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Comparative Life Histories, Demographic Statistics and Damage Potential of the Bagworms *Pteroma pendula* and *Metisa plana* in Oil Palm

Perbandingan antara Kitar Hidup, Statistik Demografi dan Potensi Kepupusan Ulat Bungkus Pteroma pendula dan Metisa plana pada Pokok Kelapa Sawit

Ho Cheng Tuck[1], Yusof Ibrahim[2] and Khoo Khay Chong[1]

[1] CABI Southeast and East Asia Regional Centre,
PO Box 210, 43400 Serdang, Selangor, Malaysia
[2] Department of Agricultural Science, Faculty of Technical dan Vocational Education, Universiti Pendidikan Sultan Idris, 35900, Tg. Malim, Perak, Malaysia

Abstract

This article provides an accurate detail of the life history of the bagworms *Pteroma pendula (P. pendula)* and *Metisa plana (M. plana)* on oil palm. *P. pendula* was confirmed to possess four larval stages with no difference in the number of instars and pupal development time between the sexes. Life history of *M. plana* followed reported by earlier workers of 5-6 larval instars for males and 6-7 for females were used. There was, however, no difference in pupal developmental time and size. Sex ratio for both species was nevertheless 1:1 and more representative r_m and λ values were obtained. The last two statistics were nevertheless superior for *P. pendula* and insects bred in the field. The r_m for *P. pendula* was 0.06459 in the laboratory and 0.07327 in the field while the λ was 1.06672 in the laboratory and 1.07603 in the field; cf the r_m. *M. plana* was 0.04783 in the laboratory and 0.06061 in the field while the λ was 1.04899 in the laboratory and 1.06248 in the field. *M. plana* clearly had the potential to be more damaging, requiring 3.5X and 3.0X more oil palm leaf area and biomass for the completion of its larval stages, however, in the field this is perhaps mitigated by its lower reproductive potential compared to *P. pendula* thus balancing the deleterious impact of both species on oil palm.

Keywords bagworms, damage potential, infestations, life history, reproductive potential

Abstrak

Artikel ini memberi butir-butir terperinci yang tepat tentang kitar hidup ulat bungkus *Pteroma pendula (P. pendula)* dan *Metisa plana (M. plana)* dalam kelapa sawit. *P. pendula* telah dipastikan mempunyai empat peringkat larva dengan tiada perbezaan antara jantina dalam bilangan instar dan masa perkembangan pupa. Kitaran hidup *M. plana* adalah mengikut laporan terdahulu di mana 5-6 instar larva bagi jantan dan 6-7 bagi betina. Walau bagaimanapun, tidak terdapat perbezaan di antara saiz dan masa perkembangan pupa. Nisbah jantina bagi kedua-dua spesies ialah 1:1 dan nilai r_m dan λ

adalah representatif. Kedua-dua statistik terakhir ini adalah superior bagi *P. pendula* serta serangga yang membiak di lapangan. Nilai r_m *P. pendula* adalah 0.06459 di makmal dan 0.07327 di lapangan, manakala λ adalah 1.06672 di makmal dan 1.07603 di lapangan; cf nilai r_m *M. plana* adalah 0.04783 di makmal dan 0.06061 di lapangan, manakala λ adalah 1.04899 di makmal dan 1.06248 di lapangan. *M. plana* jelas lebih berpotensi merosakkan, memerlukan 3.5X lebih keluasan permukaan daun dan 3.0X lebih keluasan permukaan daun dan biojisim kelapa sawit masing-masing untuk melengkapkan peringkat larva; begitupun, populasinya di lapangan agak kurang disebabkan oleh potensi pembiakan yang rendah berbanding *P. pendula*, seterusnya mengimbangkan impak kerosakan kedua-dua spesies ini pada pokok kelapa sawit.

Kata kunci ulat bungkus, potensi kerosakan, infestasi, kitar hidup, potensi pembiakan

Introduction

Information about the biology of a pest is an important component in its integrated management. Of the eight species of bagworms associated with oil palm in Malaysia (Sankaran, 1970; Syed and Shah, 1977; Norman *et al*., 1994; Robinson *et al*., 1994), life history information is only available for *Pteroma pendula (P. pendula)* (Krishnan, 1977), *Metisa plana (M. plana)* (Basri and Kevan, 1995; Rhainds *et al*., 1999) and *Mahasena corbetti* (Syed, 1978). However much of this information is incomplete, while there was inconsistent or no information on fecundity and population demography, duration of life stages of both sexes and the sex ratios for these species. Wood (1982) and Basri *et al.*, (1988) indicated that although *P. pendula* infestations were more widespread, it was less damaging than *M. plana*; a study on comparison of their damage potentials would certainly verify their reports. Damage potential was defined by Basri (1993) to be the maximum amount of foliage an unconstrained bagworm larva can eat and use for bag construction.

This paper reports the comparative life histories, demographic statistics and damage potential of the bagworms *P. pendula* and *M. plana*.

Materials and Methods

Comparative life histories

At the hatch of a new generation of a single species infestation of *P. pendula* or *M. plana* in a five-year old oil palm of Dusun Durian Estate, Golden Hope Plantation Berhad, 20 larvae in synchronous life stage were sampled randomly every two days from the same infestation source. There was no insecticide intervention in these infestations. Larvae were removed from their bags for measurement of head capsule width, bag and body length and weight. Thereafter the samples were destroyed. The change in head capsule width and occasional recovery of discarded head capsule sill stuck to or within the bag indicated change in instar, the measurement of discarded head capsule width or measurement prior to change in width being taken as the head capsule measurement for the previous instar. The bag and body length and weight measurements for each instar period were pooled to provide range and mean of the parameters. For the aforementioned, vernier callipers and a Mettler® AB204 analytical balance were used.

Daily samples of 20 pupae from a synchronous population in the 5-year old oil palm field were dissected to ascertain duration, bag and body lengths and weight of prepupa, pupa and adult. No laboratory rearing was carried out except for male adults who were kept in a plastic aquarium tank (20 x 50 x 70 cm) and fed with drops of 10% honey until death. The duration of overall developmental period was recorded.

Ratio of growth of head capsule widths between two consecutive instars was calculated. The relationship between instar and log (head capsule width+1) was established by linear regression. Significance between means of egg-to-adult and egg-to-egg for laboratory and field samples for *P. pendula* were determined by t-test at *p*=0.05, while for *M. plana* the 1-way ANOVA at *p*=0.05 was used with LSD test multiple comparisons of means (Statistica® Version 5.0).

Laboratory and field population demography

Laboratory demography Colonies of *P. pendula* and *M. plana* were established in the laboratory with initial field collected five gravid females each kept in a 500 ml plastic cup. Upon hatching, five neonates from each female were bred on an oil palm leaflet per cup with the offsprings of each female being kept separately. Leaflets were changed twice weekly, the insects being observed daily. At each larval instar change as judged by bag length, cessation of feeding and discarding of head capsule, numbers of survivors were recorded for each colony. Similar recordings of duration of female prepupae, pupae and adults were made based on bag morphology and behaviour. The emergence of adult female is characterized by intermittent protrusion of the head from the anterior opening of the bag. Duration of prepupal, pupal stages and male moth life span were recorded. The moths were fed with drops of 10% honey and their survivorship was recorded.

Field demography Hatches from five gravid females of each bagworm species were placed separately in a nylon organza sleeve cage measuring 91 cm diameter x 122 cm long at frond of 17 situated midway between lower frond and the shoot of a 5-year old oil palm cleared of bagworms in a field infested with a similar and synchronous bagworm species. Maximum enclosure of the insects within the sleeve throughout its life cycle was to exclude and thus minimize interference by parasitoids. For each species five hatched larvae from each female were observed twice weekly. The larvae were transferred using a soft brush to the immediate succeeding frond when more than 25% of leaflets were scraped or holed. When pupation occurred, observations were made daily to record duration of pupal stage, adult emergence, calling, mating and egg-laying. When a female was calling, i.e. intermittent protrusion of the head out of the posterior opening of the bag accompanied by the release of sex pheromone, the sleeve was then removed to allow mating with males from the infested field. The sleeve was replaced after all females on the frond had mated as indicated by the sealed posterior opening of the bag, and time to oviposition and fecundity of each female were recorded.

Time of oviposition was ascertained by feeling the posterior part of the bag, eggs being often laid when the bag felt hard and filled. This was confirmed by making a small slit at the back of the bag. When confirmed, the bag was dissected to count the number of eggs present. Data from egg-to-adult and egg-to-egg were recorded to determine generation time and to calculate sex ratio of offspring. The chi-square test from the non-parametric statistics module of Statistica® Version 5.0 was used to test for confirmation to a 1:1 sex ratio. Data were pooled to calculate survivorship of females and males and demographic statistics including net reproductive rate (R_o), mean generation time (T), doubling time (DT), capacity of increase (r_c), intrinsic rate of population increase (r_m) and finite rate of population increase (λ). Calculations followed that described by Birch (1948) and Laughlin (1965); calculations were made with the Microsoft Office Excel 2000. For comparison, a rough estimate of R_o from direct observation was made by dividing the number of female adults in generation t+1 by that in generation 1.

Damage potential

Damage potential of *P. pendula* and *M. plana* in oil palm was estimated following the method of Basri (1993), albeit with slight modifications; areas of leaflets scraped and cut were measured and then translated into biomass removed. One hundred neonate *P. pendula* and *M. plana* were reared individually on leaflet segments in the laboratory. Leaflets were changed twice weekly. At each change, scraped spots were cut out and their area were traced on mm square paper and estimated to the nearest mm^2. At the same time, a similar area of each scraped spot was traced on an undamaged control leaflet taken from the same frond and position as that of the treatment. This tracing was cut out, and dried at 65˚C for 48 h together with the scraped cut-out. The difference in dry weight represented the weight (mg) of biomass removed by the scraping incident. Mean leaf area and biomass removed by each larval stage was calculated, while cumulative data for the 100 larvae over all instar stages were also obtained.

Results

Comparative life histories

Chi-square tests showed all sex ratios of *P. pendula* did not differ significantly from a 1:1 ratio (Table 1). From these same colonies mean egg-to-adult and egg-to-egg generation time in the laboratory and field were obtained (Table 2). Mean egg-to-adult generation time for males and females were 50.8 and 49.6 days laboratory compared with 47.0 and 45.2 days field. Means were not significantly different for sexes for each environment but were so for each sex between environments. Generation time was shorter in the field. The same trend was seen for egg-to-egg generation time, mean of 49.8 days in the field being significantly shorter than 57.4 days in the laboratory.

As with *P. pendula*, chi-square tests showed sex ratio of *M. plana* to not differ significantly from 1:1 (Table 1). Mean egg-to-adult generation time for the different sexes were 60.0 days (five instars) and 69.0 days (six instars) for males and 73.6 days (six instars) and 82.6 days (seven instars) for females in the laboratory; males 59.8 days (five instars) and 66.6 days (six instars) and females 62.2 days (six instars) and 69.8 days (seven instars) in the field (Table 3). Values were significantly different between life stages in each environment. For each life stage, except for male larvae with a maximum of five instars

Table 1 Sex ratio of *P. pendula* and *M. plana* colonies bred in the laboratory and field.

Colony	Laboratory				Field			
	female: male	x^2	df	p	female: male	x^2	df	p
P. pendula								
1	1:1.15	0.352	1	0.553	1:1.18	0.243	1	0.622
2	1:1.12	0.111	1	0.739	1:1.06	0.625	1	0.803
3	1:1.04	0.021	1	0.884	1:1.13	0.184	1	0.668
4	1:1.17	0.307	1	0.579	1:1.24	0.532	1	0.466
5	1:1.10	0.091	1	0.763	1:1.13	0.176	1	0.674
M. plana								
1	1:0.96	0.021	1	0.884	1:0.93	0.034	1	0.853
2	1:0.94	0.032	1	0.857	1:0.73	0.615	1	0.433
3	1:0.90	0.105	1	0.746	1:0.88	0.133	1	0.715
4	1:175	0.000	1	0.317	1:0.93	0.037	1	0.847
5	1:1.63	0.385	1	0.239	1:0.91	0.037	1	0.847

Ho: sex ratio is 1:1

Table 2 Mean egg-to-adult and egg-to-egg generation time (days) of *P. pendula* in the laboratory and field.

Colony	Laboratory		Field	
	Range	Mean±S.E.	Range	Mean±S.E.
Egg-to-adult				
Male	47-53	50.8 ± 1.1 a i	45-49	47.0 ± 0.8 b i
Female	46-52	49.6 ± 1.2 a I	43-48	45.2 ± 1.0 b i
Egg-to-adult				
Male+Female	56-58	57.4 ± 0.4 a	48-51	49.8 ± 0.7 b

Means within columns and rows followed by the same letter and Roman numeral respectively are not significantly different at *p*=0.05 based on t-test.

where mean generation time was not significantly different between the laboratory and the field, significantly longer generation time was recorded in the laboratory. Mean egg-to-egg generation time was significantly longer at 91.2 days in the laboratory compared with 75.0 days in the field.

Table 3 Mean egg-to-adult and egg-to-egg generation time (days) of *M. plana* in the laboratory and field.

Colony	Maximum instars	Laboratory		Field	
		Range	Mean±S.E.	Range	Mean±S.E.
Egg-to-adult					
Male	5	58-62	60.0 ± 0.8 a i	59-61	59.8 ± 0.4 a i
Male	6	67-70	69.0 ± 0.7 a ii	65-68	66.6 ± 0.6 b ii
Female	6	70-76	73.6 ± 1.2 a ii	60-64	62.2 ± 0.8 b iii
Female	7	80-85	82.6 ± 0.9 a iv	68-71	69.8 ± 0.7 b iv
Egg-to-adult					
Male+Female	7	87-93	91.2 ± 1.2 a	73-77	75.0 ± 0.8 b

Means within columns and rows followed by the same letter and Roman numeral respectively are not significantly different at p=0.05 based on 1-way ANOVA and LSD (column) and t-test (rows).

Population demography

Egg-to-egg survivorship curves of *P. pendula* bred in the laboratory and the field are as in Figure 1 and that of *M. plana* in Figure 2. Curves in both environments were generally similar except that generation in the field was completed earlier than that in the laboratory; *P. pendula* being 51 days in the field compared with 57 days in the laboratory, while 76 days in the field compared with 92 days in the laboratory for *M. plana*. The curves followed Holling's between Type I and II patterns where mortality was initially gradual and then abruptly heavy on older individuals for *P. pendula* and less abruptly for *M. plana*. NM_{50} values for both species were similar with *P. pendula* being 48 and 52 days for the field and laboratory population while 44 and 52 days for *M. plana*, respectively.

Adult females' mortality for *P. pendula* occurred during the last three days of their life span (Figure 3). This coincide with rate of egg production, all eggs being laid within these last three days with maximum numbers during the last two. The female generation took 58 day to complete in the laboratory compared with 51 days in the field. For *M. plana* adult females (Figure 4), survivorship showed a double plateau pattern, decreases corresponding with two periods of egg laying that arose from the differential in times of pupation of females, hence those with a maximum of six larval instars laid eggs earlier than those with seven larval instars. In the laboratory, the first batch of eggs was laid over 82-85 days and the second over 91-93 days with the bulk being laid during the latter period. In the field, the first batch of eggs were laid over 68-70 fays and the second over 74-77 days. Overall, *M. plana* female generation took 93 days to complete in the laboratory compared with 77 days in the field.

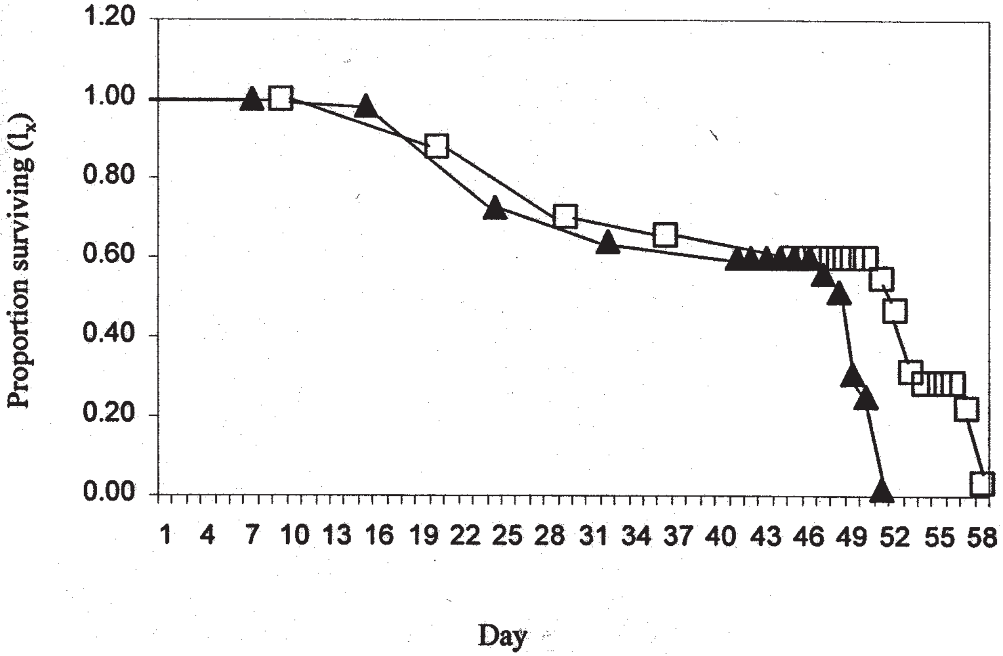


Figure 1 Overall egg-to-egg survivorship of male and female *P. pendula* reared in the laboratory (□) and field (▲)

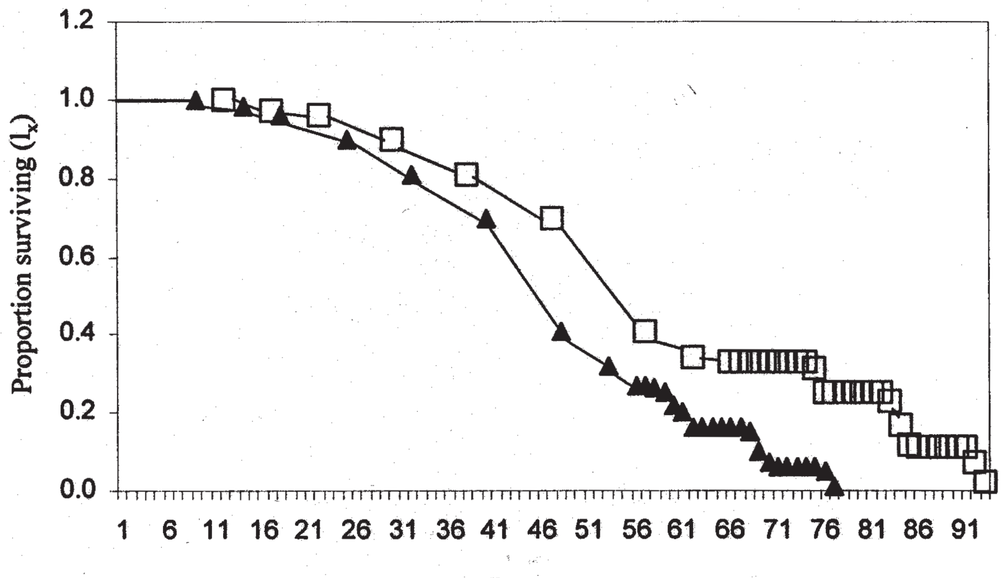
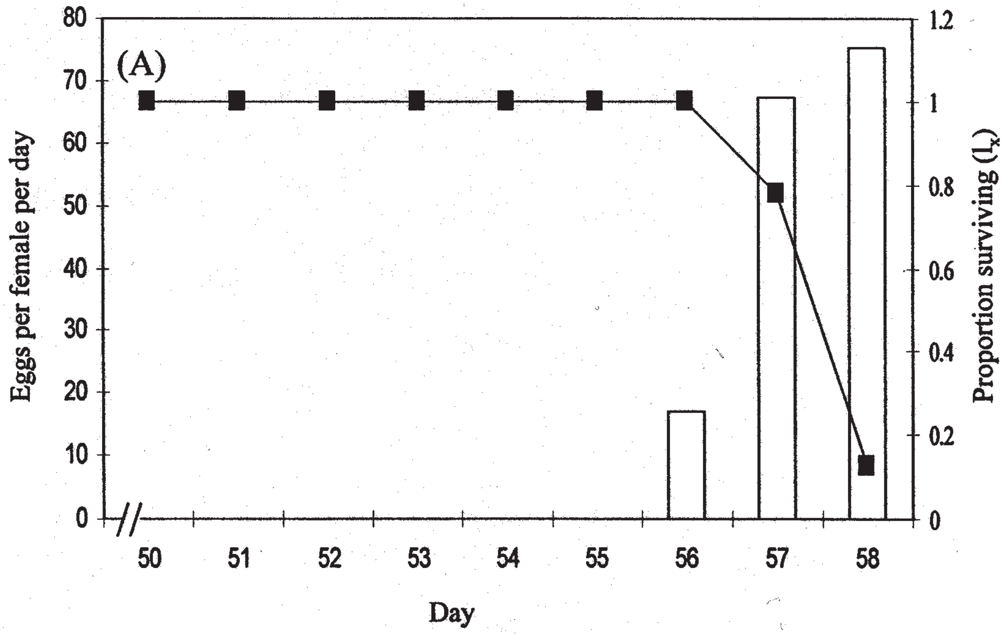


Figure 2 Overall egg-to-egg survivorship of male and female *M. plana* reared in the laboratory (□) and field (▲)



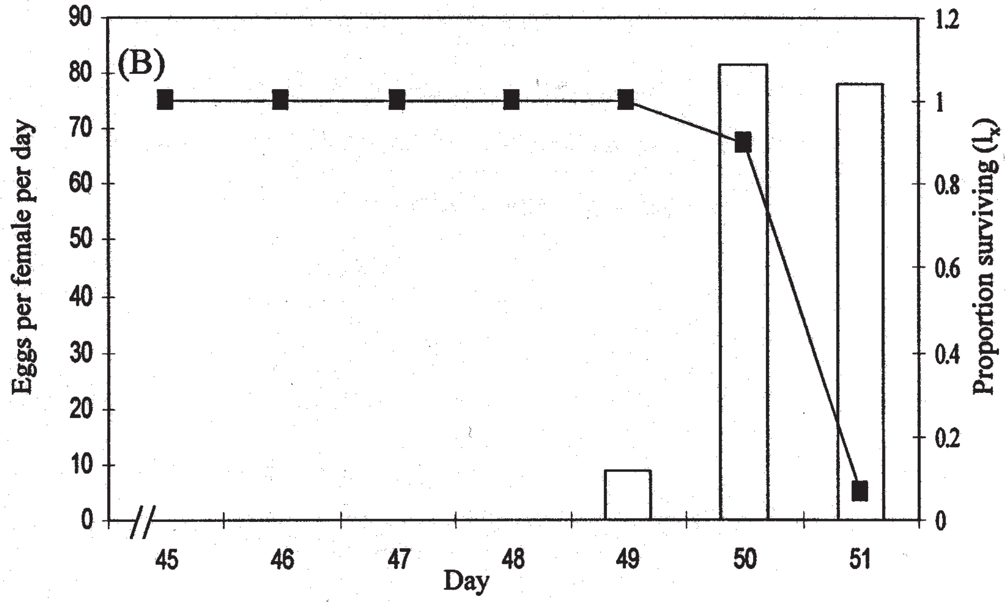


Figure 3 Egg production (□) and survivorship (■) of adult female *P. pendula* reared in the laboratory (A) and field (B)

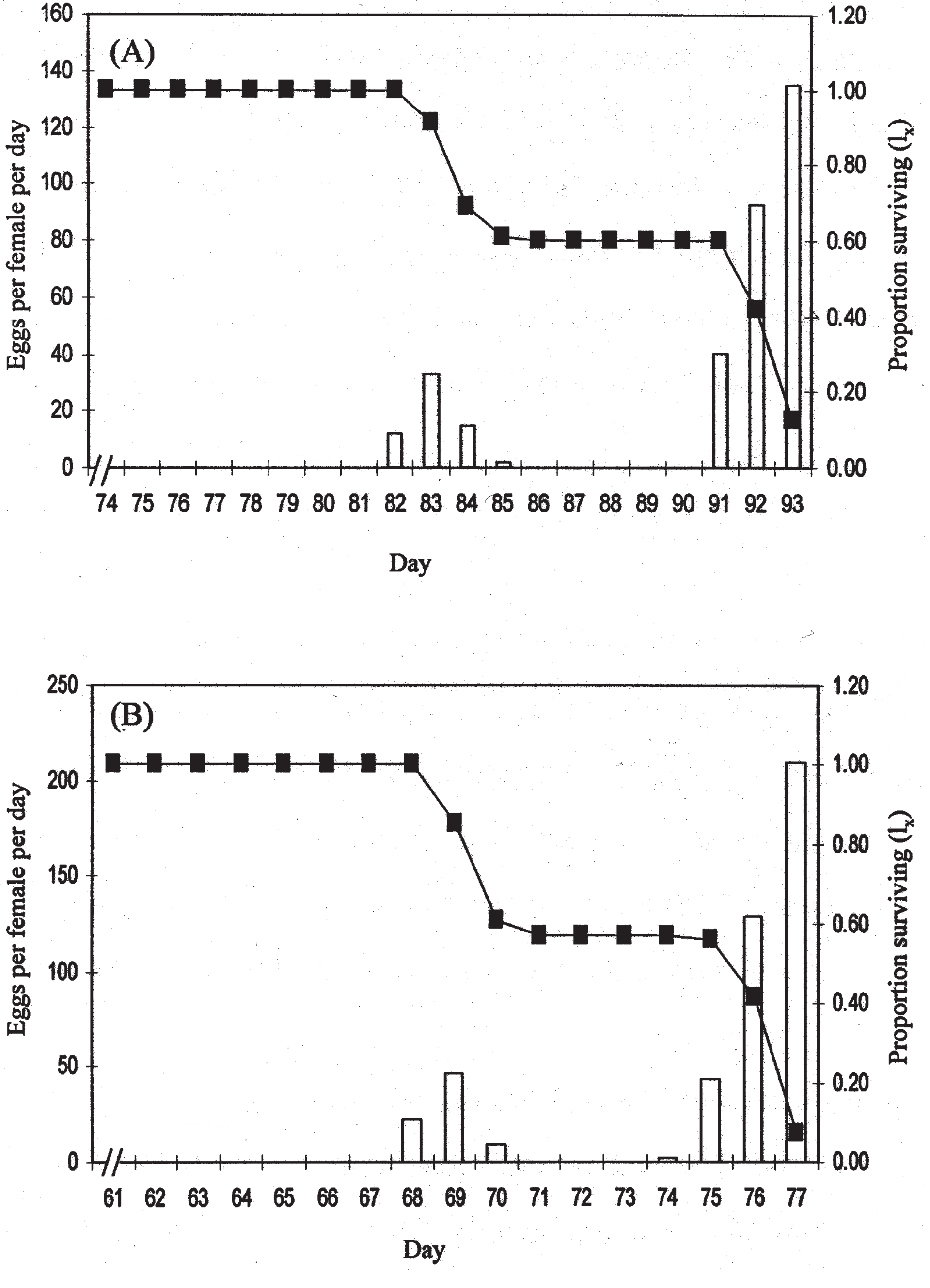


Figure 4 Egg production (□) and survivorship (■) of adult female *M. plana* reared in the laboratory (A) and field (B)

Table 4 Demographic Statistic of *P. pendula* and *M. plana* bred in the laboratory and field.

Statistic	*P. pendula*		*M. plana*	
	Laboratory	Field	Laboratory	Field
Rough R_o	23.6	23.4	20.6	16.4
Observed T (days)	58.0	51.0	93.0	16.4
r_c	0.05450	0.06182	0.03253	0.03633
Calculated				
R_o	39.0	39.0	67.0	81.0
T (days)	56.91	50.07	88.35	72.92
DT (days)	10.73	9.46	14.57	11.50
r_c	0.06458	0.07327	0.04757	0.06028
r_m	0.06459	0.07327	0.04783	0.06061
λ	1.06672	1.07603	1.04899	1.06248

$$\text{Rough } R_o = \frac{\text{no. of female adult is generation } t+1}{\text{no. of female adults in generation } t}$$

$$r_c = [\log_e(R_o)]/T$$

$$R_o = \sum l_x m_x$$

$$T = \sum x l_x m_x / R_o$$

$$DT = (\log_e 2)/r_c$$

$$r_m = \text{obtained through iterative balancing } \sum e^{-r_m x} l_x m_x = 1$$

$$\lambda = e^{r_m}$$

For *P. pendula*, all values were generally the same for both laboratory and field estimation for R_o, T, DT, but r_c, r_m and λ were superior for field population (Table 4). Calculated T was shorter than the observed (56.91 days laboratory and 50.07 days field calculated cf. 58.0 days laboratory and 51.0 days field observed). This corresponded with a high r_c of 0.06458 laboratory and 0.07327 field derived from calculated R_o and T cf. 0.05450 laboratory and 0.06182 field derived from rough R_o and observed T. The r_m and λ from actual adult female survivorship and fecundity were 0.06459 laboratory, 0.07327 field and 1.06672 laboratory and 1.07603 field respectively. In the is case of *M. plana*, except for the rough R_o, all other demographic statistics were superior for the field population. Calculated T was also shorter than the observed (88.35 days laboratory and 72.92 days field calculated cf. 93.0 days laboratory and 77.0 days field observed). This corresponded with a high r_c of 0.04757 laboratory and 0.06028 field derived from calculated R_o and T compared with 0.03253 laboratory and 0.03633 field derived from rough R_o and observed T, while r_m and λ from actual adult female survivorship and fecundity were 0.04783 laboratory, 0.06061 field and 1.04899 laboratory and 1.06248 field respectively. These values were lower than those of *P. pendula*.

Damage potential

Scraping was the predominant mode of damage to oil palm leaflets by *P. pendula* and *M. plana*. For *P. pendula* the mean area scraped per larva for L1 to L4 were 12.85, 32.40, 81.15 and 57.74 mm^2 respectively compared with 2.22, 11.33, 2.0 and 0.0 mm^2 cut leaves, respectively. Highest losses to scrapping occurred at L3, and L2 for cutting, while total leaf area loss was greatest at L3 (Table 5). Similarly with *M. plana*, scraping activity for L1 to L7 were 16.44, 88.45, 100.64, 104.75, 112.80, 102.61 and 77.71 mm^2 respectively compared with 6.63, 12.50, 11.67, 16.77, 15.40, 14.87 and 31.24 mm^2 cut leaves, respectively. Leaf damage was the least during L1, increased at L2 and remained relatively consistent at L3 to L7 (Table 6). Losses in terms of leaf biomass removed followed a similar trend for both species (Table 5, 6).

Table 5 Mean (± S.E.) leaf area (mm^2) damaged and mean leaf biomass (mg dry weight) removed by a single *P. pendula* at various instars.

Instar	Scraped Leaf			Cut Leaf			Total		
	n	area	biomas	n	area	biomas	n	area	biomas
I	100	12.85 ± 0.44	0.93 ± 0.05	18	2.22 ± 0.28	0.39 ± 0.15	100	13.25± 0.44	1.0 ± 0.08
II	93	32.40 ± 1.43	2.25 ± 0.1	3	11.33 ± 7.79	1.03 ± 0.72	93	32.76 ± 1.49	2.28 ± 0.1
III	73	81.15 ± 8.11	5.72 ± 0.57	1	2.0 ± 0.0	0.20 ± 0.0	73	81.18 ± 8.11	5.72 ± 0.57
IV	54	57.74 ± 3.34	4.04± 0.23	0	0.0	0.0	54	57.74 ± 3.34	4.04 ± 0.23

Table 6 Mean (± S.E.) leaf area (mm^2) damaged and mean leaf biomass (mg dry weight) removed by a single *M. plana* at various instars.

Instar	Scraped Leaf			Cut Leaf			Total		
	n	area	biomas	n	area	biomas	n	area	biomas
I	100	16.44 ± 0.83	1.49 ± 0.08	30	6.63 ±0.91	0.65 ±0.08	100	18.43 ±0.89	1.69 ± 0.08
II	93	88.45 ± 5.54	5.58 ± 0.4	30	12.50 ±1.68	1.13 ±0.19	93	92.48 ± 5.76	5.94 ± 0.1
III	90	100.64 ±8.11	7.07± 0.39	66	11.67 ± 1.26	1.06± 0.11	90	108.0 ± 5.22	7.77 ± 0.57
IV	80	104.75 ± 3.34	7.37 ± 0.37	64	16.77 ± 1.71	1.61± 0.18	80	118.16 ± 4.86	8.65 ± 0.23

Table 6 *(cont'd)*

V	70	112.80 ± 3.80	7.01 ± 0.22	55	15.40 ± 1.36	1.69 ± 0.25	70	124.90 ± 3.98	7.34 ± 0.21
VI	49	102.61 ± 3.58	7.14± 0.24	30	14.87 ± 3.60	1.50 ± 0.32	49	109.48 ± 3.80	7.90 ± 0.27
VII	21	77.71 ± 3.76	5.48 ± 0.25	21	31.24 ± 3.65	3.31 ± 0.38	21	108.95 ± 3.0	8.80 ± 0.29

Cumulative leaf area damage by 100 larvae over all instars were for *P. pendula* 0.76 cm^2 cut, 132.92 cm^2 scraped and 133.68 cm^2 total scraped and cut (Figure 5A). This are compared with 43.66 cm^2 cut, 418.64 cm^2 scraped and 462.30 cm^2 scraped and cut for *M. plana* (Figure 5B). A similar trend was recorded in terms of biomass removed, *P. pendula* 0.010 g cut, 0.934 g scraped and 0.944 g scraped and cut compared with *M. plana* 0.435 g cut, 2.359 g scraped and 2.794 g scraped and cut.

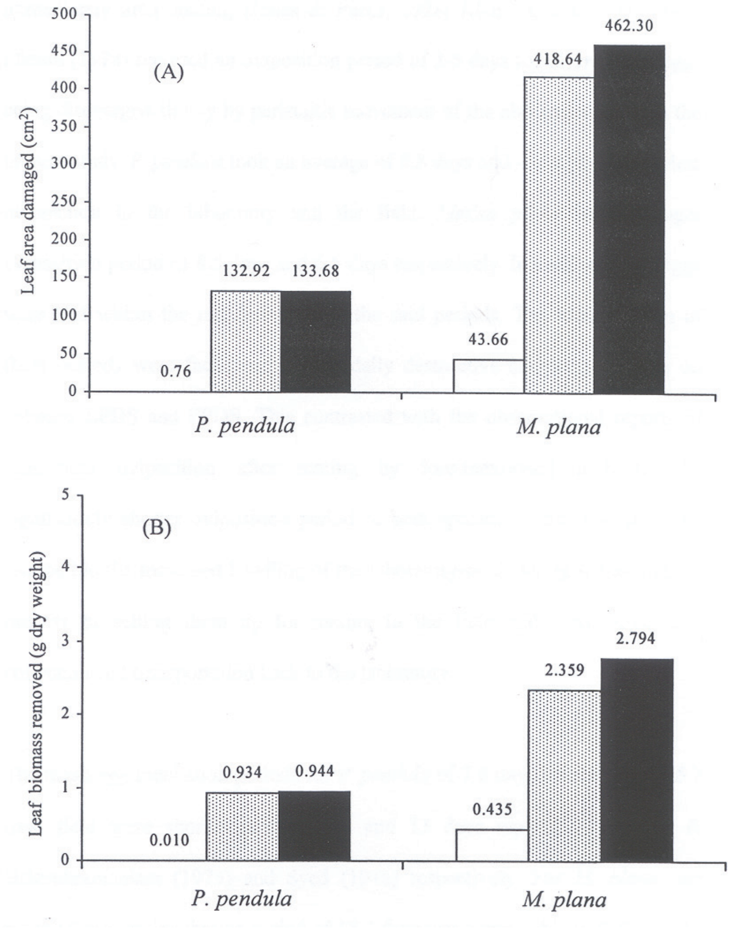


Figure 5 Potential damage (A) cumulative leaf area (cm^2) and (B) cumulative biomass removal (g) by 100 *P. pendula* and *M. plana* larvae over all instar stages. Cut □ scraped ▨ and total ■

Discussion

Sex ratio of bagworms have been recorded to be male biased, being 2.3:1 for *Hyalarcta huebneri* (Westwood) (Heather, 1975), 8:1 for *Eumeta crameri* (Ameen and Sultana, 1977), 2.2:1 for *Pteroma plagiophleps* (Howlader, 1990), 8.5:1 for *M. plana* (Basri and Kevan, 1995), the same as 1:1 for *Thyridopteryx ephemeraeformis* (Kaufmann, 1968), and female biased as 0.6:1 and 0.9:1 for *M. plana* (Basri, 1993). The contrasting results for *M. plana* arose from male biased being recorded in a destructively sampled colony (Basri and Keven, 1995) while female bias occurred in non-destructively sampled ones (Basri, 1993) whereby chi-square test was not performed. In the current report where non-destructive sampling was practised, a 1:1 ratio was consistently recorded through chi-square test in all colonies of *P. pendula* and *M. plana*; their similarity to ratios in likewise sampled colonies in the work of Basri (1993).

Both the laboratory and field populations of *P. pendula* were seen to be synchronous. Noteworthy was the almost simultaneous emergence of males and females in a generation, verifying the lack of sexual difference in generation time. This would also suggest a high probability of sib-mating, hence high mating success of the species albeit with high genetic relatedness. Duration of life cycle corresponded that of Syed (1978); however, egg-to-adult and egg-to-egg generation time was significantly shorter in the field. The fluctuating field temperatures as opposed to more constant laboratory ones were surmised to be the major contributor to a faster development times as have been recorded in other insects (Foley, 1981; Taylor and Shields, 1990).

Females were observed to emerge significantly later than males in the laboratory but there was overlapping of ranges in the field. Female bagworms have been reported to pupate preferentially on higher strata of host trees (Gross and Fritz, 1982; Cox and Potter, 1988; Cronin and Gill, 1989). However, the reported tendency of females emerging before males was possibly due to sampling of only one high frond per palm which was not to fully represent the bagworm population (Rhainds *et al.*, 1999). Syed (1978) suggested that overlapping generations occurred for *M. plana* to increase in abundance due to the large difference in larval developmental time between males and females, but this was disputed by Basri and Kevan (1995) who reported that mating of individuals from the same generation could occur. This study showed that although male and female emergence did not overlap in the laboratory, the difference in development time was big, and more importantly, ranges of male and female development time overlapped in the field, suggesting that mating of individuals of the same generation to generally apply. The lack of total synchrony of male and female emergence with a tendency towards protandry could be a mechanism for reducing genetic relatedness (Wiklund and Fagerstrom, 1977). Duration of life cycle of *M. plana* was about 1.5 times that of *P. pendula*. This is perhaps the reason for asynchronous infestations in mixed infestations of the pests.

In both *P. pendula* and *M. plana*, a superior reproductive potentials, r_m and hence λ were recorded in field colonies. With the shorter developmental time, the field insects could have a marked influence on the magnitude of r_m (Lewontin, 1965). The higher reproductive potential (r_m) of *P. pendula* compared with *M. plana* in both the laboratory and field helps explain its status as the predominant pest in oil palm.

Basri (1993) reported feeding behaviour of *M. plana* to change from scraping to cutting after L5, with L7 removing the greatest amount of tissue. In contrast, the present study showed scraping to be the predominant mode of damage by both *P. pendula* and *M. plana*. Leaf area and biomass loss was greatest in the later instars in *P. pendula* but remained relatively constant in L3 to L7 for *M. plana*. Assessment of damage potential showed *M. plana* clearly had the potential to be more damaging, but was perhaps mitigated by its lower reproductive potential than *P. pendula*, thus balancing the deleterious impact of both species on oil palm.

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