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Long-term Dynamics of Phytophagous Lady Beetle Populations under Different Climate Conditions in Sumatra and Java, Indonesia

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ABSTRACT Since 1990 we have studied population dynamics of the phytophagous lady beetles, *Epilachna vigintioctopunctata*, *E. enneasticta* and *Epilachna* sp. 3 (aff. *emarginata*), (Coleoptera: Epilachninae) in Padang, Sukarami (West Sumatra), Bogor (West Java) and Purwodadi (East Java), Indonesia. These sites have distinctly different climate conditions, e.g. Padang has a typical tropical rainforest climate without a clear alternation of wet and dry seasons, while Purwodadi has a strong dry season of 6-7 months. We have conducted censuses at 3-7 day intervals, including mark-recapture of beetles and construction of life tables for up to 9 consecutive years in order to clarify the seasonal change in abundance and mortality of the populations. In most populations the adult number changed greatly with the formation of high peaks from time to time at intervals of 6-12 months. Their increase or decrease was gradual, progressing over 3-5 months. Even under conditions with sufficient amount of rainfall in Padang, Sukarami and Bogor, oviposition intensity, number of the following immature stages and, as a result, adult emergence frequently showed discrete peaks at a fixed interval. These "generation cycles" were especially clear during the phase of population increase. There was no simple relationship between the seasonal change in rainfall and that of the beetle populations. We also discussed the impacts of the strong droughts in 1994 and 1997-1998 caused by El Niño, and the degree of synchronization in the trends of the populations among the adjacent study sites.

Key words: *Epilachna* / population dynamics / Java / Sumatra / El Niño

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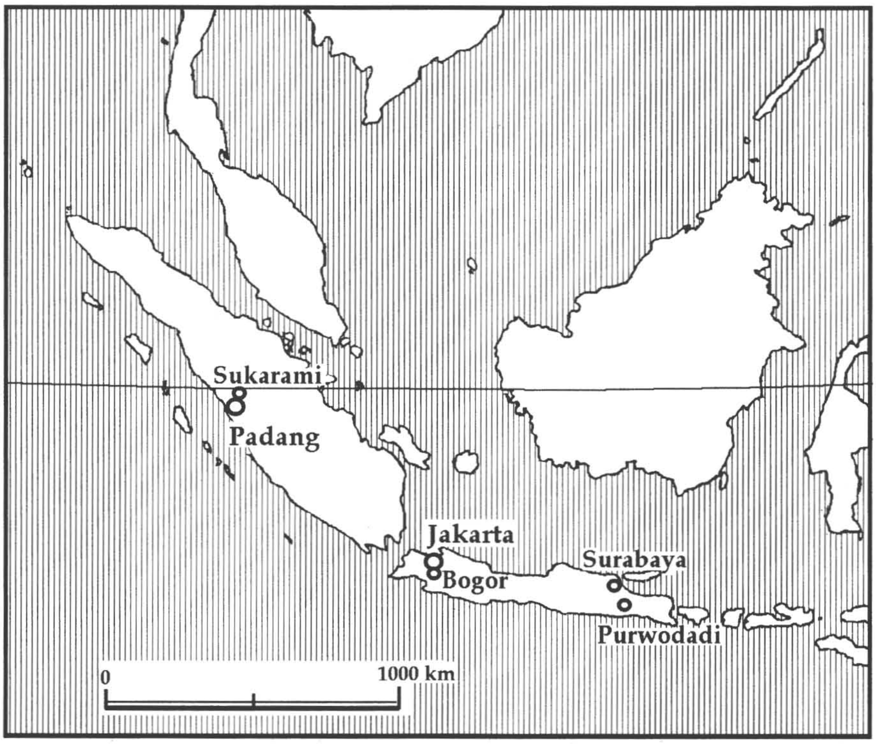

Fig. 1. Locations of the study sites, Padang, Sukarami (West Sumatra), Bogor (West Java) and Purwodadi (East Java).

In previous articles (Nakamura *et al.*, 1990; Inoue *et al.*, 1993) we reported the seasonal abundance and mortality in a population of the phytophagous lady beetle *Epilachna vigintioctopunctata* feeding on the weed *Solanum torvum* for 3 years in Padang, West Sumatra (Fig. 1). The current study aimed to overcome 2 major limitations in the studies of seasonal cycles of tropical insects: (1) most long-term data have been concentrated in the highly seasonal tropics which have a distinct alternation of wet and dry seasons. Little research have been done in humid tropics that lack clear seasonal cycles; (2) most studies used indirect methods such as light traps, pitfall traps and sweeping. These methods can collect a large number of samples of various species simultaneously and are suitable for analyses at the community or guild level; however, changes in abundance of particular species usually cannot be analyzed in detail (Nakamura *et al.*, 1990; Inoue *et al*, 1993 and literature cited therein). Therefore, we carried out the study in Padang, one of the most non-seasonal tropical areas on the earth, and used direct and intensive methods, i.e. mark-recapture of adults and construction of life tables for immature stages of the field populations. Laboratory rearings were done to analyze survivorship and reproductive schedules. Fig. 2 summarizes the results of this study: (1) adult abundance fluctuated at a magnitude of 290 and exhibited 3 major peaks during the 3 years. Their increase or decrease was gradual, progressing over 3-5 months (corresponding to 3-4 generations); (2) population increase was suppressed in months of normal rainfall (>300 mm) but reached to its highest peak during the 1982-1983 El Niño when rainfall dropped to 50% of the long-term average; (3) at this high peak, the population reached a density at which food shortage due to defoliation occurred; (4) oviposition

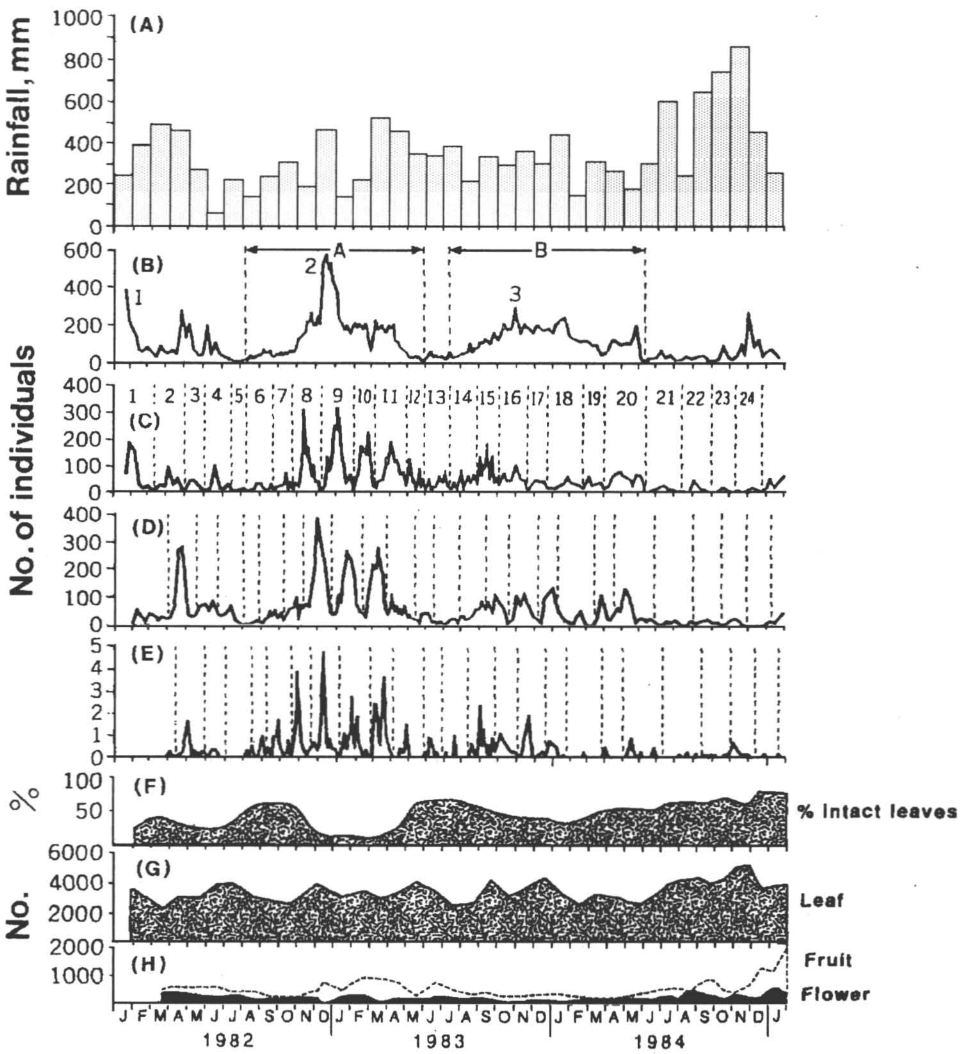

Fig. 2. Seasonal fluctuation in total amount of rainfall per month (A) , the number of *E. vigintioctopunctata* in successive developmental stages (B-E) and the condition of the host plant *S. torvum* (F-H) in Padang, West Sumatra. Number of individuals in each stage is expressed as follows: (B) adults, number estimated by the Jolly-Seber formula ($\hat{N}_i$). 1 - 3, successive peaks; A, B, 2 completely followed cycles; (C) eggs, number laid per day. Numeral indicates *i*th generation; (D) 4th instar larvae, number directly counted; (E) new adults, number of pupal exuviae collected per day; (F) percentage of intact leaves; (G) total number of leaves, number of flowers and fruits of *S. torvum*. Adapted from Nakamura *et al.* (1990).

intensity increased at an interval of 48 days, showing discrete peaks. This discreteness continued during the following immature stages and, as a result, adult emergence was also discrete. The discrete generations or "generation cycles" (Knell, 1998) occurred for most of the study period, although it was sometimes difficult to distinguish generations, particularly at low density. We have not yet been able to explain why generations were discrete. This is an interesting phenomenon because the Leslie matrix tells us that, under stable conditions, proportions of developmental stages soon reach a stable, overlapping distribution.

Indonesia has extremely diverse environments, so that the results obtained in one location cannot be applied to others with different environmental conditions. Recently "abnormal" deviations of climate have been reported from various regions of the world. In Indonesia, El Niño brings drier seasons and has occurred at an average interval of 4-5 years, but its periodicity and intensity have greatly changed from time to time (Inoue & Nakamura, 1990; Inoue *et al.*, 1993 and literature cited). In recent decades, the impact of severe droughts associated with the 1982-1983 (Leighton & Wirawan, 1986) and 1997-1998 El Niños were extremely strong (Nakagawa *et al.*, 2000). We need long-term studies of population dynamics to cover whole episodes of environmental changes in order to understand their impact. Only such long-term studies can detect influences of rare disturbances on animal populations and the adaptive traits associated with them. The responses of insects to environmental change may be different in various taxa due to different adaptive traits.

Since 1990 we have extended our research in space, time, and study materials. First, we have established many study sites with distinctly different climate conditions and elevations. For example, Padang (West Sumatra) has a predominantly non-seasonal tropical climate with an annual rainfall of 5000 mm, while, Purwodadi (East Java) has an annual rainfall of about 2000 mm with 6-7 months of a strong dry season. Second, we have been conducting routine censuses of some epilachnine and other insect populations for more than 9 years. Third, the study materials include not only the phytophagous ladybird beetles *Epilachna* (Coleoptera: Coccinellidae: Epilachninae), but also the tortoise beetles *Aspidomorpha* (Coleoptera: Chrysomelidae: Cassidinae), and the banana skipper *Erionota thorax* (Lepidoptera: Hesperiidae). Finally, we carried out the censuses simultaneously at more than one site. The aim of the "multi site" study was to determine whether the populations fluctuate synchronously or independently. The previous study could not answer this question because it was conducted in only one small patch (Nakamura *et al*, 1990; Inoue *et al.*, 1993).

Since the early 1980's we have studied several *Epilachna* species at various localities in Sumatra and Java (Table 1). The present article will document an outline of seasonal abundance of adult populations of the epilachnine beetles which have been studied since 1988. Our questions were: (1) How large is the amplitude of the fluctuation ? (2) How are peaks of adult numbers formed ? (3) Do discrete generations occur or not ? (4) How does the rainfall change, especially strong droughts due to El Niño, affected the host plants and populations. (5) How frequently does food depletion occur ? (6) Do adjacent populations fluctuate independently or synchronously? We will present the detailed analyses of adult populations and immature stages elsewhere.

MATERIALS AND METHODS

Study species

Basic information on 3 study species are summarized below from reviews of the epilachnine beetles in Sumatra and Java done by Katakura *et al.* (1988, 2001).

Epilachna vigintioctopunctata (Fabricius) (henceforth abbreviated as EV) : This species is one of the most common and widespread epilachnines in Southeast Asia (Richards, 1983), and is found on

Table 1. List of *Epilachna* populations studied on population dynamics in Indonesia. *Populations whose long-term fluctuations in adult population size are mentioned in the present article.

Species	Location			Food plant (Faimly)	Study period	Reference
	Province	City	District (elavation, m)			
E. vigintioctopunctata	Sumatera Barat (West Sumatra)	Padang	Lubuk Minturun (80)	*Solanum torvum* (Solanaceae)	1980	Nakamura et al., 1988.
		ditto	Ulu Gadut (140)*	ditto	1982-1984	Abbas, 1985; Nakamura et al., 1990; Inoue et al., 1993.
		ditto	8 locations around Padang (40-140)*	ditto	1988-1989	Nakano et al., 1991.
		ditto	Limau Manis (260)*	*Centrosema pubescens* (Leguminosae)	1995-1996	Abbas, 1996; Abbas & Nakamura, 1997.
		Solok	Sukarami (928)*	*Solanum torvum* (Solanaceae)	1991-present	Hasan et al., unpublished.
	Jawa Timur (East Java)	Pasuruan	Purwodadi Botanic Garden (300)*	ditto	1993-1996	Kahono, 1996.
	Jawa Tengah (Central Java)	Wonogiri	Baturetno (120)	ditto	1995-1997	Kahono & Nakamura, unpublished.
	Jawa Barat (West Java)	Bogor	Bogor Botanic Garden (260)*	ditto	1993-present	Kahono, 1999.
		ditto	ditto	*Brugmansia suaveolens* (Solanaceae)	1995-present	ditto
		ditto	ditto	*C. pubescens* (Leguminosae)	1995-present	ditto
E. septima	Sumatera Barat (West Sumatra)	Padang	Lubuk Minturun (80)	*Momordica charantia* (Cucurbitaceae)	1982	Abbas & Nakamura, 1985.
E. sp. 3 (aff. *emarginata*)	Jawa Barat (West Java)	Bogor	Bogor Botanic Garden (260)*	*Mikania micrantha* (Compositae)	1990-present	Nakamura et al., 1992; Kahono & Nakamura, unpublished.

various kinds of crops and weeds belonging to Solanaceae. The most important host plants of this species in Indonesia may be eggplant and the weed, *Solanum torvum* (Solanaceae). In both West Sumatra and Java, this species was common everywhere in the rural areas (Katakura *et al.* 1988, 2001). Recently, we found epilachnine beetles occurring on an herbaceous vine weed, *Centrosema pubescens* (Leguminosae). The beetles on the legume discovered in Padang (West Sumatra) and Bogor (West Java) are smaller in size than EV on solanaceous plants, but otherwise the two are morphologically very similar. Host preferences of legume feeding beetles appeared to be different from *Solanum* feeding beetles (Nishida *et al.*, 1997). The legume beetle is treated here as *E. vigintioctopunctata* (Katakura *et al.*, 2001).

E. enneasticta Mulsant (EN): Like EV, this species is a pest of solanaceous crops and weeds. Distribution is restricted to cooler highlands more than about 400 m above sea level, where it occurs together with EV at much lower density.

Epilachna sp. 3 (aff. *emarginata*, EM): This common species feeds on an herbaceous weed, *Mikania micrantha* (Compositae) in West Java and West Sumatra.

Study populations

General climatic conditions of Indonesia and Sumatra are given in Inoue and Nakamura (1990) and rainfall conditions of Java in Nakamura *et al.* (1994).

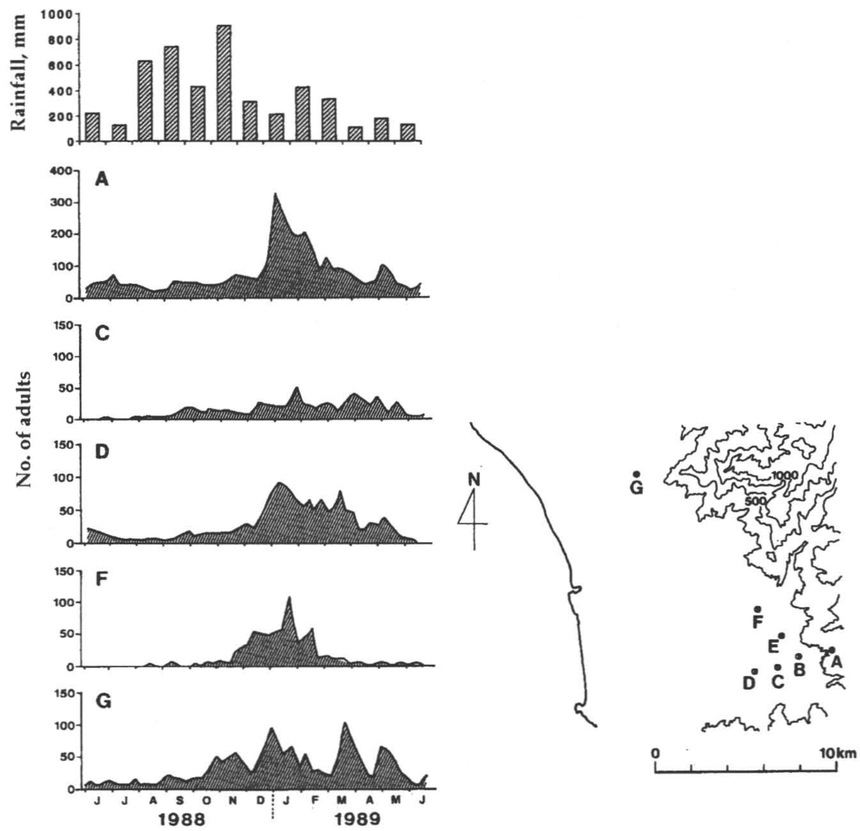

Fig. 3. Seasonal fluctuations in the number of adult *E. vigintioctopunctata* feeding on *S. torvum* in several local populations around Padang, West Sumatra. (Right) locations of populations studied (A-G). (Left) top: seasonal fluctuation in total amount of rainfall per month recorded at Tabing, 4 km southwest of G. A-G: local populations of *E. vigintioctopunctata*. Adapted from Nakano *et al*. (1991 and unpublished).

Padang

Padang lies nearly on the Equator (0°53'S, 100°21'E) and has a predominantly tropical humid-equatorial climate: Mean monthly air temperature fluctuated only between 26.7 (September to December) and 27.5°C (May) and the annual rainfall was 4764 mm without a clear alternation of wet and dry seasons (Ogino, 1984).

EV in multi sites. Seven EV populations feeding on *S. torvum* were chosen within a radius of 10km around Padang with elevations from 40-140 m (Fig. 3). Daily rainfall and EV populations were monitored at each site for 13 months from June 1988 to June 1989. The aim was to learn whether or not the local populations fluctuate synchronously, and how the reproductive and mortality processes differ among the populations.

EV feeding on *Centrosema*. An EV population feeding on *C. pubescens* was studied at the edge of the Limau Manis Campus of Andalas University (260 m altitude) from September, 1995 to December, 1996. A patch of *C. pubescence*, 70 m×1.5-3.0 m, was chosen as the study site on an overgrown piece of ground with short bushes and weed, dominated by *Imperata cylindrica* and *Mimosa* spp.

Sukarami

Sukarami is a highland (928 m altitude) about 40km northeast of Padang and is very wet with drizzling rain almost everyday. The average values over 22 years (1960-1982) were: annual rainfall of 2917 mm, monthly rainfall fluctuated from 145 mm (July) to 340 mm (November) and mean monthly temperature from 20.8 to 21.4°C.

EV and EN. The main study site was established in December, 1991 by planting 10 *S. torvum* seedlings, and an additional 6 were added in January, 1993. Two sub-sites (A and B) were established in January, 1992, each containing 10 seedlings to compare the seasonal trends of EV and EN among the 3 sites. On April, 1996 10 *S. torvum* seedlings were additionally planted in all sites. The main site, site A, and site B are linearly located at about a 900 m interval on a hilly slope on the Experimental Field of Sukarami Rese Assessment arch Institute for Agricultural Technology (BTPT Sukarami).

Bogor

Bogor (6°37'S, 106°32'E, 260 m altitude) is located at the eastern end of the area of tropical rainforest climate in which Padang is center. The average annual rainfall in Bogor was 3850 mm (range = 2000 to 5500 mm) and the cycles of dry and wet seasons are less distinct and more irregular than those of east Java. Compared with Padang, Bogor has less but more seasonal rainfall and severe droughts are more frequent (Nakamura *et al.*, 1994).

EV. In March of 1991 we established study sites U and S, located about 400 m apart, in Bogor Botanic Garden and planted 10 *S. torvum* seedlings in each site. Two other host plants of EV, *Brugmansia suaveolens* (Solanaceae) and *C. pubescens*, were also censused in these sites, but the findings on these plants will be published elsewhere.

EM. The host plant, *Mikania micrantha*, was distributed sporadically, covering fences and vegetation in the Bogor Botanic Garden. We chose 4 clumps in the Garden for this study; their size ranged from 2m-12 m width×1.5 m height. Two of them were in sites U and S. The study began at Orchid and River sites in December, 1990. The latter site was destroyed in mid-1991, and the Orchid site at the end of 1994. The populations in sites S and U were censused from November 1991 and September, 1994 onwards, respectively. Nakamura *et al.* (1992) presented the results from October, 1990 to November, 1991 and Nakamura *et al.* (1995) presented survivorship and fertility schedules of the species under laboratory conditions.

Purwodadi

This study was conducted in Purwodadi Botanic Garden, LIPI, located at 7°47'S, 112°41'E, 300 m altitude, about 70 km south of Surabaya, East Java (Table 1). In general, rainfall in East Java is distinctly seasonal (Inoue and Nakamura, 1990; Nakamura *et al.*, 1994). According to the rainfall record kept by the Purwodadi Botanic Garden for 15 years (1982-1996), the average annual rainfall was 2622.5 mm, ranging from 1836 (1990) to 3776 mm (1995). Monthly rainfall ranged from 0 to

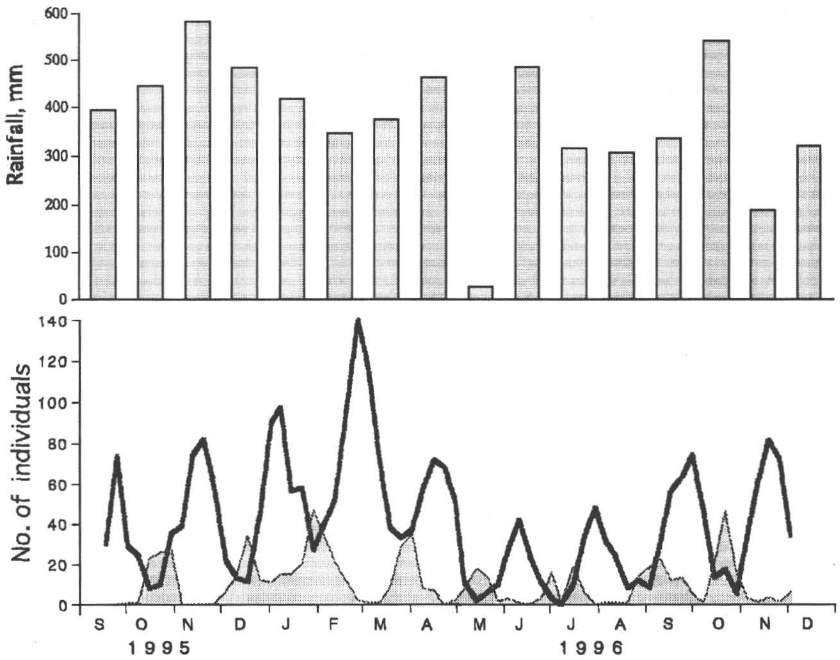

Fig. 4. Seasonal fluctuation in total amount of rainfall per month (top) and in the size of *E. vigintioctopunctata* population feeding on *C. pubescens* (bottom) in Padang, West Sumatra. Bold and thin lines indicate adults and 4th instar larvae, respectively.

1165 mm. Rainfall in Purwodadi is distinctly seasonal: dry months usually last 5 to 7 months from May or June to October or November (Kahono, 1996).

EV. EV was studied in 3 study sites (A, B and C), established in November of 1993 by transplanting 10 seedlings of *S. torvum*. In site A, the host plants were planted on a sunny bank of a small pond (5×12 m), which dried up in mid dry season. Site B was established on the bank of a larger pond (10×30 m) located in the shade of forest trees. During the dry season, the surface area of the pond decreased considerably, but the pond never completely disappeared. Site C was established on a sunny, dry field without a nearby water source. These 3 sites formed a triangle with sides 275 m (A-B), 500 m (A-C) and 440 m (B-C). The growth of the host plants was the greatest in site A, where they flowered regularly at the start of the dry season and produced abundant fruits. In sites B and C, the plant growth, flowering and fruiting were less than in site A, due to the shady (site B) and hot and dry (site C) conditions, respectively.

Census methods

Censuses were carried out at 3 to 7 day intervals. The adult population was censused by mark and recapture methods and population parameters were estimated by the Jolly (1965)-Seber (1973) method. Immatures (egg to pupa) were counted directly with mortality factors recorded to construct life tables. Host plant conditions, e.g. the number of leaves, flowers and the intensity of feeding were

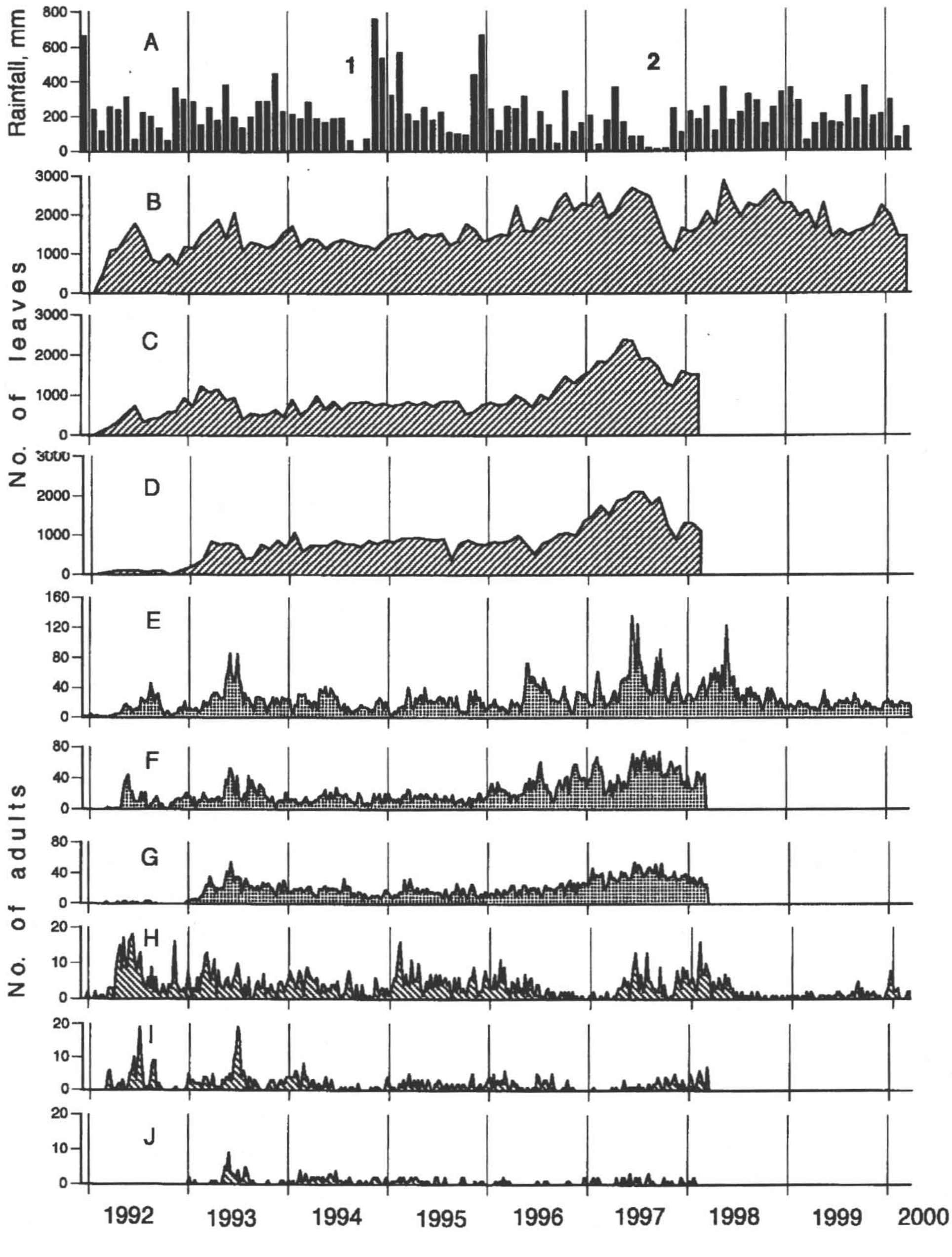

Fig. 5. Seasonal fluctuation in total amount of rainfall per month (A) , total number of *S. torvum* leaves on the main site (B), sites A (C) and B (D), the number of adult *E. vigintioctopunctata* feeding on *S. torvum* on the main site (E), sites A (F) and B (G), and the number of adult *E. enneasticta* on the main site (H), sites A (I) and B (J) in Sukarami, West Sumatra. Numerals in (A) indicate Droughts 1 and 2.

censused monthly. Detailed procedures are described in Nakamura *et al.* (1988, 1990).

RESULTS AND DISCUSSION

Padang

EV in multi sites Fig. 3 (top) shows the changes in monthly rainfall at Tabing, near site G (top) and that in adult number at 5 study sites in and around Padang. At Tabing, annual rainfall was 5240 mm and 3393 in 1988 and 1989, respectively, and monthly rainfall ranged from 126 mm (July, 1988) to 904 mm (November, 1988) during the study period. The general seasonal trends in rainfall were the same at all sites, though the total amount of annual rainfall ranged from 3393 mm to 4626 (Nakano *et al.*, 1991). Fig. 3 (2nd to bottom) indicates that, as a whole, EV populations apppeared to change synchronously. The populations began to increase between October and December, 1988. Peaks were observed from December, 1988 to March, 1989, when the monthly rainfall was less than 400 mm, while during a high rainfall period from August (628 mm) to November (904 mm), 1988, the populations remained low.

***EV feeding on* Centrosema** Fig. 4 (top) shows that during the 15 months (September, 1995-December, 1996), monthly rainfall was more than 300 mm except for May and November (26.6 mm and185.5 mm, respectively). That of April 1996 was 461.2 mm and it dropped suddenly to 26.6 mm in May (this extreme value may seem doubtful, but the rainfall in Sukarami also dropped suddenly in the same period, Fig. 5A), and then recovered to 483.9 mm in June. The number of adults and 4th instar larvae fluctuated with distinct peaks and valleys at almost fixed intervals (Fig. 4, bottom). We found only a few egg masses and the number of 4th instar larvae probably greatly underestimated, because the creeping weed tangled with other weeds and shrubs in a complicated manner. The intervals of the peaks of adults and 4th instar larvae averaged 52.6 days (SD, 5.2; range, 49-63) and 51.1 (SD, 9.9; range, 42-64), respectively. The serration of 4th instar larvae lagged a fixed period behind that of the adults (i.e. the average interval between the peaks of the 2 stages was 30.0 days (SD, 7.8 days, range, 21-42 days)). Therefore, distinct valleys were considered to be changes of generations. During the study period, adult number ranged from 0 to 140: peak number gradually increased from the onset of the study (September, 1995) to the highest peak (late February, 1996), spanning 4 successive generations, and then descended to the lowest peak (June, 1996) over 2 generations, and then again began to increase during the next 4 generations (until the end of this study). Adult population size began to decrease before the low rainfall of May, 1996.

Sukarami

Climate during the study period Sukarami is normally a very wet place, but droughts occurred frequently during the study period (Fig. 5A). From 1992 to 1999, annual rainfall ranged from 1489 (1997) to 3321 mm (1995), and 15 out of the 96 months were dry (<100 mm), 6 being <50 mm. Two droughts were extremely severe: (1) August to October 1994 (3 successive dry months), (2) June to October, 1997 (5 successive dry months due to the strong 1997-1998 El Niño). These are referred as to Droughts 1 and 2, respectively, in Fig. 5A, and during these droughts Sukarami and its surrounding areas were covered with a heavy, thick haze.

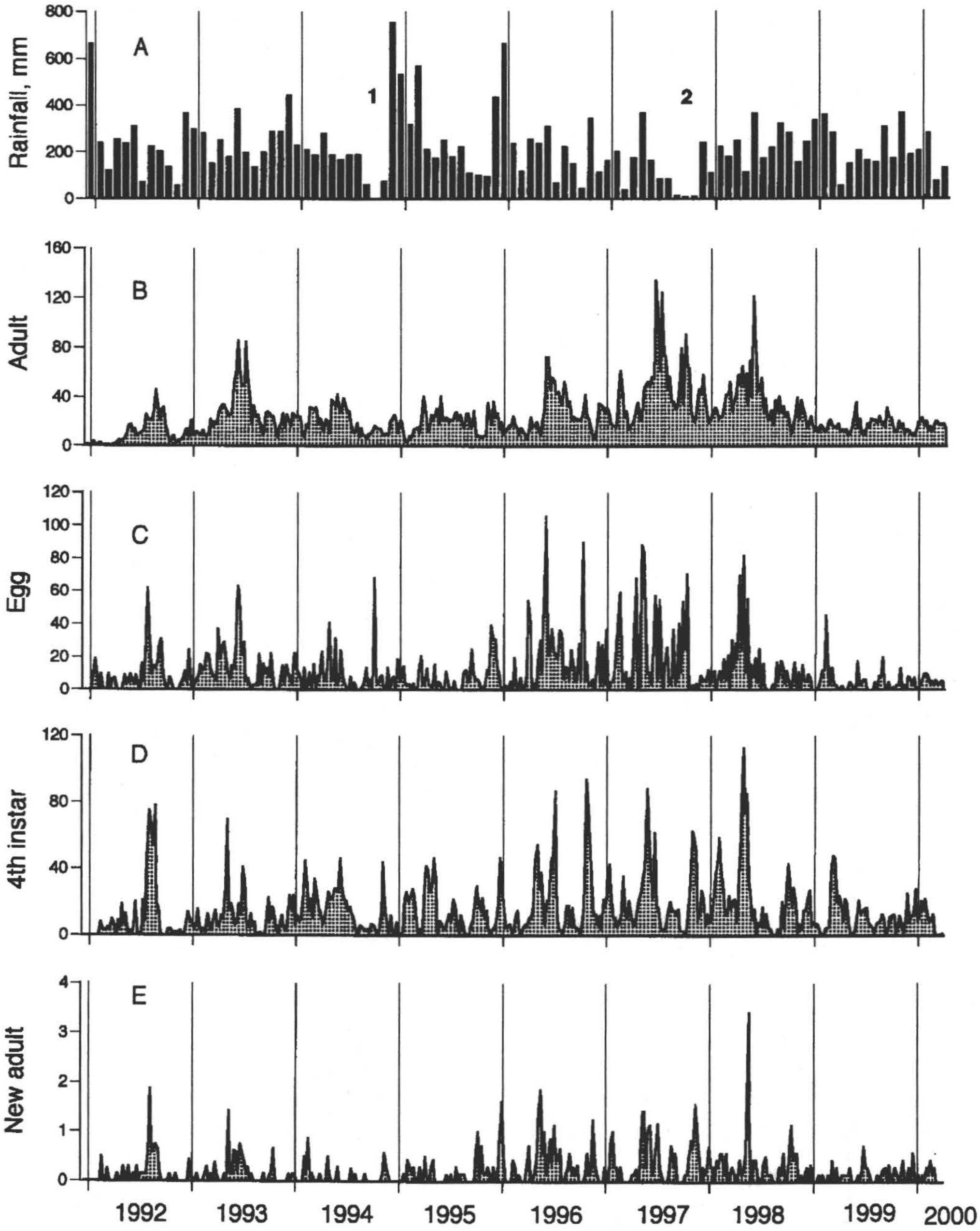

Fig. 6. Seasonal fluctuation in total amount of rainfall per month (A) and total number of *E. vigintioctopunctata* in successive developmental stages (B-E) on the main site in Sukarami, West Sumatra. Number of individuals in each stage is expressed as follows: (B) adults, number directly counted; (C) eggs, number laid per day; (D) 4th instar larvae, number directly counted; (E) new adults, number of pupal exuviae collected per day. Numerals in (A) indicate Droughts 1 and 2.

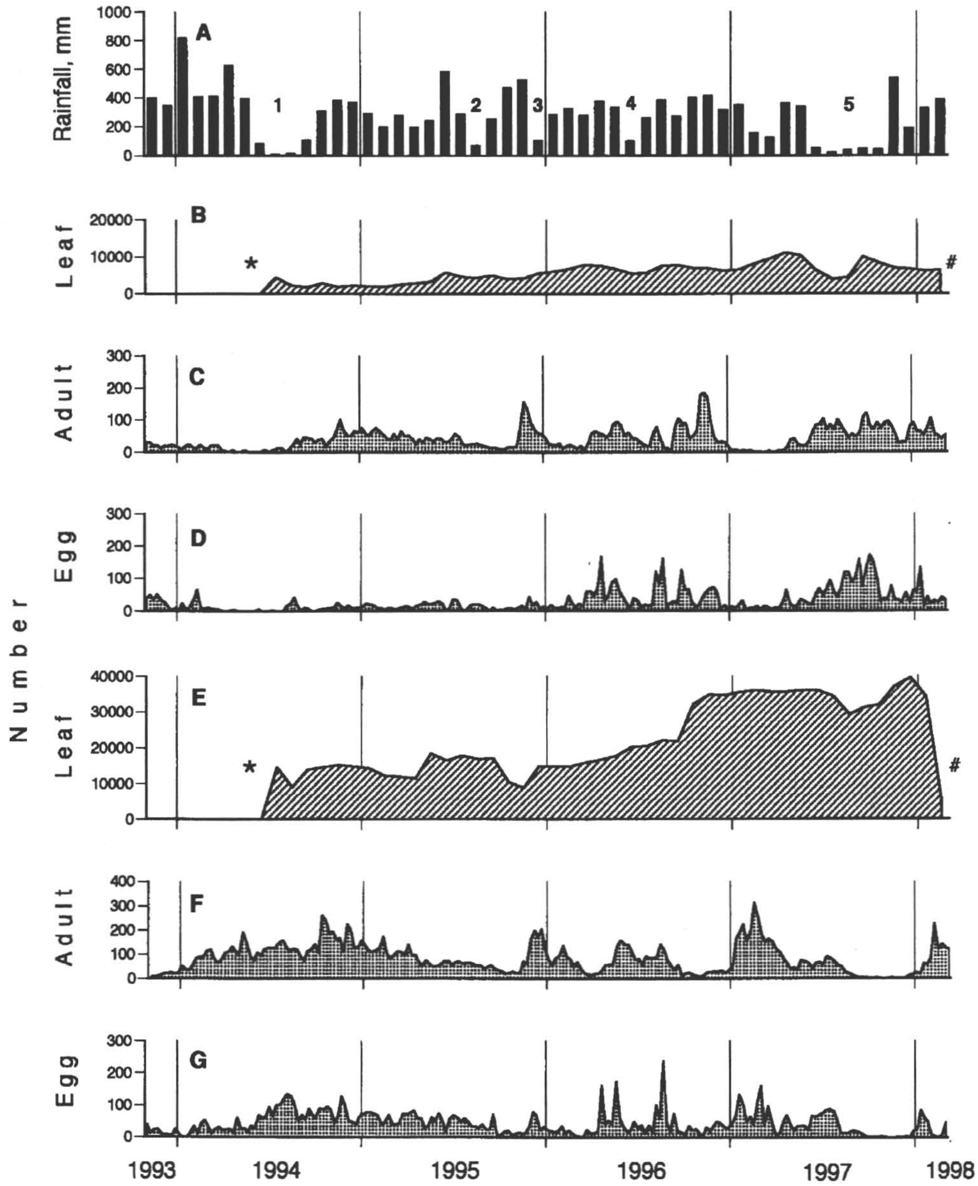

Fig. 7. Seasonal fluctuation in total amount of rainfall per month (A) , total number of *S. torvum* leaves on sites U (B) and S (E), the number of adult *E. vigintioctopunctata* feeding on *S. torvum* on sites U (C) and S (F) and total number of eggs laid per day on sites U (D) and S (G) in Bogor Botanic Garden, Bogor, West Java. Numerals in (A) indicate droughts. * and # in (B) and (E) indicate the onset and end of the record, respectively.

Host plant Total leaf number in the 3 sites fluctuated synchronously (Figs. 5B-D). The amount of leaves increased quickly after onset of the study, and reached a plateau from 1993 to mid 1997. It did not decrease during Drought 1, but dropped dramatically during Drought 2, due to the severe dryness and to the advanced age of the plants (> 8 years old in mid-1998) .

Adult Population

Main site

EV Adult number fluctuated from 0 to 135, with 6 major peaks occurring from time to time (see numerals in Fig. 5E): Peak 1 in early July 1992, Peak 2 in late April, 1993, Peak 3 in early May, 1996, Peak 4 in late May, 1997, Peak 5 in mid September, 1997 and Peak 6 in mid May, 1998. Adult number was at a rather constant low level for 2.5 years from mid 1993 to early 1996, and for more than 1 year from late 1998 to early 2000. Fig. 6 shows the seasonal change in number of eggs laid per day, 4th instar larvae and emergence of new adults, indicating the generation cycles. As found with EV in Padang (Fig. 2), the increase and decrease gradually progressed over 5-6 months, corresponding to 3-4 generations. The EV population here had 5-6 generations per year, while there were 8 generations in lowland Padang (Nakamura *et al.*, 1990) (Fig. 2) (see Concluding Remarks for comparison with Padang).

EN EN always coexisted with EV on the host plants. Its adult number, ranging only from 0 to 18, was always lower than EV except early in 1992 (Fig. 5H). Several low peaks were found during the study period.

Sub sites A and B

EV In site A the adult number fluctuated from 0 to 75 and in site B from 0 to 54 (Figs. 5F, G). Peaks were less distinct than at the main site. Adult numbers at the sites A and B fluctuated synchronously with each other and with that in the main site as well.

EN In site A, adult number fluctuated from 0 to 19, with 2 sharp peaks in late May, 1992 and mid May, 1993 (19 adults in both sites) (Fig. 5I). From 1994 onwards, it remained at a low level, ranging only from 0 to 3 in site B (Fig. 5J).

Bogor

Climate during the study period

Average annual rainfall from 1993 to 1997 was 3537.6 mm, ranging from 2218 (1997)-4347 (1993) mm. Fig. 7A shows the monthly rainfall during the study period. Eleven out of 52 months were dry months (<100) (referred to by numerals in Fig. 7A). The longest dry spell was 5 months from June to October, 1997 and was caused by 1997 El Niño (19-48 mm per month, Drought 5); the 2nd longest spell was 3 months from June to August, 1994 (8-82 mm per month, Drought 1). Dry months also occurred sporadically in August (66 mm, Drought 2) and December (99 mm, Drought 3), 1995 and June, 1996 (99 mm, Drought 4).

Adult population

(1) EV

Host plant

In site U (Fig. 7B), the total leaf number increased gradually during the study period, but dropped during the drought periods, especially during Droughts 1 and 5, the most drastic decrease occurring during Drought 5. Leaf number began to recover quickly in the middle of this drought (reason is unknown), and then decreased again and continued even after the end of the drought. Droughts 2 and 4, which lasted only 1 month also decreased the leaf number to some extent. In site S (Fig. 7E), total

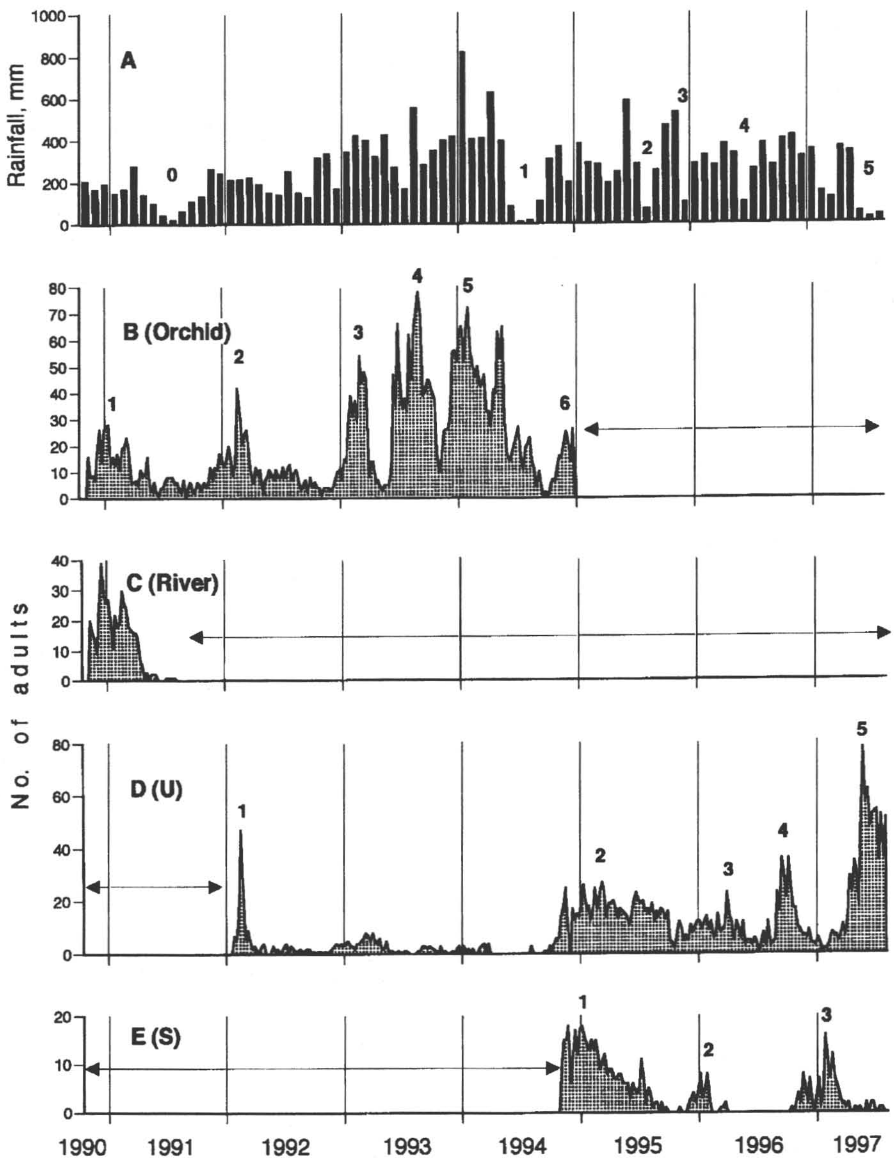

Fig. 8. Seasonal fluctuation in total amount of rainfall per month (A) , number of adult *Epilachna* sp. 3 (aff. *emarginata*) on each site (B-E) in Bogor Botanic Garden, Bogor, West Java. Arrow indicates the period with no data. Numerals in (A) indicate droughts, and (B), (D) and (E) peaks in adult numbers, respectively.

leaf number increased gradually during the study period, then dropped during the droughts but to a lesser extent than in site U. As on site U, the number began to recover in the middle of Drought 5, but then quickly decreased toward the end of the study. Some host plants, especially aged ones, in both sites lost most of their leaves and/or were dead during or after Drought 5.

Adult

Change in adult number in site U (Fig. 7C) was as follows: (1) it increased from mid 1994 to late

1995, reaching a plateau of around 50 beetles with repeated small peaks; (2) from late 1995 to late 1996, higher and sharp peaks were formed at 3-6 month intervals (156 and 187 adults in December, 1995 and November, 1996, respectively); (3) even during the Drought 5, it increased again, forming a plateau around 100, and then decreased after the drought. In site S (Fig. 7F), adult number increased and decreased gradually with small peaks beginning in November, 1993 and ending in late 1995. Thereafter acute peaks were formed at irregular intervals (4-8 months) until April, 1997. The highest one was 315 beetles in February, 1997. After Drought 5, there was a high peak of 228 in January, 1998.

Comparison of the seasonal change in adult number between the 2 sites showed that (1) the trends were opposite from November, 1993 to mid 1994, and thereafter became synchronous until late 1996. They were then out of phase until the end of 1997, i.e. (1) the formation of the highest peak in site S was 3 months later than in site U; (2) in site S, the adult number remained lowest during Drought 5, while it was on a plateau in site U. The serration in number of eggs laid per day in both sites (Figs. 7D, G) was more discrete than the number of adult especially from late 1995 to the end of 1997. The generation cycle was again found in these populations (also see Kahono, 1999).

(2) EM

The amount of *Mikania* leaves seemed rather stable compared to *S. torvum*, although no exact count was made. The plants were damaged seriously when the density was high. In the Orchid site (Fig. 8B), adult number fluctuated from 0 to 67, and exhibited 5 major peaks during the 4 years (October, 1990-December, 1994). Peak 1 (28 beetles) occurred in December, 1990-January, Peak 2 (42) in January-February, 1992, Peak 3 (54) in February, 1993, Peak 4 (78), and Peak 5 (72) in January-February, 1994. In the River site (Fig. 8C), which was destroyed in late March, 1991, a high peak was formed in December, 1990 (39). In site U (Fig. 8D), it ranged from 0 to 78 during 6.5 years (November, 1991 to June, 1997) with 5 major peaks: Peak 1 in late January of 1992, Peak 2 from late 1994 to mid 1995, Peak 3 in early 1996, Peak 4 around October, 1996, and Peak 5 around May, 1997. In site S (Fig. 8E), it changed from 0 to17 during 3 years (September, 1994-July, 1997) with 3 major peaks: Peak 1 in early 1995, Peak 2 at the end of 1995, and Peak 3 in early 1997. Generation cycles were again found in this species (see Nakamura *et al.*, 1992 for seasonal change in number of eggs and the following immature stages).

The negative effect of the drought on the population size of EM was clear: Drought 0 on the population on Orchid and River sites (Figs. 8B, C), Drought 1 on Orchid site (Fig. 8B) and Drought 5 on sites U and S (Figs. 8D, E). On Orchid site, 3 major peaks (Peaks 3, 4 and 5) were formed successively during 2 years (1993 and 1994) when rainfall was constantly high. The reduction in population size was caused, at least partly, by depletion of host plants by EM, as in EV in Padang (Nakamura *et al.*, 1990; Inoue *et al.*, 1993).

Generally, the trends in adult numbers in each site were synchronous: e.g., Orchid and River sites from late 1990 to early 1991, Orchid and U sites from the end of 1991 to the end of 1994, and sites U and S from the latter half of 1994 onward, though Peak 3 in site S occurred between Peaks 4 and 5 of site U. It should be noted that the trends in adult number of EM on sites U and S (Figs. 8 D, E) were the same as those of EV on respective sites (Figs. 7C. F), suggesting the importance of micro-habitat conditions such as soil moisture rather than amount of rainfall.

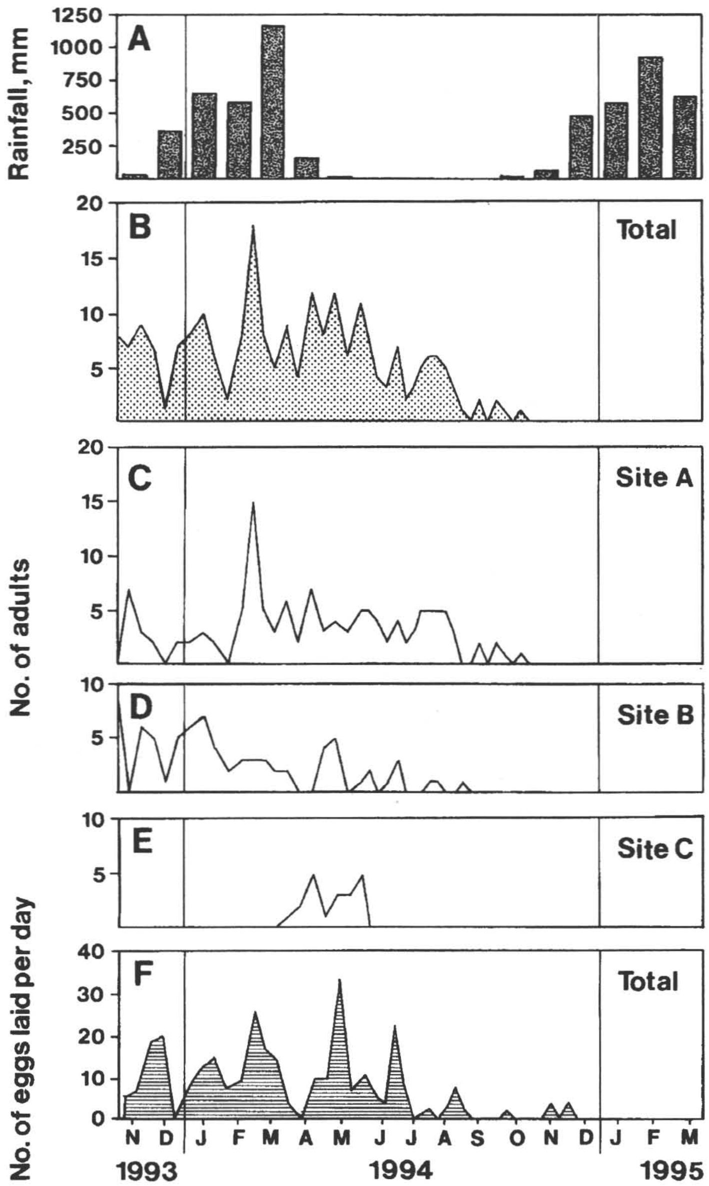

Fig. 9. Seasonal change in total amount of rainfall per month(A), total number of adult *E. vigintioctopunctata* for the 3 sites (B), that for sites A (C), B (D), C (E) and number of eggs laid per day for the 3 sites (F) in Purwodadi Botanic Garden, East Java.

Purwodadi

Climate during the study period

Fig. 9A shows the rainfall during the study period. Annual rainfall was 2196 mm (1993), 3140 (1994), and 3776 (1995). Dry and wet seasons were very distinct in 1994, i.e. average monthly rainfall was 578.2 mm in the rainy season, followed by a severe dry season from May to November when there were 4 months without rain. The following wet season started in December, 1994. Temperatures tended to be higher toward the end of the dry season (September to November) and to drop as the rainy season started (December): monthly temperature fluctuated from 24.8°C (July) to 28.1 (November) in 1993, and from 24.9°C (March) to 27.8 (November) in 1994.

Host plant

In general, total leaf number decreased as the dry season progressed, and began to increase again with the beginning of the rainy season. It should be noted that (1) the trends in the total leaf numbers varied among the sites, and among the individual plants even in the same site, and (2) leaves sprouted and dropped rather constantly in the dry seasons as well as in the rainy seasons (Kahono, 1996).

Adult

Seasonality in number When the study was launched in November, 1993, the end of the dry season, adults and eggs were already abundant on the host plants. The entire adult population remained at the same level until early the next rainy season (May, 1994) (Fig. 9B), then decreased as the dry season progressed. No rainfall was recorded from June to September of 1994 (Fig. 9A), however, adults and eggs were found on the host plants at low density until very late in the dry season (October of 1994) and reached zero in November 1994 (Fig. 9B). On sites A and B (Figs. 9C,D), trends in adult numbers were similar to that of the entire population. However, on site C (Fig. 9E), where the field conditions were very dry, adults were found only for a short period from March, 1993 to May, 1994 (late rainy season to early dry season). The 1994 dry season spanned 8 months, in which some host plants lost their leaves. They regained a normal number of leaves after the rainy season started in December, 1994 (Fig. 9A), but adults did not thereafter appear in the study sites during the rest of the study period (March, 1995) (Fig. 9B). The reason for this is unknown.

Oviposition Number of eggs laid per day for the entire population coincided with the number of adults (Figs. 9 B, F). Oviposition continued until the end of the 1994 dry season (Figs. 9A, F), with the duration of oviposition varying among sites depending on the habitat conditions; eggs were laid even until the very late dry season on sites A and B which were located beside ponds and until the mid dry season on site C which was located in a dry area. Kahono (1996) derived the fecundity index by E_i/NA_i, where E_i is the number of eggs laid per day during ith census and NA_i the number of female adults at ith census (a 1:1 sex ratio of beetles was assumed). Seasonal change in the fecundity index generally coincided with that of adult numbers, although it showed the highest peak in December, 1993 (early rainy season) and a 2nd one in July, 1994 (mid dry season).

Number of generations per year Serration in number of adults and eggs (Figs. 9B, F) indicate that EV here had 3-4 generations a year. Adult number and oviposition activity decreased to zero as the dry season progressed, making the adverse effect of the dry season on EV reproduction apparent in 1994 (Fig. 9F). Response of EV to the dry season was different between the years: (1) many adults and eggs were found in November, 1993, the end of dry season; yet (2) adults did not return to the study sites even after the onset of the 1994/1995 rainy season (Figs. 9B, F) Therefore, EV is not simply dependent on the cycle of the rainy and dry seasons but is also determined by other factors of host plant condition and natural enemies. To analyze the causes, we should examine adult diapause and migration, seasonal change in quantity and quality of host plants and in the action of natural enemies.

CONCLUDING REMARKS

Magnitude of fluctuation and formation of major peaks in adult numbers

Previous results showed that EV in Padang reproduced throughout the year with the adult number fluctuating dramatically and exhibiting 3 major peaks in 3 years. In peak formation, increase or decrease was gradual over 3-5 months or 3-4 generations. Shape and height of the peaks varied, and the intervals of major peaks were not regular, ranging from 8-12 months (Figs. 2) (Nakamura *et al.*, 1990; Inoue *et al.*, 1993). The present results show that EV in Sukarami (Fig. 5E) and Bogor (Figs. 7C, F) and EM (Figs. 8B-D) reproduced throughout the year and exhibited the same features in fluctuation and peak formation as EV in the previous study. EV feeding on *C. pubescens* was studied for only 14 months, so that only 1 major peak was recorded during the study period. EV in the multi-site study showed similar features (Fig. 3). EN in Sukarami, however, remained at a low level during most of the study period (Figs. 5H-J).

Occurrence of generation cycles

Nakamura *et al.* (1990) speculated that the process in which the serration in number became pronounced during high density was probably related to emigration. Overcrowding of adults in a small study area not only evoked a density-dependent emigration and shortened adult residence time, but, the duration of oviposition periods by each female was also probably shortened, producing serrated curves in the egg and subsequent stages. Godfray and Hassell (1987, 1989) proposed a model to explain the discreteness of generations in a constant "tropical" environment, based on the host parasitoid interaction. But their model cannot be supported in our study, because parasitism did not increase prior to drop in beetle density (Nakamura, *et al.*, 1990; Inoue *et al.*, 1993). The present study found the generation cycles in most of the populations studied (Figs. 4 and 6-9), with EV feeding on *C. pubescens* showing the most distinct serration (Fig. 4). Our preliminary analysis showed that EV, EN and EM populations suffered from a high wasp parasitism in egg, larval and pupal stages. However, there was neither clear seasonal trend nor simple density-dependency in the parasitism. Host plants were seriously damaged by them when they formed high peaks. Therefore, we hold to our assumption derived from the previous study in Padang. We found the large fluctuation in number, peak formation and generation cycles similar to the epilachnine beetles in our study of the banana skipper, *E. thrax* in Padang and Sukarami (Hasyim, 1994) and in Bogor (Erniwati, unpublished) and of the tortoise beetles, *A. miliaris* and *A. sanctaecrucis* in Bogor (Noerdjito, 1998).

Number of generations per year

The present study indicated that EV feeding on *Centrosema* in Padang had 8 generations, which is the same as EV feeding on *S. torvum* in Padang (Fig. 2) (Nakamura *et al.*, 1990). EV in Sukarami had 5-6 generations per year. Average temperature in Sukarami is about 5°C lower than that in lowland Padang. In Sukarami, EV needed 32.1 days to complete the immature stages and the generation time *T*, derived by $l_x m_x$ schedules was 72.9 days (Hasan *et al.*, in prep.). In Padang, the corresponding values were 23.4 and 47.6 days, respectively (Abbas *et al.*, 1985). Thus the difference in the number of generations between EV in Sukarami and Padang can be explained by temperature. In Purwodadi, in contrast, with a 6-7 month dry period, EV could reproduce only 3-4 generations during the short rainy season (Fig. 9; Kahono, 1996).

Synchronization of trends among local populations

Population trends of epilachnine beetles could be determined by factors such as rainfall, host plant conditions and natural enemies, which may work in combination in a complicated manner. Since we have not yet analyzed these data completely, we examine below only the trends in adult population in relation to rainfall and leaf number of the host plants.

The trends in the amount of *S. torvum* were generally synchronous among the 3 sites in Sukarami (each 900 m apart) and between the 2 sites in Bogor (400 m apart), as were trends in EV number in Sukarami (Fig. 5) and in EM in Bogor (Fig. 8). However, in Bogor, EV populations on the adjacent sites were not always synchronous (Fig. 7), but EV and EM on the same site showed the same trends (Figs. 7 and 8). This suggests that some micro-habitat condition such as soil moisture was more important than rainfall in determining populations.

In Padang the EV populations located within a radius of 10 km, where the general trends in rainfall were the same, were synchronous (Fig. 3). This suggests that rainfall is important in determining the trends. However, neither female fecundity nor the rate of wasp parasitism was clearly related to the seasonal distribution of rainfall (Nakano *et al.*, 1991). It should be noted that (1) the study period was only 13 months, which is too short to generalize the results, and (2) at the onset of the study, we planted seedlings of similar age, which might have canalized the trends.

Effects of drought on seasonal trends of host plants and epilachnine beetles

The previous study of EV in Padang showed that high peaks occurred during a period of decreased rainfall associated with the 1982-1983 El Niño. Heavy rainfall, on the other hand, suppressed the population increase, perhaps because of its negative effects on egg hatchability and adult longevity (Nakamura *et al.*, 1990; Inoue *et al.*, 1993). On the contrary, an earlier report on EM in Bogor (Nakamura *et al.*, 1992) which dealt with only one year at the onset of the study, showed the negative effect of drought on population size. The drought appeared to lower the adult survival rate and adult fecundity (Figs. 5 and 9, op. cit.), resulting in a decreasing population throughout the drought period (Figs. 2 and 3 op. cit.).

Although we have not yet analyzed this in detail, the present results showed that (1) there was no simple correlation between the trends of rainfall and those of the beetle populations; (2) the severe drought in 1994 did not suppress *S. torvum* in Sukarami (Figs. 5B-D), but it did in Bogor (Figs.7B, E). Its effects on adult numbers were not clear in either locality; (3) the drought in 1997-1998 apparently suppressed host plants and EV in both Sukarami and Bogor, but EV and EM on site U in Bogor nontheless increased during the drought.

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インドネシア共和国スマトラ島とジャワ島の気候条件の異なる環境における食葉性 テントウムシ類（テントウムシ科：マダラテントウ亜科）個体群の長期動態

1．インドネシア共和国スマトラ島とジャワ島の気候の異なる環境に定点観測地を設置し，食葉性テントウムシ類の長期個体群動態を，成虫の個体識別マーク法と卵，幼虫，蛹の生命表作成を用いた３～７日おきの定期センサス調査によって最長９年間継続して調査した。

2．定点観測地は，スマトラ西部州のパダン（海岸低地の典型的な熱帯多雨林気候，年間降雨量は4000ミリ以上，乾雨季の区別なし），スカラミ（海抜 928 mの高地環境，2917 mm），西ジャワ州のボゴール（海抜 260 m，熱帯多雨林気候帯の東端に位置する，3850 mm，通常明瞭な乾季はないが，時々強い干ばつがある），東ジャワ州のプルウォダディ（海抜 300 m，2000～2500 mm，６～８月間の強い乾季あり）に設置し，３種の食葉性テントウ類，①ナス科の半低木*Solanum torvum*を食草とするニジュウヤホシテントウ*Epilachna vigintioctopunctata*（ツル草*Centrosema pubescens*を食草とする個体群を含む），② *E. enneasticta*（食草は*S. torvum*），③ キク科のツル草*Mikania micrantha* を食する*Epilachna* sp. 3（aff. *emarginata*）を調査した。

3．個体数変動の特性（*S. torvum*食のニジュウヤホシテントウを中心に述べる）

（1）乾雨季が不明瞭なパダン，スカラミ，ボゴールでの結果。①成虫数は時々大ピークを形成し，個体数の変動幅は大きい（パダンでは約290 倍に達した）。ピークへの個体数の増減は，それぞれ3～5カ月ずつかけて徐々に生じた（３～４世代にあたる）。② 卵，幼虫，蛹の個体数変化はノコギリ状であり，generation cycleが生じた)。③ 数百m～数 km 離れた複数の個体群での成虫数の増減は，全般的に同調した。④個体群サイズの変動と降雨量の消長との同調性は全般に低かった（ただしボゴールの*E.* sp. 3 では，降雨の増減と個体数変動の同調性が比較的高かった)。調査期間中に生じた非常に強い干ばつ（1982/1983, 1997/1998のエル・ニーニョなど）の際には，食草葉量が減少したが，個体数が急減するとは限らなかった。

（2）強い乾季のあるプルウォダディでの結果。①雨季～乾季初期にかけて個体数が増加した。その後，乾季が進むにつれて個体数は減少したが，乾季後半まで成虫は食草上にとどまり続けた。② 食草への産卵数は，成虫数の推移と一致した。メス成虫あたりの産卵数は，雨季の初期と乾季の中期にピークが見られた（前者が最大値)。