ORIGINAL PAPER

Makoto Kato

Structure, organization, and response of a species-rich parasitoid community to host leafminer population dynamics

Abstract The parasitoid community dynamics of an agromyzid honeysuckle leafminer, *Chromatomyia suikazurae* (Agromyzidae, Diptera) were studied between 1981 and 1990 in a natural forest in Kyoto, Japan. The parasitoid fauna composed three koinobionts (all larval-pupal solitary parasitoids) and 22 idiobiont species (11 larval solitary, nine pupal solitary and one pupal gregarious).The parasitoid community was dominated by early-attacking oligophagous braconid koinobionts at early periods, but was gradually displaced by late-attacking polyphagous eulophid idiobionts. Accordingly, the diversity index of the parasitoid community peaked at an intermediate point in the intra-generational succession. The succeeding attack-in-waves by the late-attacking idiobionts greatly reduced not only the survival rates of early-attacking parasitoid larvae but also the survival rates of hosts. The density-dependence observed in the host pupal mortality was thought to result from density-dependent host-switching by a keystone polyphagous pupal idiobiont parasitoid, *Chrysocharis pubens*, whereas high host pupal mortality was potentially attained by an early-attacking koinobiont braconid. Supposed aggregation of polyphagous parasitoids at high host density resulted in intense within-host competition and in an increase of host-feeding attack, both of which contributed to low emergence rates of parasitoids at high host densities. Parasitoid emergence rates were also reduced at low host densities, probably by inter- and intra-specific hyperparasitism among oligophagous parasitoids for limited hosts. The regulation effects of the species-rich parasitoid community upon the host population dynamics are thought to derive from succeeding attack-in-waves by polyphagous late-attacking idiobionts, especially by the keystone species.

M. Kato
Biological Laboratory, Yoshida College, Kyoto University,
Sakyo, Kyoto 606–01 Japan

Introduction

Insect parasitoids can constitute an important mortality factor for insect herbivores. A host insect's feeding niche affects the number of associated parasitoid species per host species, which is generally highest in leafminers, followed by semi-concealed herbivores, gall formers, external folivores, concealed feeders and root feeders (Hawkins and Lawton 1987; Hochberg and Hawkins 1992). Parasitoid community richness is linked to the effect of parasitoids on host populations and the driving mechanism is the susceptibility of hosts to parasitoid attack (Hawkins and Gross 1992; Hawkins 1993; Cornell and Hawkins 1993). To detect the effects of parasitoid community richness upon the host population dynamics, the following questions should be addressed: (1) parasitoid community structure; (2) community organization through interspecific competition; and (3) responses of parasitoid community to host population dynamics.

Parasitoid community structure can be interpreted in terms of interactions among parasitoid species with different modes of parasitism, which involves solitary versus gregarious, endo- versus ecto-, koinobiont versus idiobiont (parasitoids permit or not the host to grow), primary versus secondary, early- versus late-attacking, polyphagous versus oligophagous, larval- versus pupal- and pro-ovigenic versus synovigenic (wasps emerge with a full complement of eggs or mature eggs after emergence) parasitoids (Force 1974; Askew and Shaw 1979, 1986; Spiers et al. 1991). Parasitoids, however, do not always clearly segregate their patterns of host utilization temporally and spatially. For example, host phylogeny and host ecological properties such as 'apparency' influence their host utilization patterns (Askew and Shaw 1986). The structure and diversity of para-

sitoid communities vary not only among host species but also in the same host species among habitats or in a gradient of ecological succession (Price 1973, 1991; Washburn and Cornell 1981).

Parasitoid communities may be organized through interspecific competition for exploitation of individual hosts (within-host competition) and for their discovery (across-hosts competition) (Taylor 1988). Within-host competition generally occurs not only between parasitoids with similar modes of parasitism but also between ones with different modes (Askew and Shaw 1979), and this suggests that niche segregation in relation to host exploitation is incomplete among parasitoid species. The issue of across-hosts competition is mainly determined by differences in host-searching and egg-production rates. In general, inferiority in within-host competition may be compensated by superiority in across-hosts competition (Price 1973, 1975; Ywölfer 1979; Zwölfer 1979; Sholz and Höller 1992).

Density-dependent foraging of host-specific parasitoids has been viewed as an important attribute contributing to the regulation of host populations (Beddington et al. 1976; Hassell 1985). The dynamics of multiparasitoid-host interactions and the factors affecting parasitoids' coexistence and host equilibrium levels have been analyzed by mathematical models (e.g., May and Hassell 1981; Kakehashi et al. 1984). These models predict that when two parasitoid species have different niches in relation to host utilization the host equilibrium level can be depressed, but that when the niches are similar the host equilibrium level would rise. These predictions, however, have not been tested in field populations. Contrasting the equilibrium viewpoint, there is evidence for instability and local extinction of hosts by density-dependent parasitoid attack in multiparasitoid-host systems (Washburn and Cornell 1981; Huffaker et al. 1986). Murdoch et al. (1985) concluded that predators and parasitoids adopting lying-in-wait or search-and-destroy strategies are candidates for biological control in a non-equilibrium state. It is an intriguing problem whether host populations might be regulated in multi-parasitoid host system, and if so which parasitoid species could be a candidate for regulation, host-specific host-synchronous parasitoid species adopting a density-dependent foraging strategy or polyphagous parasitoid species adopting density-dependent host-switching, or both (Tscharntke 1992; Hawkins and Gross 1992). Long-term field studies on both host population dynamics and parasitoid community dynamics in a natural ecosystem are necessary to address the problem.

The aim of this study is to describe the dynamics in a multiparasitoid-host interaction in a natural ecosystem and to address the three issues raised above. I carried out a population study of a leafminer, *Chromatomyia suikazurae* (Agromyzidae, Diptera), and its parasitoid community for 10 years in Kyoto, Japan. The leafminer passes two discrete generations on *Lonicera gracilipes* leaves in spring; the first generation is completely free from parasitoid attack but the second is subject to in-tense attack by a diverse parasitoid community (Kato 1985). The population in the first generation was resource limited, but the population in the second generation was regulated by density-dependent parasitoid attack in pupal stage (Kato 1994). In this paper, I focus my attention on the intra-generational process of the parasitoid community in the second generation and investigate structure, organization and dynamics of the parasitoid community. By analyzing the interactions between host population dynamics and parasitoid community dynamics, I examine the parasitoids' response to host population dynamics and then discuss the regulatory role of the parasitoid community on host populations.

Materials and methods

Life history of the leafminer

Chromatomyia suikazurae Sasakawa is an agromyzid leafminer species mining in the palisade parenchyma of leaves of *Lonicera* spp. (Caprifoliaceae) (Kato 1985, treated as *Phytomyza lonicerae*). The third instar larva pupates in spongy parenchyma in the leaf by making its puparium at the inner side of the lower epidermis. The population passes two generations on deciduous *L. gracilipes* at Iwakura (G1 and G2, respectively), and a third one on evergreen *L. japonica*. The G1 population was parasitoid free and resource-limited and the G2 population suffered intense parasitoid attack (for detail, see Kato 1994). Seasonal patterns of larval development and death in G2 in 1981 are shown in Fig. 1.

Field sampling

Field observations were made at a site at Iwakura (135°47'E, 35°5'N, 170 m in altitude), about 5 km north of Kyoto city, Japan from 1981 to 1990. In G2, stratified complete samples were taken. All mined leaves of randomly selected plants were sampled sequentially at an interval of 1–7 days from late April to middle May. In later analyses, the samples were sorted by sampling date
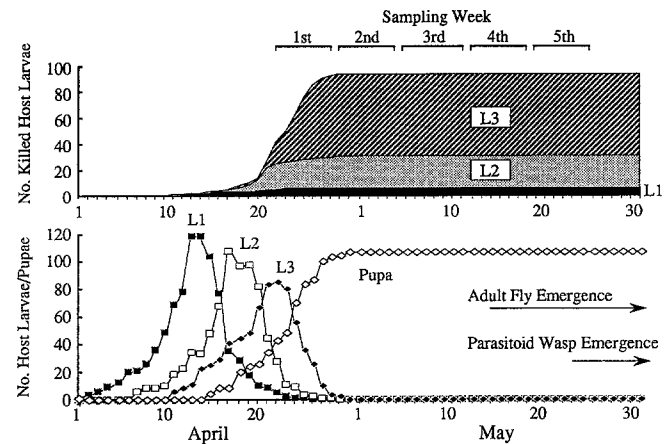

Fig. 1 Changes in the numbers of living host larvae and pupae and in the cumulative numbers of killed host larvae on an intensively censused shrub from April to May in 1981. Parasitoid community structure was compared among data sorted by the sampling date into the five weeks: 1st week, 22–28 April; 29 April–5 May; 3rd, 6–12 May; 4th, 13–19 May; 5th, 20–26 May. *L1–L3* refer to 1st–3rd instar larvae

into five sampling weeks; 1st week, 22–28 April; 2nd, 29 April–5 May; 3rd, 6–12 May; 4th, 13–19 May; 5th, 20–26 May (Fig. 1). The number of sampled plants ranged from 13 to 61 (mean = 34.4, SD = 16.3). All sampled mined leaves were sorted by leafminer stage (first to third instar larvae and pupae) and state (removed by predators, missing or intact), and their numbers recorded. Emergence of adult flies before sampling was checked by a characteristic emergence slit of each puparium. The sorted leaves were incubated separately in glass bottles (7 cm in diameter, 13 cm in height) covered with pin-perforated film (parafilm, American Can Company). After October, when all host flies and parasitoids had emerged, they were sorted and counted by species and sex. Ovipositor lengths of each parasitoid species were measured.

The leafminer density per leaf for each sampled plant was estimated by dividing the number of sampled leafminers by the total number of leaves per plant. The total number of leafminers in the quadrat was estimated by multiplying the mean leafminer densities per leaf by the total number of leaves in the quadrat.

To obtain detailed information on the intra-generation process in G2 from 1981 to 1985, all the leafminers (including eggs) on a selected plant were marked by putting sticky tape on a branch, and then the stage (first to third instar larvae and pupa; judged from length of pharyngeal skeleton) and vigor (live or dead; judged from swinging movements of the pharyngeal skeleton) of each leafminer were traced daily from the start of G2 until all leafminers had pupated. About a week after pupation, all mined leaves were sampled and incubated in glass bottles (2 cm in diameter, 4.5 cm in height, sealed by perforated parafilm) were used to track. After October, emerged flies and parasitoids were counted.

Preliminary dissections of hosts parasitized by various parasitoid species in the laboratory enabled identification of species by examining eggs, larvae, pupae or head capsules of dead parasitoid larvae. A total of 33 host larvae sampled on 24 April 1985 and 38 killed larvae and 49 pupae sampled on 2 May 1985 in the field were dissected to check the number and sex of parasitoid progeny.

Results

Parasitoid community structure

A total of 24 parasitoid species were recorded from C. suikazurae at the study site (Table 1). Three braconid species were solitary, endoparasitic, larval-pupal koinobionts. Three pteromalids were solitary, endoparasitic, pupal idiobionts. All 19 eulophids were idiobionts, and their modes of parasitism were diverse. Tetrastichus sp. 5 was the only gregarious parasitoid species, and the mean number of emerging parasitoids per host was 4.0 (SD = 1.1, n = 18). Facultative multiparasitism occasionally occurred in some solitary species such as Tetrastichus spp. 1–3, Chrysocharis pentheus and Teleopterus erxias. The rate of multiparasitism in Chry. pentheus was 4.2% (n = 42).

Table 1 Parasitoid wasp species which emerged from *Chromatomyia suikazurae* and some of their ecological characteristics. *K* koinobiont, *I* idiobiont, *L* larva, *P* pupa.

SUBORDER Family Subfamily	Code	Species	Mode of para- sitism	Endo/ ecto- parasit- ism	Host stages of oviposition/ emergence	Number of eggs/ host[a]	Host range[b]	Mean (±SD) length (mm) of ovipositor
ICHNEUMONOIDEA								
Braconidae								
Opinae	1	*Opius* sp.	K	endo	L/P	1	s	0.35 ± 0.01
Alysiinae	2	*Dapsilarthra* sp.	K	endo	L/P	1	f	0.44 ± 0.01
	3	*Dacnusa nipponica* Takada	K	endo	L/P	1	f	0.32 ± 0.00
CHALCIDOIDEA								
Pteromalidae								
Miscogasterinae	4	*Sphaeripalpus* sp.	I	endo	P/P	1	f	0.73 ± 0.00
	5	*Merisumus* sp.	I	endo	P/P	1	f	0.80 ± 0.01
	6	*Halticoptera* sp.	I	endo	P/P	1	f	0.85
Eulophidae								
Elacheritinae	7	*Cirrospilus diallus* Walker	I	ecto	L/L(P/P)	1	f	0.83 ± 0.02
Eulophinae	8	*Diglyphus minoeus* (Walker)	I	ecto	L/L	1	f	0.40 ± 0.01
	9	*Pnigalio katonis* (Ishii)	I	ecto	L/L(P/P)	1	o	0/90 ± 0.03
	10	*Pnigalio* sp.	I	ecto	L/L	1	o	0.82 ± 0.02
Tetrastichinae	11	*Tetrastichus* sp. 1	I	endo	L/L	1+	o	0.41 ± 0.01
	12	*T.* sp. 2	I	endo	L/L	1+	o	0.40 ± 0.01
	13	*T.* sp. 3	I	endo	L/L	1+	o	0.42 ± 0.00
	14	*T.* sp. 4	I	endo	L/L	1	o	0.34 ± 0.02
	15	*T.* sp. 5	I	endo	P/P	4	s?	0.51 ± 0.01
Entedontinae	16	*Chrysocharis pubens* (Delucchi)	I	endo	P/P	1	f	0.61 ± 0.03
	17	*C. phryne* (Walker)	I	endo	P/P	1	o	0.72 ± 0.02
	18	*C. pentheus* (Walker)	I	endo	L/L	1+	o	0.52 ± 0.02
	19	*C. albipes* (Ashmead)	I	endo	L/L(P/P)	1	o	0.62 ± 0.03
	20	*C. ujiyei* Kamijo	I	endo	L/L(P/P)	1	o	0.71
	21	*Cotterellia japonica* Kamijo	I	endo	P/P	1	o	0.91 ± 0.01
	22	*Closterocerus trifasciatus* Westwood	I	endo	L/L(P/P)	1	o	0.24 ± 0.02
	23	*Teleopterus erxias* (Walker)	I	endo	L/L	1+	o	0.23 ± 0.01
	24	*Pediobius acantha* (Walker)	I	endo	P/P	1	o	0.72 ± 0.01

[a] 1+ refers to facultative multiparasitism
[b] s specific to *Chro. lonicerae* (and related species); f confined to Agromyzidae; o utilizing leaf-miners of more than one order

The evidence of host range was accumulated both from my observations and from the literature (Kamijo 1978; Takada and Kamijo 1979; Hansson 1985). Only *Opius* sp. and *Tetrastichus* sp. 5 seemed to be oligophagous specialists which might switch hosts to related agromyzid leafminers in the next generation. The other 22 species were polyphagous, although their hosts were restricted to Agromyzidae (8 species) or to leafminers (14 species). Ten species oviposited only into host larvae, eight species only into host pupae. Six species (*Cirrospilus diallus*, *Pnigalio* spp. *Chry. albipes*, *Chry. ujiyei* and *Closterocerus trifasciatus*) oviposited mainly on larvae but occasionally into pupae. Ovipositor lengths of pupal parasitoids were usually more than 0.6 mm (except for *Tetrastichus* sp. 5) while those of larval and larval-pupal parasitoids were less than 0.6 mm. All parasitoids (even pupal parasitoids) host-fed; that is, they inserted their ovipositors into the host's body and sucked fluid exuding from the wound. Although some species refrain from ovipositing on parasitized hosts for a while after the preceding oviposition (e.g., *Diglyphus minoeus*; Kato 1989), hyperparasitism generally occurred in most idiobiont species.

Parasitoid community organization

The data on emerging parasitoid communities were sorted by sampling date into the five sampling weeks (Fig. 2). The proportion of the number of *i*th parasitoid species per total emerging parasitoid wasps at *j*th sam-

pling week, i.e., $P_i(j)$, was estimated. An assembly of $P_i(j)$ was defined as the parasitoid community at time *j*. Figure 2 shows the changes of $P_i(j)$ over the five sampling weeks. The dominant species whose fraction attained more than 10% at least once were restricted among the following six species: *Opius* sp., *D. minoeus*, *Tetrastichus* sp. 5, *Chry. pubens*, *Chry. phryne* and *Chry. pubens*. The parasitoid community changed over the sampling weeks. For example in 1982, the parasitoid community in the first week was dominated by *Opius* sp. and followed by *Chry. pentheus*, *D. minoeus* and *Tetrastichus* sp. 5, whereas that in the third week was dominated by *Chry pubens*, followed by *Chry. pentheus*, *Tetrastichus* sp. 5 and *Opius* sp. The most conspicuous tendencies in the change were a decrease in the fraction of *Opius* sp. (significant for 1982–1990 by Spearman correlation, $P < 0.05$), and an increase in the fraction of *Chry. pubens* (significant for 1982–1989 by Spearman Correlation, $P < 0.05$).

To detect some trends of variations, a principal component analysis on the parasitoid communities was carried out. The variable used for the analysis was $P_i(j)$. Two principal components (PC1 and PC2) accounted for 21.6% of the standardized variance and three components explained 35.6%. In Fig. 3, indicating trends on the plot of PC1 and PC2, plots in later weeks were arranged toward PC1, which had high positive loadings on *Chry. pubens* and *Pediobius acantha* and high negative loadings on *Opius* sp., *D. minoeus* and *Pnigalio katonis* (Fig. 4.). The PC1-oriented trend indicates that the parasitoid community structure was organized by re-

Fig. 2 Changes in species composition of parasitoid wasps, $P_i(j)$, over the five sampling weeks for 1981–1990. See Table 1 for parasitoid *species codes*
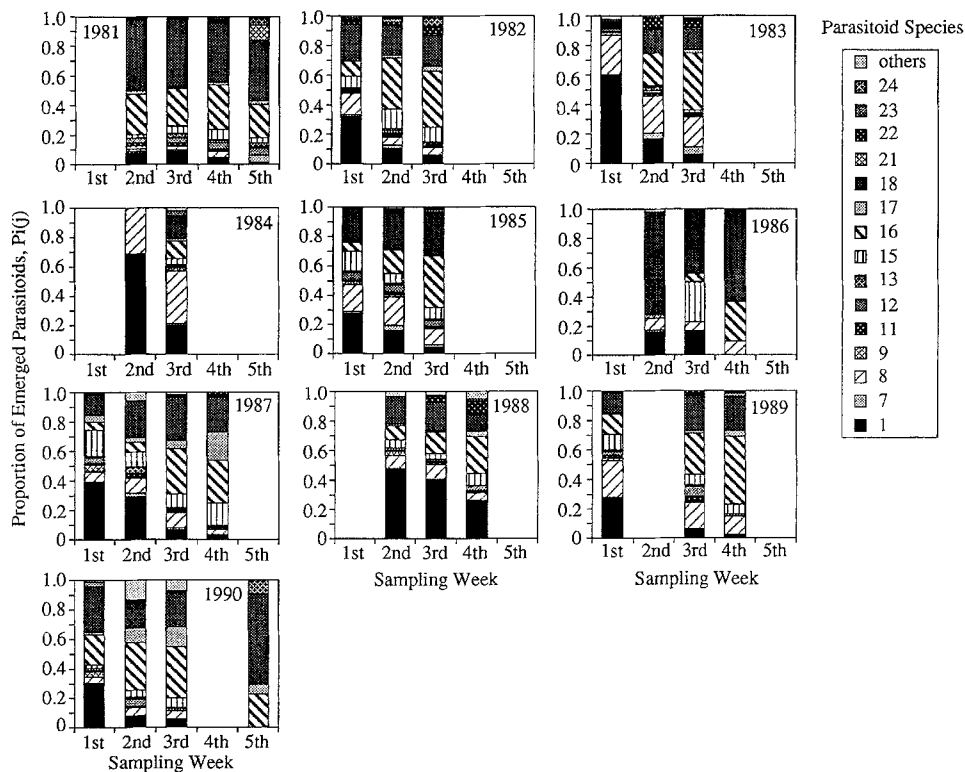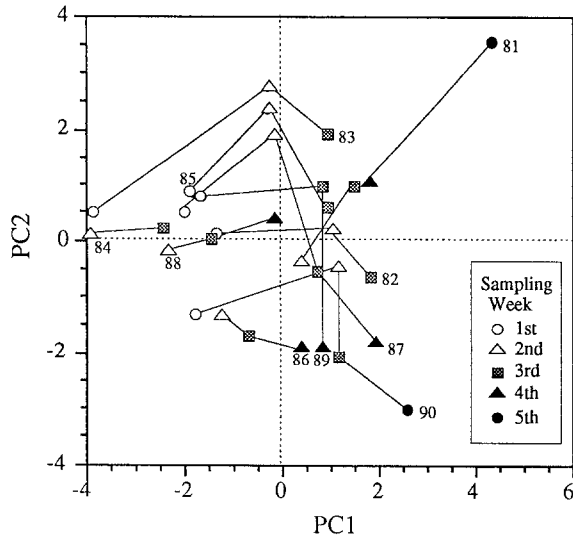
Fig. 3 Result of a principal component analysis on parasitoid communities during five weeks in 1991–1990. Variables used for the analysis were $P_i(j)$. *Numerals* beside the symbols refer to years: 81–90 for 1981–1990. Loadings of variables upon the components are shown in Fig. 4
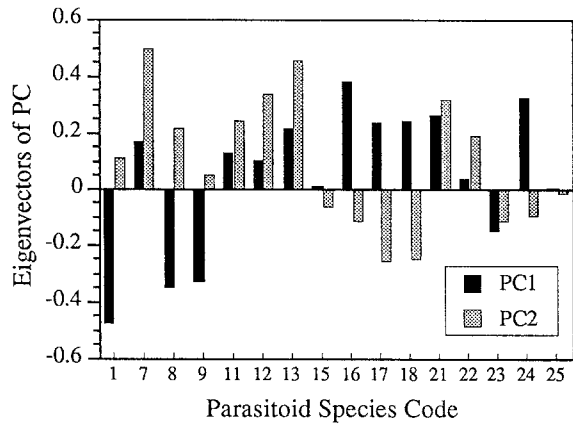

Fig. 4 Eigenvectors of 16 parasitoid species upon the first and the second primary components (PC1 and PC2) in a primary component analysis on parasitoid communities (Fig. 3). See Table 1 for parasitoid *species codes* (25 refers to other species)
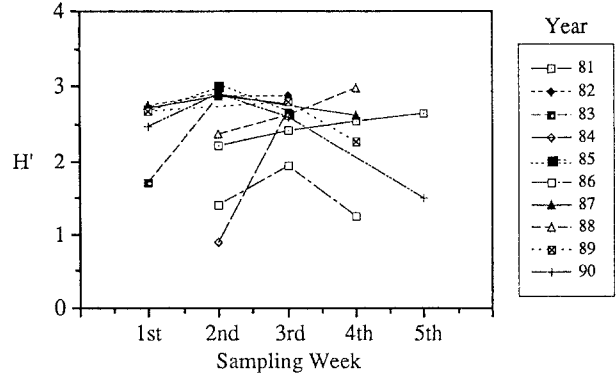

Fig. 5 Changes in Shannon-Wiener diversity index (H') of parasitoid community over the five sampling weeks
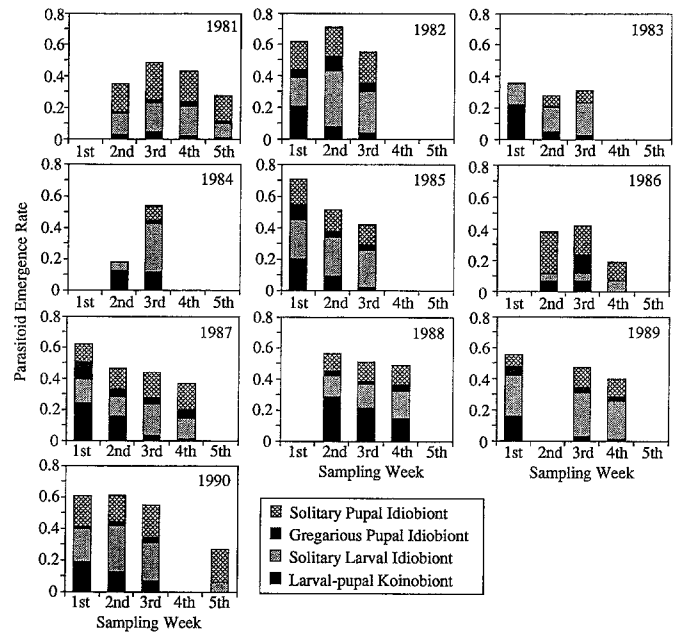

Fig. 6 Changes in emergence rates (%) of parasitoids over the five sampling weeks for 1981–1990. Parasitoid species were sorted by mode of parasitism

placements of early-attacking parasitoids such as *Opius* sp., *D. minoeus* and *P. katonis* by late-attackers such as *Chry. pubens* and *Pediobius acantha*. Figure 3 also indicates early upward and late downward trends along the PC2 axis (excluding 1981). PC2 had high positive loadings on *Cirrospilus diallus* and *Tetrastichus* sp. 3 and high negative loadings on *Chry. phryne* and *Chry. pentheus* (Fig. 4). This suggests that the former two species at first displaced the early-attackers before the 3rd week but were replaced by the latter two species after then.

Accompanied by the replacement of early attackers by late attackers, the Shannon-Wiener diversity index H' for the parasitoid community at first increased and then decreased except for 1981 and 1988 (Fig. 5). The

peak of H' was usually between 2.5 and 3.0, but went down to less than 2.0 in 1986 when host density reached a minimum.

Changes in the emergence rates of parasitoid species were next investigated over the five sampling weeks. Figure 6 shows the changes of parasitoid emergence rates, which were combined by mode of parasitism. Total emergence rate tended to decrease with time. A low emergence rate in early weeks in 1981, 1984 and 1986 might be attributable to high parasitoid larval mortality caused by sampling too early in a delayed spring. The most conspicuous tendency is the decrease of the fraction of koinobiont parasitoids (Fig. 6).

Dissection of hosts in 1985 helped me to understand the process of parasitoid succession. Of living larvae

Table 2 Results of dissection of *Chromatomyia suikazurae* larvae and pupae sampled in 1985

Date	Host stage	Condition	Number	Percent
24 April	Living larva	Unparasitized	10	30.3
		Parasitized by		
		one *Opius* sp. egg/larva	17	51.5
		two *Opius* sp. eggs/larvae	4	12.1
		≥3 *Opius* sp. eggs/larvae	2	6.1
		Total	33	100.0
2 May	Killed larva	Unparasitized (suffered parasitoid's host-feeding)	11	28.9
		Parasitized by		
		≥1 *Chrysocharis pentheus* eggs/larvae	3	7.9
		≥1 *Diglyphus minoeus* eggs/larvae	3	7.9
		one *Opius* sp. larva	6	15.8
		one *Opius* sp. larva and ≥1 *C. pentheus* eggs/larvae	3	7.9
		one *Opius* sp. larva and ≥1 *D. minoeus* eggs/larvae	8	21.1
		one *Opius* sp. larva and ≥1 *C. pentheus* and *D. minoeus* eggs/larvae	3	7.9
		two *Opius* sp. larvae	1	2.6
		Total	38	100.0
2 May	Pupa	Unparasitized	1	2.0
		Parasitized by		
		one *Opius* sp. larva	35	71.4
		one *Opius* sp. larva hyperparasitized by one *C. pubens* egg/larva	9	18.4
		one *Opius* sp. larva hyperparasitized by *Tetrastichus* sp. 5 larvae	1	2.0
		two *Opius* sp. larvae	2	4.1
		one *C. pubens* larva	1	2.0
		Total	49	100.0

67% had already been parasitized by the koinobiont *Opius* sp. on 24 April (Table 2). On 2 May, parasitism of *Opius* sp. was 96% and at least 19.1% of them were hyperparasitized by *Chry. pubens*. On 2 May when all healthy host larvae had pupated, 55.3% of killed host larvae also contained ≥ 1 *Opius* sp. larvae. The first and second instar larvae of *Opius* sp. had heavily sclerotized mandibles and head capsules and eliminated competitors in the same host. The later-instar larvae, however, lost their mandibles and were subject to hyperparasitism by late-attacking idiobionts. A comparison of Table 2 with Fig. 6 suggests that the potential pupal mortality caused by koinobiont parasitoids was higher than estimated from parasitoid emergence and that there was asymmetric competition between koinobionts and idiobionts.

Total host mortality increased, associated with intra-generational succession of the parasitoid community (Fig. 7); the increase was significant except for 1986 and 1989 (Spearman correlation, $P<0.05$). This suggests that late-attacking pupal idiobionts, especially *Chry. pubens*, acted not only as hyperparasitoids but also as primary parasitoids of host pupae.

Responses of parasitoid community to host population dynamics

The densities of emerging parasitoid wasps were next investigated in relation to host densities. The emerging parasitoid densities were estimated from the emergence rates of the samples in the 3rd week. The changes in emerging parasitoid densities were shown in Fig. 8 with
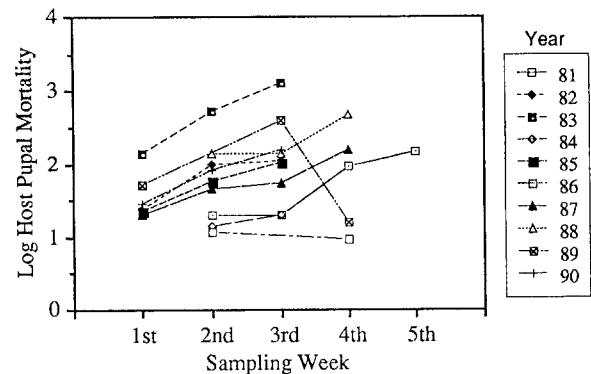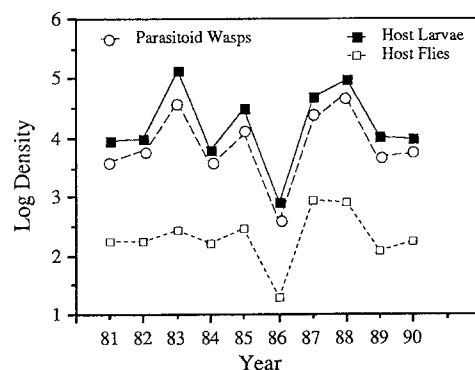

Fig. 7 Changes in host pupal mortality (log) over the five sampling weeks for 1981–1990

Fig. 8 Ten-year changes in log densities of host larvae, host adult flies and emerging parasitoid wasps

Fig. 9 Relationships between the log-odd ratio (=logit) and the log host larval density for four dominant parasitoid species, *Opius* sp. *Diglyphus minoeus*, *Chrysocharis pubens* and *Chry. pentheus*. Maximum likelihood regression equations are: *Opius* sp., $y = 0.13x - 1.87$, $r^2 = 0.023$, $P = 0.67$; *D. minoeus*, $y = 0.13x - 1.87$, $r^2 = 0.049$, $P = 0.54$; *Chry. pubens*, $y = 0.23x - 1.88$, $r^2 = 0.23$, $P = 0.163$; *Chry. pentheus*, $y = -0.21x + 0.006$, $r^2 = 0.441$, $P = 0.047$
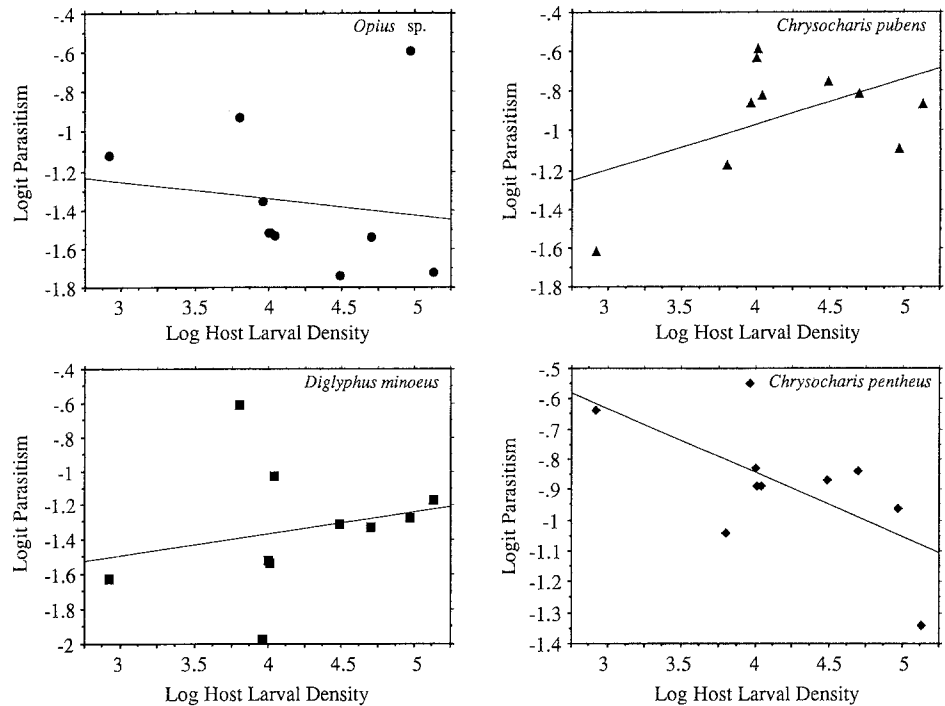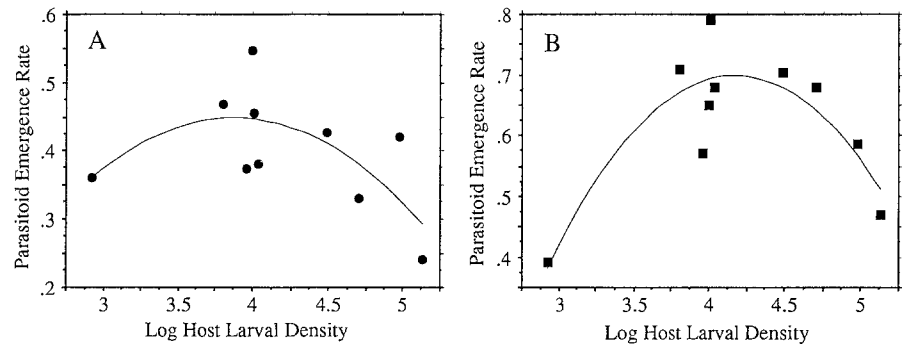

Fig. 10A Relationship between the emergence rate of larval parasitoids per killed host larvae and the host larval density. A regression line is shown ($y = -1.014 + 0.756x - 0.98x^2$, $r^2 = 0.31$, $P = 0.31$). **B** Relationship between the emergence rate of pupal parasitoids per killed host pupae and the host larval density. A regression line is shown ($y = -2.839 + 1.697x - 0.203x^2$, $r^2 = 0.69$, $P = 0.007$)

changes in host larval and adult densities. The log emerging parasitoid densities were significantly correlated with log host larval densities ($y = 0.96x - 0.29$, $r^2 = 0.99$, $P < 0.001$).

Density dependence of parasitoid attack was tested by applying logistic regression as suggested by Hails and Crawley (1992). The proportion of leafminers that were parasitized by parasitoid species (*p*) was transformed into the log-odd ratio, namely, $\log[p/(1-p)]$ by assuming a binomial distribution of sampling error, and regressed against the log host density. *Opius* sp. and *D. minoeus* were density independent (Fig. 9). Significant inverse density-dependence was detected in parasitism of *Chry. pentheus*. Logit parasitism of *Chry. pubens* suggested an optimum curve with a peak at log host larval density 4. The linear correlation was positive whereas the regression was not significant. *Chrysocharis pubens* was the dominant polyphagous pupal idiobiont species that can shift host species. Alternative hosts of *Chry. pubens* include *Cerodonta caricicola*, *Phytomyza heringiana*, *P. jucunda* and *P. milii*, all of which are

agromyzid leafminers that putate in the mine (Hansson 1985). These results suggest that the density dependence in pupal mortality reported in Kato (1994) might result from attack of the polyphagous pupal parasitoid, *Chry. pubens*, with its density-dependent host shifts.

The emergence rate of larval parasitoids per killed host larvae peaked at intermediate host densities and was reduced at low and high host density (Fig. 10A). Similarly, the emergence rate of pupal and larval-pupal parasitoids per killed host pupa peaked at intermediate host density and decreased at low and high host density (Fig. 10B). The emergence rates reflected not only the intensity of within-host competition but also the intensity of feeding attack by female parasitoid wasps.

Discussion

The parasitoid community of *C. suikazurae* was dominated by eulophid idiobiont species and accompanied by less abundant braconid koinobionts, and was largely

similar to that of lepidopterous leafminers described by Askew and Shaw (1979). Koinobiont species where characterized by (a) narrow host range, (b) early attack, (c) high fecundity and small eggs, (d) simple and immediate handling behaviour and (e) pro-ovigeny (wasps emerge with a full complement of eggs) but partially synovigenic (wasps can mature some eggs). One of the important behavioral cues in host searching by the koinobiont *Opius* sp. was vibration of host larvae, as reported for braconid parasitoids of tephritid larvae (Lawrence 1981) and of agromyzid larvae (Sugimoto et al. 1988). These characteristics of the koinobionts ensure potentially high attack rates and have formerly been regarded as necessary properties for biological control (Beddington et al. 1976). *Opius* sp. did not immediately kill the host and did not discriminate between parasitized and unparasitized hosts as long as the host larva is alive, and thus hyperparasitism occasionally occurred (Table 2). The sclerotized mandibles of young instar larvae are suspected to be used to eliminate intraspecific competitors as shown in a braconid species by Lawrence (1988).

The idiobiont species were characterized by (a) wide host range, (b) late attack, (c) low fecundity and large eggs, (d) elaborate host-handling behavior (e) synovigeny (wasps can mature more eggs). Synovigeny is linked with frequent feeding on the host by the female wasp. They do not refrain from attacking parasitoid larvae, and inter- and intraspecific hyperparasitism occurred quite commonly. Hyperparasitism can be viewed as an active foraging strategy rather than as a passive process in some circumstances (Speirs et al. 1991). The idiobionts of *C. suikazurae* fit this case. Late-attacking female wasps generally had advantages over erarly-attacking ones because they could kill previously deposited parasitoids using their ovipositors and venoms. Their relatively low attack rates resulting from features (b), (c) and (d) might be compensated by density-dependent host switching (a) and probably by high host-feeding rates deriving from their synovigenic habits (e).

Apparent succession in the parasitoid community within a host generation was observed (Figs. 3 and 4): early-attacking koinobionts were gradually replaced by late-attacking idiobionts. The process of within-host competition among parasitoids in host larvae was different from that in host pupae. Succession series in host larvae were from *D. minoeus* to *Chry. pentheus*; those in host pupae were from *Opius* sp. to *Chry. pubens*. Although pupal-parasitoid larvae cannot escape from the sclerotized host puparium, larval-parasitoid larvae can escape from host larvae to safer positions in a mine when they have finished larval development. Since the swelling of the larval body on a leaf surface and the chemical sign of parasitized hosts are important cues for parasitoid searching, it is adaptive for parasitoid larvae to move away from the host corpse for pupation.

This asymmetric within-host competition (i.e., late attackers are always winners) structured the parasitoid community (Fig. 2). The result of the contest between early-attacking and late-attacking parasitoids was usually determined not only by direct competition between parasitoid larvae coexisting in or on hosts but also by the female wasp's attack. The succeeding attack-in-waves by the late-attacking idiobionts greatly reduced not only the survival rate of early-attacking parasitoid larvae but also the survival rate of hosts (Figs. 6 and 7). These idiobionts can be regarded not only as hyperparasitoids but also as candidates for host regulation. As significant density dependence was detected in the pupal mortality (Kato 1994), it is hypothesized that the extended succession of a species-rich parasitoid community in host pupae might cause the density-dependent host pupal mortality. If these parasitoids have even slight propensities to prefer intact hosts to parasitized hosts of those and fed on by female wasps, the regulatory effect of their successive attack-in-waves will be stronger. The period during which parasitoid attack affects host mortality will be also important in determining the regulatory effect, because density-dependence was detected only in the host pupal stage, not in the larval stage.

The classical properties of biological control candidates deduced from equilibrium theory are specialist parasitoids which act in a density-dependent manner (Beddington et al. 1976; Huffaker 1971). This concept of regulation has been questioned, and predators and parasitoids adopting lying-in-wait and search-and-destroy strategies are viewed as suitable candidates for biological control in non-equilibrium systems by Murdoch et al. (1985). The leafminer population studied was subject to intense parasitism by koinobionts whose ecological properties were comparable to empirically developed criteria of biological control candidates. However, the host population was actually subject to density-dependent attack by pupal idiobionts (especially *Chry. pubens*), which are regarded as lying-in-wait polyphagous parasitoids. The density-dependent host switching has been detected in a pteromalid, *Nasonia vitripennis*, in a laboratory condition (Cornell and Pimentel 1978).

This study detected a regulatory effect of the species-rich parasitoid community upon host population dynamics, and proposed a hypothesis that the regulatory effect derived from succeeding attack-in-waves by polyphagous late-attacking idiobiont parasitoids, especially by a keystone species, *Chry. pubens*. This hypothesis coincides with the implication that parasitoid community richness is linked to the effect of parasitoids on host populations (Hawkins 1993; Cornell and Hawkins 1993). This study predicts that some host populations fostering differently structured parasitoid communities may not always be regulated by them, and the prediction was partly confirmed by Kato (in prep.). As most species constituting the parasitoid community were polyphagous, studies on dynamics of both the leafminer community and the parasitoid community will be necessary.

References

Askew RR, Shaw MR (1979) Mortality factors affecting the leaf-mining stages of *Phyllonorycter* (Lepidoptera: Gracillaridae) on oak and birch. 2. Biology of the parasite species. Zool J Linn Soc 67:51–64

Askew RR, Shaw MR (1986) Parasitoid communities: their size, structure and development. In: Waage J, Greathead D (eds) Insect parasitoids. Academic Press, New York, pp 225–264

Beddington JR, Free CA, Lawton JH (1976) Concepts of stability and resilience in predator-prey models. J Anim Ecol 45:791–816

Cornell HV, Hawkins BA (1993) Accumulation of native parasitoid species on introduced herbivores: A comparison of hosts as natives and hosts as invaders. Am Nat 141:847–865

Cornell H, Pimentel D (1978) Switching in the parasitoid *Nasonia vitripennis* and its effects on host competition. Ecology 59:297–308

Force DC (1974) Ecology of insect host-parasitoid communities. Science 184:624–632

Hails RS, Crawley MJ (1992) Spatial density dependence in populations of a cynipid gall-former *Andricus quercuscalicis*. J Anim Ecol 61:567–583

Hansson C (1985) Taxonomy and biology of the Palearctic species of *Chrysocharis* Foster, 1856 (Hymenoptera: Eulophidae). Entomol Scand Suppl 26:1–30

Hassell MP (1985) Insect natural enemies as regulating factors. J Anim Ecol 54:323–324

Hawkins BA (1993) Parasitoid species richness, host mortality, and biological control. Am Nat 141:634–641

Hawkins BA, Gross P (1992) Species richness and population limitation in insect parasitoid-host systems. Am Nat 139:417–423

Hawkins BA, Lawton JH (1987) Species richness for parasitoids of British phytophagous insects. Nature 326:788–790

Hochberg ME, Hawkins BA (1992) Refuges as a predictor of parasitoid diversity. Science 255:973–976

Huffaker CB (1971) Biological control. Plenum, New York

Huffaker CB, Kennett CE, Tassan RL (1986) Comparisons of parasitism and densities of *Parlatoria oleae* (1932–1982) in relation to ecological theory. Am Nat 128:379–393

Kakehashi M, Suzuki M, Iwasa Y (1984) Niche overlap of parasitoids in host-parasitoid systems: its consequence its single versus multiple introduction controversy in biological control. J Appl Ecol 21:115–131

Kamijo K (1978) Chalcidoid parasites (Hymenoptera) of Agromyzidae in Japan, with description of a new species. Jpn J Entomol 46:455–469

Kato M (1985) Life history and mortality pattern of the honeysuckle leaf-miner *Phytomyza lonicerae* Robineau-Desboidy (Diptera, Agromyzidae). Jpn J Entomol 53:604–615

Kato M (1989) Host-handling behavior of the parasitoid, *Diglyphus minoeus* (Hym.: Eulophidae), parasitizing the honeysuckle leaf-miner *Phytomyza lonicerae* (Dip.: Agromyzidae). Entomophaga 34:503–509

Kato M (1994) Alternation of bottom-up and top-down regulations in a natural population of an agromyzid leafminer, *Chromatomyia suikazurae*. Oecologia

Lawrence PO (1981) Host vibration – a cue to host location by the parasite, *Biosteres longicaudatus*. Oecologia 48:249–251

Lawrence PO (1988) Intraspecific competition among first instars of the parasitic wasp *Biosteres longicaudatus*. Oecologia 74:607–611

May RM, Hassell MP (1981) The dynamics of multiparasitoid-host interactions. Am Nat 117:234–261

Murdoch WW, Chesson J, Chesson PL (1985) Biological control in theory and practice. Am Nat 125:344–366

Price PW (1973) Parasitoid strategies and community organization. Environ Entomol 2:623–626

Price PW (1975) Reproductive strategies of parasitoids. In: Price PW (ed) Evolutionary strategies of parasitic insect and mites. Plenum, New York, pp 87–111

Price PW (1991) Evolutionary theory of host and parasitoid interactions. Biol Control 1:83–93

Scholz D, Höller C (1992) Competition for hosts between two hyperparasitoids of aphids, *Dendrocerus laticeps* and *Dendrocerus carpentesi* (Hymenoptera: Megaspilidae): the benefit of interspecific host discrimination. J Insect Behav 5:289–300

Speirs DC, Sherratt TN, Hubbard SF (1991) Parasitoid diets: does superparasitism pay? Trend Ecol Evol 6:22–25

Sugimoto T, Shimono Y, Hata Y, Nakai A, Yahara M (1988) Foraging for patchily-distributed leaf-miners by the parasitoid, *Dapsilarthra rufiventris* (Hymenoptera: Braconidae) III. Visual and acoustic cues to a close range patch-location. Appl Entomol Zool 23:113–121

Takada H, Kamijo K (1979) Parasite complex of the garden pea leaf-miner, *Phytomyza horticola* Gourea, in Japan. Jpn J Entomol 47:18–37

Taylor AD (1988) Parasitoid competition and the dynamics of host-parasitoid models. Am Nat 132:417–436

Tscharntke T (1992) Coexistence, tritrophic interactions and density dependence in a species-rich parasitoid community. J Anim Ecol 61:59–67

Washburn JO, Cornell HV (1981) Parasitoids, patches, and phenology: their possible role in the local extinction of a cynipid gall wasp population. Ecology 62:1597–1607

Zwölfer H (1979) Strategies and counterstrategies in insect population systems competing for space and food in flower heads and plant galls. Fortschr Zool 25:331–353