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Alternation of bottom-up and top-down regulation in a natural population of an agromyzid leafminer, *Chromatomyia suikazurae*

Abstract The population dynamics and the relative importance of bottom-up and top-down effects in a plant-leafminer-multiparasitoid interaction was studied between 1981 and 1990 in a natural forest in Kyoto, Japan. The leafminer, *Chromatomyia suikazurae* (Agromyzidae, Diptera), passed two generations (G1 and G2) on *Lonicera gracilipes* (Caprifoliaceae). The G1 population in February was free from parasitoid attack, and the mortality in G1 was mainly caused by resource limitation. Intraspecific competition for resources occurred at the larval stage in G1, and the larval mortality was density-dependent. The G1 adult density was resource-limited (the number of newly opened leaves), and its variability was lower than that of G2. The G2 population in April was not resource-limited but subject to intense attack by a species-rich parasitoid complex, and thus total mortality was much larger than that in G1. Significant density dependence was detected not in larval but in pupal mortalities, which were mainly caused by parasitism by parasitoids that attacked the pupa. The host population alternately experienced "bottom-up" effects during the larval stage in G1 and "top-down" effects during the pupal stage in G2. Overall population fluctuation was non-cyclic and mainly due to climatically-induced fluctuation of available plant resources in G1.

Key words Population dynamics · Density dependence · Resource limitation · Leafminer · Parasitoid

Introduction

The population dynamics of insect herbivores can be understood in the context of plant-herbivore-enemy interactions (Price et al. 1980; Faeth 1987) and the relative importance of "bottom-up" (due to variations in resource base) and "top-down" (due to variations in mor-

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tality caused by natural enemies) effects differs among insects in various tritrophic interactions (Price 1992; Hunter 1992). Recent detailed studies emphasize the stronger effects of resource quantity and quality compared to top-down effects (Price et al. 1980; Price and Clancy 1986; Stiling 1987, 1988; Price 1988; Ohgushi 1992). Top-down regulation has sometimes been studied in the context of introduction of parasitoids to attempt to control exotic pests (De Bach et al. 1971; Embree 1966; Murdoch et al. 1985; Greathead 1986; Quednau 1990) and by field experiments excluding natural enemy effects (Faeth and Simberloff 1981; Mason 1987).

Endophytic insects such as gallmakers and leafminers generally have species-rich parasitoid complexes (Askew and Shaw 1986; Hawkins and Lawton 1987; Hochberg and Hawkins 1992), and the insects associated with more parasitoid species are subject to more intense parasitoid attack (Hawkins 1993; Cornell and Hawkins 1993). Alternatively, endophytic insects suffer death from abscission because their feeding stages are encased in leaf tissue and are dependent on the leaf for food and moisture (Faeth et al. 1981; Potter 1985; Bultman and Faeth 1986; Stiling et al. 1987; Kahn and Cornell 1989). However, there have been few long-term population studies of natural plant-herbivore-multiparasitoid systems. The aim of this study is to describe population dynamics over 10 years of a leafminer, its host plant leaves and its parasitoids, and to find the relative importance of bottom-up and top-down effects.

Chromatomyia suikazurae (Agromyzidae, Diptera) is a leafminer on *Lonicera* species (Caprifoliaceae). The leafminer passes two discrete generations on host leaves in spring; the first generation is completely free from parasitoid attacks but the second is subject to intense attack by a diverse parasitoid community (Kato 1985). I made a detailed 10-year population census of this species and its parasitoid community in a natural forest in Kyoto, Japan. In this paper, I describe, the dynamics of the leafminer population and the available plant resource, and explore key factors using the methods presented by Royama (1977, 1984). Next, density-depen-

dent sources of regulation are examined by applying logistic regressions as presented by Hails and Crawley (1992). Structure, organization and responses of its parasitoid community to the host population dynamics are reported in Kato (1994).

Materials and methods

Life history of the leafminer

Chromatomyia suikazurae Sasakawa, 1993 is an agromyzid species mining in the palisade parenchyma of leaves of *Lonicera* spp. (Caprifoliaceae) (Sasakawa 1993; 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* (Fig. 1). The larval period is about 15 days in G2. Adult flies emerge from overwintering pupae in evergreen leaves of *Lonicera japonica* and oviposit on newly opened leaves of *L. gracilipes* on mild warm days in early February (Fig. 1). Larvae (G1) pupate from late February to early March, and new adult flies emerge from late March to early April. Most living larvae (G2) have pupated by the end of April. Adult flies emerge from the pupae in G2 in late May and June. From June to October very few living mining larvae are found in *L. gracilipes* and *L. japonica*. In late September to October, mining larvae are found on newly opened leaves of *L. japonica*, but at very low densities.

Study area

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. The study site is covered by a natural (partly secondary) deciduous forest dominated by *Quercus serrata, Q. variabilis* and *Castanea japonica*. The understory (consists mostly of shrubs such as *Lindera obtusibola, L. umbellata, Ilex crenata, Osmanthus heterophyllus, Callicarpa mollis, Viburnum erosum, Abelia septhulata, A. serrata* and *Lonicera gracilipes*. All these plant species are native. A 100 × 100 m quadrat was established in the forest containing 76 plants of *L. gracilipes*, which were numbered. Climbers of *L. japonica* were present at the forest margin near the study site, but their density was much lower than that of *L. gracilipes*. Meteorological observations were made at Kamigamo experimental forest of Kyoto University (135 m in altitude), 3.3 km southwest of the study site. Changes in the monthly mean of daily maximum temperature of the site from January to May between 1981 and 1990 are shown in Fig. 2.

Field sampling

The population of *L. gracilipes* was censused from 1981 to 1990. The numbers of mined and unmined leaves and leafminers on all the plants in the quadrat were counted in late February and early March (G1). At least 100 mined leaves were randomly sampled in early March and the numbers and instars of larvae they contained were recorded. All mined leaves collected were incubated in glass bottles under outdoor conditions. After April, the numbers of emerging adult flies were counted.

In G2, stratified complete sampling was done. All mined leaves of haphazardly selected plants were sampled sequentially at an interval of 1–7 days from late April to middle May. The number of sampled plants ranged from 13 to 61 (mean = 34.4, SD = 16.3). All mined leaves collected were sorted by leafminer stage (first- to third-instar larvae and pupae) and state (removed by predators,
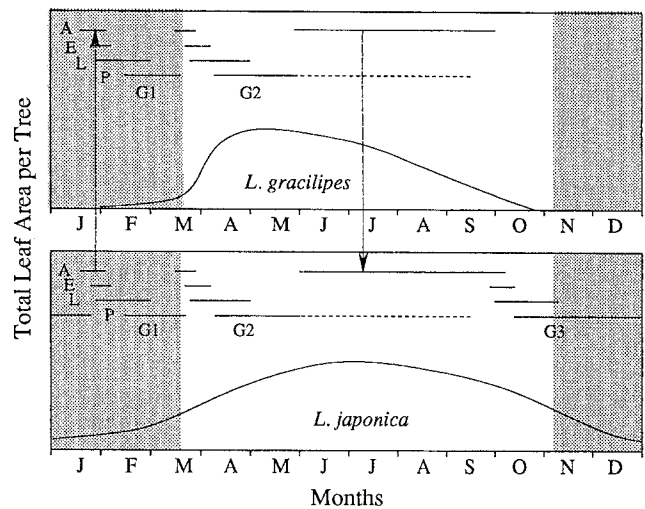

Fig. 1 Life history patterns of *Chromatomyia suikazurae* and changes in the total leaf area of the two host plant species, *Lonicera gracilipes* and *L. japonica*, in Kyoto: *A*, adult fly; *E*, egg; *L*, larva; *P*, pupa. Uncertain processes are shown in broken lines. *Arrows* refer to host plant shifts by adult flies. *Shaded areas* refer to the period during which parasitoid wasps are not active
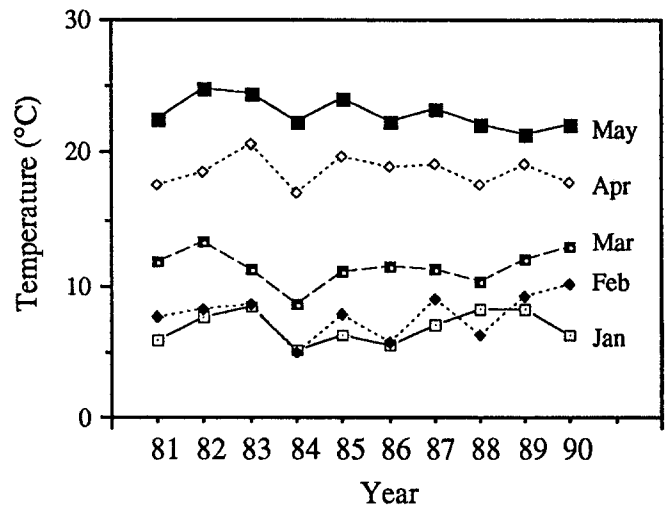

Fig. 2 Annual changes in monthly mean of daily maximum temperature (°C) from January to May at Kamigamo Experimental Forest (after Kyoto University Forest 1981–1990).

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. Forewing and ovipositor lengths of individuals of each parasitoid species were measured.

The density of leafminers 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 their mean densities per leaf by the total number of leaves in the quadrat. The log-transformed leaf, larval, pupal and adult densities per quadrat at the g th generation ($g = 1-2$) in the t th year ($t = 1981-90$) are given

as $L(t, g)$, $NL(t, g)$, $NP(t, g)$ and $NA(t, g)$, respectively. $L(t, 1)$ was directly counted every year. $L(t, 2)$ was directly counted in 1981 and was estimated to be largely constant afterwards.

Results

Demographic patterns and mortality factors were very different between G1 and G2. Life table studies (Table 1) show that larvae and pupae in G1 were free from parasitism and predation. Mean larval and pupal mortalities ($\pm$ SD, range) were 32.9% ($\pm$21.4, 3.8–64.5) and 41.6% ($\pm$28.1, 1.8–71.7), respectively. Because the mortality and adult size were strongly affected by the leaf area (Kato 1985), the mortality factor is thought to be food limitation.

Life-tables for G2 are shown in Table 2. The egg density was estimated from the egg mortality measured on the intensively studied plants. Egg mortality was generally very low ($\leq 2\%$, mean $= 0.31\%$). There were no egg parasitoids and unhatched eggs might have been infertile. Mean mortalities ($\pm$ SD, range) of first to third instar larvae were 2.4% ($\pm$1.5, 0.7–5.8), 12.8% ($\pm$5.3, 4.6–21.8) and 52.9% ($\pm$10.5, 37.2–68.6), respectively. Most larval mortality was caused by parasitism and host-feeding by parasitoids. Mean percentage ($\pm$SD, range) parasitism in first to third instar larvae was 0% ($\pm$0), 24.3% ($\pm$11.9, 5.2–46.3) and 48.3% ($\pm$21.9, 30.0–87.8), respectively, based on parasitoid emergence. Accordingly, the fraction of parasitism might have been underestimated, especially for younger instars, because host death not accompanied by parasitoid emergence might be caused not only by either host-feeding or parasitism and parasitoid death. Parasitoid larval mortality is caused by food limitation, superparasitism, within-host competition and host-feeding by other parasitoids.

Mean pupal mortality ($\pm$SD, range) was 95.7($\pm$2.9, 89.8–99.5)%. Mean percentage ($\pm$SD, range) parasitism of pupae was 59.4($\pm$11.8, 39.1–79.0)%. On average, 8.4($\pm$4.0, 2.9–14.5)% of pupae were predated by unknown organisms. There were two types of predation traces: empty puparia and puparia removed from mines. The predators are presumed to be predacious insects and passerine birds. Mortality by pupal parasitism might have been underestimated, and a large proportion of the fraction of unknown mortality (28.0%) is thought to be also caused by parasitism.

Over the period 1981–1990, G1 larval density peaked in 1983 and 1990 (Fig. 3). In G2, larval density peaked in 1983 [5.13 (log)] and was about an order of magnitude lower than the leaf density [6.2 (log)], which was two orders of magnitude higher than that in G1. The mean larval and pupal densities in G1 was not significantly different from those in G2 (larvae, $t = 1.36$, $df = 18$, $P > 0.05$; pupa, $t = 0.50$, $df = 18$, $P > 0.05$), but mean adult density in G1 was significantly higher than that in G2 ($t = 6.13$, $df = 18$, $P < 0.001$). The variances of log larval and pupal densities were significantly smaller in G1 than in G2 (Table 3; larva, $F = 3.371$, $P < 0.05$; pupa,

Table 1 Life-tables of *Chromatomyia suikazurae* for G1 in 1981–1990 at Wakura site, Kyoto. (lx proportion of original cohort surviving to start of each stage, qx mortality %).

Stage	Mortality factor	1981		1982		1983		1984		1985		1986		1987		1988		1989		1990		Mean	
		lx	qx	lx	qx	lx	qx	lx	qx	lx	qx	lx	qx	lx	qx	lx	qx	lx	qx	lx	qx	lx	qx
Larva	Food limitation	1000	48.8	1000	30.9	1000	64.5	1000	41.5	1000	47.2	1000	3.8	1000	41.2	1000	21.9	1000	28.0	1000	41.3	1000	36.9
Pupa	Food limitation	513	71.7	691	51.5	355	64.5	585	65.6	528	28.6	962	8.4	588	57.6	781	1.8	720	62.8	587	4.7	631	41.7
Adult		145		335		126		201		377		880		249		766		267		560		391	
Female sex ratio (%)			?		54.2		?		?		?		?		?		39.1		62.2		52.1		51.9

Table 2 Life-tables of *Chromatomyia suikazurae* for G2 in 1981–1990 at Iwakura site, Kyoto. [lx proportion of original cohort (1000) surviving to start of each stage, and qx is the mortality (%); the number of 1st instar larvae is set as 1000].

Stage	Mortality factor	1981 lx	1981 qx	1982 lx	1982 qx	1983 lx	1983 qx	1984 lx	1984 qx	1985 lx	1985 qx	1986 lx	1986 qx	1987 lx	1987 qx	1988 lx	1988 qx	1989 lx	1989 qx	1990 lx	1990 qx	Mean lx	Mean qx
Egg	Unknown	1017	1.7	1011	1.1	1000	0.0	1000	0.0	1002	0.2	1000	0.0	1001	0.1	1000	0.0	1000	0.0	1000	0.0	1003	0.3
Larva I	Host-feeding	1000	2.6	1000	1.2	1000	1.8	1000	3.1	1000	2.4	1000	5.8	1000	1.0	1000	0.7	1000	2.9	1000	2.5	1000	2.4
Larva II		974	21.8	988	9.5	982	13.4	969	15.7	975	13.1	942	20.5	990	8.5	993	4.6	971	10.5	974	10.8	976	12.8
	Parasitism		5.1		3.5		0.7		3.9		3.3		2.1		1.5		1.1		3.1		5.0		2.9
	Host-feeding		16.7		6.0		12.7		11.8		9.8		18.4		7.0		3.5		7.4		5.8		9.9
Larva III		762	54.2	894	42.7	850	58.0	817	58.0	848	60.4	749	68.6	906	54.8	947	37.2	869	58.2	869	36.7	851	52.9
	Parasitism		25.5		21.0		17.4		33.1		29.7		60.2		19.9		16.9		28.5		22.7		27.5
	Host-feeding		28.7		21.7		40.6		24.9		30.7		8.4		34.9		20.3		29.7		14.0		25.4
Pupa		349	94.3	512	96.7	357	99.5	343	92.4	336	97.2	235	89.8	409	95.6	595	98.5	364	96.7	550	96.7	405	95.7
	Parasitism		53.8		76.4		46.9		61.9		68.4		35.1		64.9		57.7		65.7		62.9		59.4
	Predation		11.7		14.0		7.1		2.7		9.0		4.3		12.9		7.1		10.5		4.8		8.4
	Unknown		28.8		6.3		45.5		27.8		19.8		50.4		17.8		33.7		20.5		29.0		28.0
Adult		19.8		16.8		1.9		26.2		9.5		24		17.9		8.8		11.5		18.4		15.5	
Female sex ratio (%)		34.8		48.9		46.4		46.8		45.0		70.0		47.1		39.1		46.7		46.7		47.2	

Table 3 Means, ranges and variances of log larval, pupal and adult densities for G1 and G2. Means with same letters are not significantly different (t-test, $P > 0.05$)

Generation	Variable	Mean	Range	Variance
G1	NL(t, 1)	3.89a	3.13–4.36	0.12
	NP(t, 1)	3.67b	3.11–4.01	0.07
	NA(t, 1)	3.40c	3.08–3.99	0.10
G2	NL(t, 2)	4.20a	2.92–5.13	0.42
	NP(t, 2)	3.80bc	2.29–4.75	0.51
	NA(t, 2)	2.31d	1.30–2.96	0.21

Table 4 Regressions of SV (t, g) and OV(t, g) upon log larval and adult densities, respectively

Dependent variable	Independent variable	Value of y	r^2	P
SV(t, 1)	NL(t, 1)	1.20−0.44x	0.29	0.11
OV(t, 1)	NA(t, 1)	0.75+0.02x	0.00	0.98
SV(t, 2)	NL(t, 2)	−0.31−0.38x	0.54	0.02
OV(t, 2)	NA(t, 2)	4.26−1.17x	0.73	0.004

$F = 7.125$, $P < 0.005$). The maximum amplitude of fluctuation in larval density was 16.9 times [1.23 in (log)] in G1 and 161 times [2.21 in (log)] in G2. In contrast, the variance of adult density was not significantly different between G1 and G2 ($F = 2.12$, $P > 0.05$).

I now analyze the key factors of population fluctuations using the methods presented by Royama (1977, 1984). Inter-generational rate of larvae, RL(t, g) can be given as

$$RL(t, g) = SV(t, g) + OV(t, g),$$

where SV(t, g) is survival rate of larvae to adults and OV(t, g) is oviposition rate and given as follows:

$$SV(t, g) = NA(t, g) - NL(t, g)$$
$$OV(t, 1) = NL(t, 2) - NA(t, 1)$$
$$OV(t, 2) = NL(t + 1, 1) - NA(t, 2).$$

As the population data of G3 on *L. japonica* are lacking, OV(t, 2) actually represents the combined effect of oviposition rate in G2 and survival and oviposition rates in G3.

Annual changes of RL(t, g), SV(t, g) and OV(t, g), indicate that in G1, RL(t, 1) paralleled OV(t, 1), and the two were significantly correlated ($r^2 = 0.74$, $P < 0.002$), whereas RL(t, 1) and SV(t, 1) varied independently ($r^2 = 0.02$, $P > 0.05$) (Fig. 4). In G1, neither survival nor oviposition were significantly density dependent (Table 4).

NL(t, 1) had a higher correlation with the monthly mean of daily maximum temperature in February ($r^2 = 0.19$, $P > 0.05$) than those in January ($r^2 = 0.07$) and March ($r^2 = 0.00$) and than any monthly means of daily mean temperature. When log numbers of newly opened leaves were regressed against log numbers of G1 larvae, pupae and adults, there was a weak positive correlation of NL(t, 1) and NP(t, 1) with L(t, 1) ($r^2 = 0.27$ and 0.57, respectively) (Fig. 5) and a strong correlation between

Fig. 3 Ten-year changes in larval [NL(t, g)], pupal [NP(t, g)] and adult [NA(t, g)] densities (in log) of *Chromatomyia suikazurae* for G1 (left) and G2 (right). Changes of leaf densities [L(t, g)] are also illustrated
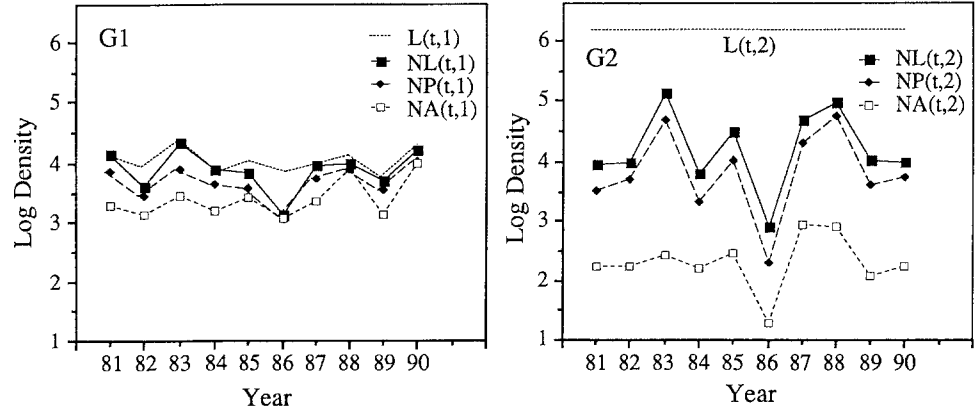

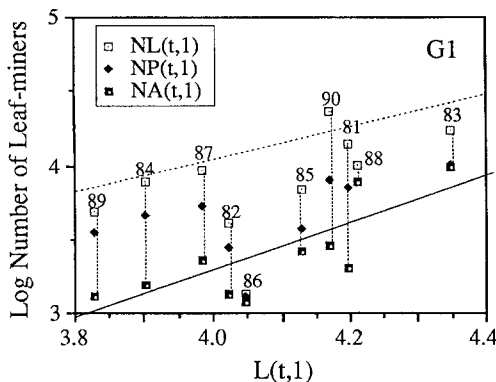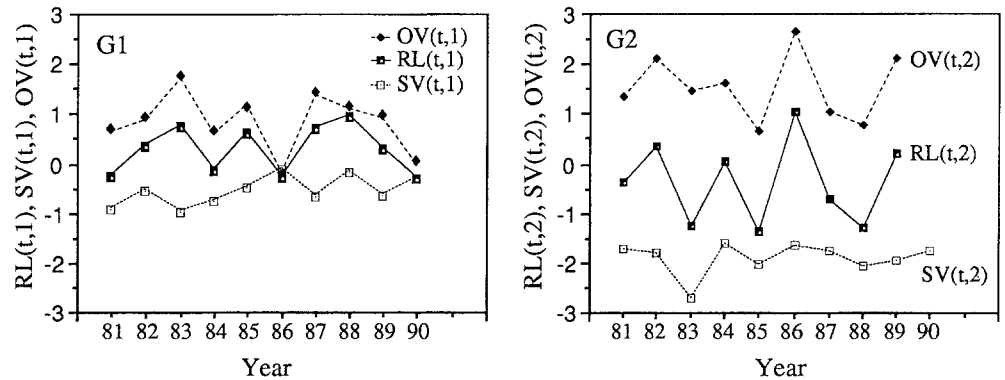**Fig. 4** Ten-year changes in SV(t, g), OV(t, g) and RL(t, g) for G1 (left) and G2 (right)

Fig. 5 Log larval, pupal and adult densities against log number of leaves at G1. The *regression line* of NA(t, 1) upon L(t, 1) is shown ($y = -3.1243 + 1.59x$, $r^2 = 0.66$). The *broken line* refers to $y = x$

NA(t, 1) and L(t, 1) ($r^2 = 0.64$, $P < 0.05$). This suggests that leafminer population size at G1, especially adult density, was limited by the number of newly opened leaves of *L. gracilipes*. Although exploitative competition in a multiple-oviposited leaf acted in a density-dependent fashion, it had minor effects on the population fluctuation compared with oviposition. OV(t, 1) was independent of NA(t, 1) (Table 4) and had higher correlation with the monthly mean of daily maximum temperature in February ($r^2 = 0.43$, $P < 0.05$) than in those in March ($r^2 = 0.00$) and in April ($r^2 = 0.23$). This suggests that the temperature at the G1 larval stage in February

might have affected the oviposition rate of the adult fly in April via plant quality (i.e., leaf area).

In G2, the fluctuation of RL(t, 2) largely paralleled that of OV(t, 2), and their regression was significant ($r^2 = 0.85$, $P < 0.001$) (Fig. 4). SV(t, 2) was also positively correlated with RL(t, 2), although not significantly ($r^2 = 0.43$, $P > 0.05$). These results show that the key factor determining population fluctuation is the change in OV(t, 2), i.e., the unknown process in G3. In contrast with G1, SV(t, 2) and OV(t, 2) were significantly negatively correlated with NL(t, 2) and NA(t, 2), respectively (Table 4).

The key factors determining the total mortality in G2 were next investigated. Annual fluctuations of sub-mortalities (k) for larvae and pupae and of combined K are shown in Fig. 6. Values of slope b in the regression of k on K in G2 were -0.0007 ($r^2 = 0.12$, $P > 0.05$), -0.022 ($r^2 = 0.05$, $P > 0.05$), 0.0044 ($r^2 = 0.00$, $P > 0.05$) for first to third instar larvae and 1.034 ($r^2 = 0.88$, $P < 0.05$) for pupae. This result shows that the key factor in the survival process in G2 was pupal mortality, a large proportion of which was caused by larval-pupal parasitoids in host larval stages (Kato 1994).

Density dependence of larval and pupal mortalities was tested by applying the logistic regression presented by Hails and Crawley (1992). The proportion of leafminers that died (p) was transformed into the odd-ratio, namely, $\log[p/(1-p)]$, by assuming a binomial distribution of sampling error, and regressed against the log host density. Significant density dependence was detect-
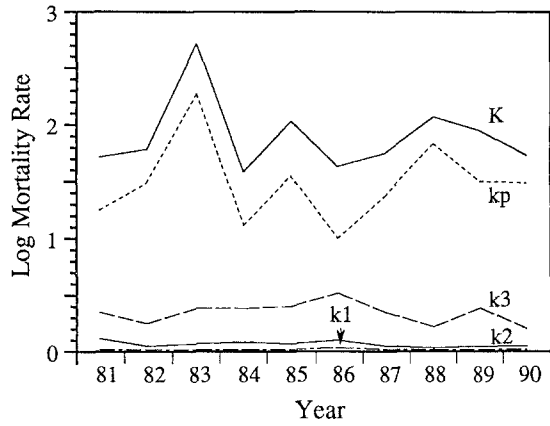
Fig. 6 Key factor analysis of the G2 population: k_1-k_3, submortalities (k) for first to third instar larvae: kp, k for pupae; K, total of ks

ed in larval mortalities in G1 ($P < 0.002$) and in pupal mortalities in G2 ($P < 0.001$) (Fig. 7).

Discussion

The first and second generation of the host displayed contrasting mortality patterns and annual fluctuations (Fig. 3). The first generation was distinguished from the second generation by lower larval and pupal mortality and less variable annual fluctuations. The density of adults in the first generation was limited largely by the number of newly-opened leaves available for the larvae; their size by the size of the leaves and the number of

larvae per leaf (Kato 1985). The larval density in the second generation was largely proportional to the adult fly density in the first generation. The mean OV(t, 1) was 0.897 (i.e., 7.9 times growth), and OV(t, 1) was independent of NA(t, 1) (Table 4). Thus, the fluctuation of larval density in the second generation was mainly created in the resource availability in the first generation. This leafminer species was unique in having a parasitoid-free generation. Although the first generation can be regarded as temporal refuge of the leafminer from parasitoid attack, resource limitation causes high mortality (the mean SV(t, 1) was -0.493) and the mean inter-generational population growth rate [RL(t, 1)] was only 0.315 (about 2.1 times).

In the second generation, the initial larval density (range 2.92–5.13 in log) was much lower than the available (i.e., suitable for adult female's oviposition and larval development) leaf density [6.2 in (log)], thus the population level was not resource-limited. The total mortality in the second generation was 23 times [1.39 in (log)] higher than in the first generation. Unknown mortality during pupal stage were probably caused by parasitoid attack, because most failures of parasitoid emergence were thought to be caused by interspecific competition in host pupae (Kato 1994). About 8.4% (range 2.9–14.5%) of pupae were killed by predators, but most of them were probably previously parasitized. Thus, almost 100% of larval mortality and 91.6% of pupal mortality in the second generation were estimated to be caused by parasitoids (Table 2). The estimated parasitoid attack rates (97.6–99.8%) were much higher than those on agromyzid leafminers on cultivated host plants (48–84%, Takada and Kamijo 1979; 2–58%, Drea et al.

Fig. 7 Relationships between the log-odd ratio (=logit) and log host density for G1 (*left*) and G2 (*right*) and for host larvae (*upper*) and pupae (*lower*). *Regression lines* and 95% *confidence bands* for the true mean of y are shown. Maximum likelihood regression equations are: G1 larvae, $y = 1.088x-4.527$, $r^2 = 0.74$, $P = 0.001$; G1 pupae, $y = -0.156x + 0.257$, $r^2 = 0.00$, $P = 0.88$; G2 larvae, $y = 0.091x - 0.210$, $r^2 = 0.07$, $P = 0.45$; G2 pupae, $y = 0.244x - 2.52$, $r^2 = 0.88$, $P = 0.0001$
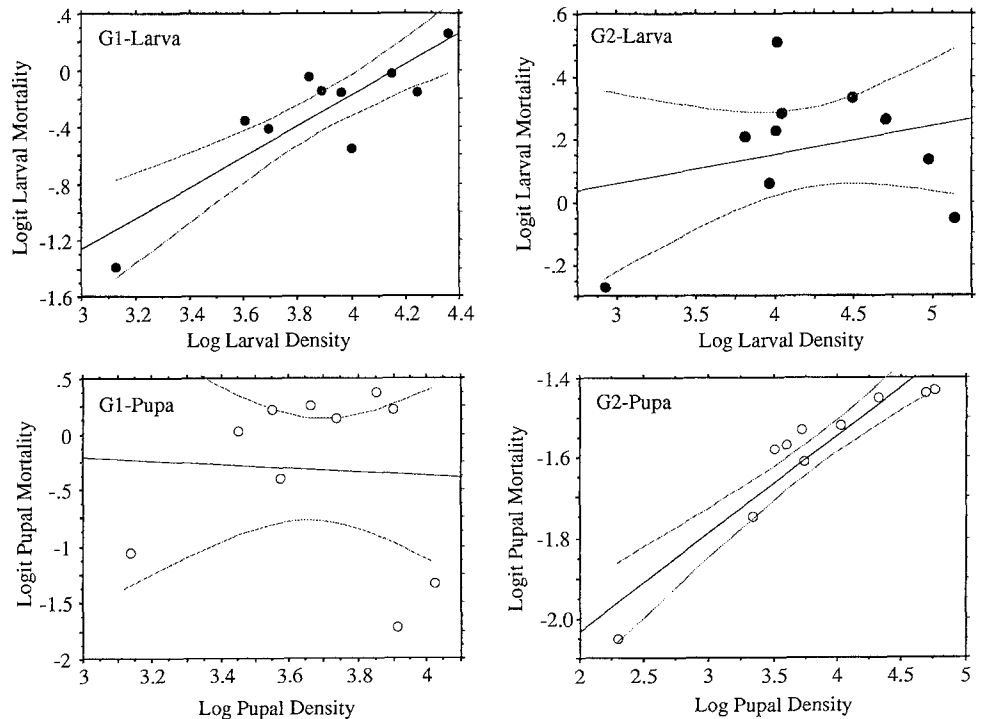
1981; 3–58%, Potter 1985). This coincides with the implication that herbivore populations associated with species-rich complexes of native parasitoids suffer more intense attack than populations on exotic host plants associated with less species-rich complexes on exotic host herbivores (Cornell and Hawkins 1993).

Significant density-dependence in the second generation was detected in pupal but not in larval mortality (Fig. 7). This density-dependence was thought to be caused by succeeding attack-in-waves by many species of parasitoids and by density-dependent host switching by a polyphagous late-attacking idiobiont parasitoid, *Chrysocharis pubens* (Kato 1994). The density-independence at host larval stage is thought to result from shortness of the host's larval period.

Long-term population studies of forest herbivores have shown that many species display population cycles with average periodicities of 8–11 years, and that mechanisms that have been proposed to cause cyclic dynamics include genetic variation, qualitative variation, climatic release, food quality deterioration, food quality improvement following plant stress and disease susceptibility (Myers 1988). Royama (1977) showed that second-order processes characterized by time-lags arising from the impact of one generation on the reproduction and survival of the next or later generation result in cyclic behavior. The second-order factors determining the basic oscillation of eastern spruce bud worm were disease, specific parasitoids and some unknown causes (Royama 1984). The population dynamics of *C. suikazurae* contrasted with these cyclic fluctuations. The absence of oscillation might result from (1) presence of the parasitoid-free generation and (2) paucity of second-order mortality factors such as attacks by specialist parasitoids and diseases (Kato 1994). The larval density fluctuation in the second generation paralleled the resource availability in the first generation, whose fluctuation was created by non-cyclic meteorological changes.

The 10-year study suggests that the leafminer population was regulated by bottom-up effects at the larval stage in the first generation and top-down effects at the pupal stage in the second generation. The bottom-up and the top-down effects alternated between generations. If the relative importance of these effects is compared by the extent to which they reduce the adult population level, top-down effects would be stronger than bottom-up effects because the total mortality was much larger in the second generation than in the first (Fig. 4). If it is compared by the variability of adult population level, bottom-up effects would be stronger because the variance of $NA(t, 1)$ was less than that of $NA(t, 2)$ (Table 1). Resource limitation in the first generation acted as an upper ceiling when adult population level in the third generation increased. When unusually high temperature in early spring triggered an increase of available new leaves, the larval density in the second generation attained a high level but the adult density in the second generation was regulated by parasitoid attack. Correlation among factors does not mean causation, and experiments removing enemies or resource limitation are needed to evaluate causation of regulation (Price 1984; Royama 1992). A comparison between such experiments and this long-term population study will be needed to evaluate the relative importance of bottom-up and top-down effects in such unusual situations.

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