. This monophagous insect group include 9 endophagous species supporting an argument that endophagous insects tend to have narrower host ranges than ectophagous species (CRAWLEY, 1989).

The many remaining oligo- and polyphagous species of Kudzu are generally excluded as key control agents but they may contribute to some extent as native agents together with key species.

Kudzu feeding species are mostly foliage or sap feeders, and few flower or seed feeders have been found. Together with the less numerous monophagous species, the paucity of species attacking reproductive organs of the plant and the rhizomes is not encouraging for the biological control of the weed. It is generally thought that insects which attack seeds or reproductive organs are most efficient in control by preventing the spread of the weed. In the case of Kudzu, however, the rhizome is also important since it is rather large which provides vigorous growth to new shoots the next season. It is discouraging that no species known to attack this portion was found.

Larvae of the weevil, *Mesalcidodes trifidus*, bore into the stem forming a remarkable gall, but are not responsible for the death of the plant.

Though the fact that there are apparently few insects that cause fatal damage to the plant is not immediately encouraging, there is still hope since weed control by insects in the past has been pursued both by a single key species such as prickly pear in Australia (DODD, 1940) and by compound agents or factors such as St. Johnswort (HUFFAKER and KENNETT, 1959; HUFFAKER, 1966). In the latter case, the insect agent, *Chrysolina quadrigemina* and climatic factors were used in combination against the weed. Biological data obtained in the present study may thus be utilized in a future biological control program.

Next, oligo- and polyphagous species should be noted, speccies, especially those feeding on various crops in addition to Kudzu. Some of these species are believed to move from Kudzu to other crops (TAKASU and HIROSE, 1986), and groups with this habit can have an important position in crop pest managements as suggested by van EMDEN (1965, 1981). These species are therefore regarded as generally negative in both Kudzu control and crop pest management.

It was not possible to estimate the effect of feeding by phytophagous species on Kudzu growth, because the surveys were carried on vigorously and extremely rapid growing plants. It is remarkable that the population densitites of all the monophagous species were relatively low so that many leaves of the host plant remained unused. In general, when plenty of food is available for feeding, insect populations particularly of multivoltine species increase. However, the present study showed that most of the multivoltine species did not increase in number even though many new branches successively appeared until November. Data to explain this phenomenon may be available by a study of the activity of parasitoids or predators, seasonal changes in the chemical components of the plant and the mutual interaction of each species. It may be possible to argue that the resistance against each phytophagous species is stronger in wild plants than in cultivated crops, and the pressure of natural enemies on the population of each phytophagous species is greater in natural vegetation than in a cultivated crop fields.

4.3 Summary

The data obtained are fundamental and diverse and provide a plat form from which to discuss a practical procedure for establishing a biological control program for the Kudzu plant. In the two areas of species composition and the food and feeding habits of Kudzu-feeding species, the following findings have been described.

The phytophagous insects and mites associated with Kudzu are, rich in species number and range widely in their taxonomic position. In spite of the high diversity, the present survey found that few species actually cause severe damage to the plant, though 14 monophagous species including leafminers are rather remarkable in their feeding on it.

Since the biological control of weeds by organisms is a rather complicated procedure in some cases (HARRIS, 1991), the fundamental data obtained will be invaluable in setting up a future biological control program.

General remarks

Weed control has been an endless problem for agriculture, and the arguments for

biological weed control have been made in this century (TILLYARD, 1929, 1930; SWEETMAN, 1936, 1958; HUFFAKER, 1964, DeBACH, 1974). The first definite work using an insect was done only fifty years ago when the prickly pear cactus, *Opuntia* spp., was successfully controlled by an introduced moth, *Cactoblastis cactorum* (BERGORTH) in Australia (DODD, 1959; ANDRES and GOEDEN, 1971; ANDRES *et al.*, 1976), though an early trial against the plant by insects was made nearly 200 years ago (JOHNSTON and TRYON, 1914). Biological weed control by exotic insects and other organisms has been attempted against 86 species of weed and by domestic organisms against 25 weed species worldwide (JULIEN, 1987). Kudzu plant, however, has not been undertaken as the target weed to date, though it is a rather serious problem in both Japan and the United States.

This study of insects associated with the Kudzu plant investigated and described: (1) species composition found in field surveys and a bibliographical survey, (2) seasonal abundance and habitat of 19 species, (3) distribution of 4 leafminer species within the plant, and (4) development and reproduction of 3 dominant species. These data are focused into the following two points of view.

Basic biological data and species composition has been provided on the feeding species. This is eagerly requested for the selection of effective biological control agents (HARRIS and Zwölfer, 1968; Zwölfer and HARRIS, 1971; WAPSHERE, 1974). High diversity and various life histories of the dominant species show that the ecosystem is complex even in a single Kudzu plant. Biological and ecological relationships between the species and with adjacent ecosystems such as movements between Kudzu and crops are intricate. This means the data may have potential for use in an applied situation such as a biological control program, yet it also reveals difficulties in crop pest management as many species attack various crops of economic important (Table 1 of Part I).

The great diversity of insects indicates Kudzu is almost a native plant now rather than an invader, and the argument can also be put forth that the plant is part of the native ecosystem except in some limited areas such as roadsides and riverbanks.

A second value of the data is concerned with the biological control of Kudzu. The potential or possibility of using one or more of identified species in a biological control program was evaluated and may be summarized as follows.

No species which causes fatal damage to the plant has yet been found in the Kagoshima area, and this makes it difficult to select a control agent from among those species known to date. There is, however, a total of 14 monophagous species, and some of these are leafminers. This is positive data for a control program, especially if the program is implemented using a combination of several agents or factors against a single weed. Each of the agents may play role in the program by inflicting indirect or partial damage.

The biological information on life cycles, habitat and reproductive data obtained and detailed here is a first step in preventing Kudzu from becoming an even more serious weed problem.

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Explanation of Plate I

- Fig. 41. Adult Trachys auricolis feeding on the leaves of Pueraria lobata.
- Fig. 42. Blotch mines of Japanagromyza tristella on a leaf of Pueraria lobata.
- Fig. 43. Tetranychus kanzawai on the undersides on a leaf of Pueraria lobata.
- Fig. 44. Larval nest of Matsumuraeses falcana or M. vicina on young leaves of Pueraria lobata.
- Figs. 45 and 46. Midge-galls on the leaf of *Pueraria lobata* made by *Pitydiplosis* sp. (45: upperside; 46: underside).
- Fig. 47. Midge-galls made by a cecidomyiid sp. on the underside of a leaf of Pueraria lobata.
- Fig. 48. Blotch mines made by the later larval stages of *Liocrobyla lobata* on the upperside of the leaf of *Pueraria lobata*.
- Fig. 49. Blotch mines of Spulerina dissotoma on a leaf of Pueraria lobata.
- Fig. 50. Blotch mines of Neolithcolletis hikomonticola on the underside of Pueraria lobata.

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^{*} Other references listed in Part I are also pertinent to this report.

