Defoliation to maintain multivoltinism:

Host regulation by a sawfly *Strongylogaster osmundae*

(Hymenoptera: Tenthredinidae) on osmund fern *Osmunda japonica*

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15 Text pages
5 Tables
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Abstract. Voltinism and host plant utilization of a sawfly *Strongylogaster osmundae* were investigated. This species was multivoltine (5 or 6 generations per year) and emerged from late April to July or early August in Kyoto, Japan. Female sawflies deposited eggs on new leaves of an osmund fern, *Osmunda japonica*, and larvae fed on them. The host plant usually developed new leaves from late April to early May (primary shoots), and intact ferns rarely shot new leaves thereafter. As primary shoots were new and available to the sawfly until the beginning of June at latest, only the first and second generations could utilize them. The eggs were laid in clusters, and the larvae fed gregariously and frequently defoliated leaves. The defoliation by the first and second generations induced the fern's compensatory regrowth, which produces food resource of the third and subsequent generations. Therefore, egg clumping and defoliation by *S. osmundae* is a kind of host regulation to maintain its multivoltine life history.

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The number of generations in a year (voltinism) of a phytophagous insect must be determined by the phenology of host plant(s) as well as environmental conditions such as temperature and photoperiod. It would be difficult for insects which depend on seasonally limited resources to complete two or more generations a year. For instance, flower and immature seed feeding two pierid butterflies, *Anthocharis scolymus* and *A. cardamines*, are univoltine while most of leaf feeding pierid butterflies in Japan are bi- or multivoltine (Fukuda et al. 1982).

Many sawflies (Tenthredinoidea) are univoltine (e.g. Naito 1982). According to Okutani (1959), 26 species (63%) out of 41 Japanese Tenthredinidae are univoltine. Among 38 Japanese Selandriinae (Tenthredinidae), larvae of which feed ferns or moss, 26 species (68%) are univoltine (Naito 1971, 1975, Naito personal communication). High frequency of univoltine must be partly due to the fact that sawflies always utilize new leaves and/or other parts of new shoots, which are abundant in spring.

Both univoltine and bivoltine (or multivoltine) sawflies, however, sometimes occur on a same host plant (e.g. sawflies on a bracken *Pteridium aquilinum*, Lawton 1976). If new leaves are essential diet, how do multivoltine species get its food? Two congeneric sawflies, *Strongylogaster secunda* and *S. osmundae* (Selandriinae), feed on new leaves of an osmund fern, *Osmunda japonica*: the former is univoltine (Okutani 1959, Naito personal communication), the latter is bivoltine (Okutani 1959)

or multivoltine.   I investigated voltinism and resource utilization of *S. osmundae* and the reaction of *O. japonica* in the field.   In this paper I report that *S. osmundae* regulates its host plant by feeding, prolongs the leaf-opening season, and enables multivoltine life history on the fern.

Materials and methods

   Field observations

   To know the seasonal fluctuation of population size and voltinism and the pattern of host plant utilization of *S. osmundae* outdoors, I studied 1) number of generations that this sawfly repeats in a year and seasonal change of its population size, 2) ovipositing and larval feeding habit on its host plant *Osmunda japonica*, 3) preference for host plant leaf age by the sawfly, and, 4) the host plant phenology and its alternation by the sawflies.

   I selected six small areas in Kyoto City (Ca. 35°N): four areas at Ichijoji (altitude: 150 - 200m; one area was named "JIZO" and another was named "M") and two at Kamigamo (altitude: 130 - 160 m, Kamigamo Experimental Forest Station, Kyoto University). Each area contained 20 to 40 individual plants of *O. japonica*. An intensive field survey was carried out every day from April to October in 1985. Each individual fern as well as all its leaves were distinguished. The dates of following three

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growth stages of each leaf were recorded: the beginning of leaf opening (OB), the end of opening (OE), and the end of elongation (EE) (Fig. 1). The number of pinnules of each leaf was also counted. When some pinnules disappeared, date, pinnule number and cause of defoliation were recorded. The eggs and larvae of the sawfly, on each leaf were counted. For some leaves, the distribution of eggs, the location of larvae, and their feeding sites were recorded.

Similar survey was carried out from 1986 to 1989 at some of the six areas.

Laboratory experiments

All adult sawflies which were used in the experiments on oviposition were collected in the field when they were fifth instar larvae and reared in the laboratory. Some of their offsprings were also used in the experiment on larval growth. All these insects were reared under constant temperature of 25°C and a photoperiod of 16L8D.

1) Oviposition. In June and July in 1985, 7 female sawflies, were put in plastic containers (ca. 2000 cc.). A container kept one female and almost the same amount of young and aged leaves (approximately 20 pinnules each) of the host fern on the day of eclosion; "young" leaves were leaves which passed the stage OE several days before, "aged" leaves were those opened in April and were more than a month after EE. The number of eggs deposited on young leaves, aged leaves and wall of the

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container was counted on the next day. A similar experiment in which 5 females were kept in a container with only aged leaves was also carried out.

2) Larval Growth. The newly hatched larvae were reared with either young, semi-aged (about 2 week after EE), or aged leaves, and their suitability as food was tested. Leaves were changed every day, and the survival of the larvae was recorded. The head width of the adult sawflies was measured.

Results

Field observations.

1) Voltinism and seasonal change of population size. Seasonal fluctuation of the number of eggs and larvae at JIZO area, Ichijoji in 1985 is shown in Fig. 2. Five generations were observed from late April to the end of July in this area. Emergence of the individuals of each generation were well synchronized. The population size of eggs and larval stage reached maximum in the second generation, and in the subsequent 3 generations it decreased gradually. Table 1 shows the number of eggs of each generation from 1985 to 1988 at two areas in Ichijoji. Five or 6 generations were observed from late April until the end of July or early August within and/or out of these areas (Otsuka unpublished) and population size fluctuated almost the same way every year, though population density differed by

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years.

On the other hand, in Kamigamo, synchronized emergence of the sawfly was not observed and the generations overlapped with each other. But it is certain that *S. osmundae* was multivoltine in Kamigamo as well, for eggs and larvae were found from April until the end of July or the beginning of August every year. Duration of the eggs and the larval stages did not differ between the two populations.

2) Manner of oviposition and feeding pattern of the larvae. Usually on the upper surface of a leaf of the osmund fern, female *S. osmundae* thrusted her ovipositor into the leaf so deeply that the tip of the ovipositor emerged on the lower side of the leaf. Then she deposited an egg and the egg appeared as if it was placed from the lower side of the leaf. She repeated this egg-laying procedure in a close distance, and a "loose egg mass" appeared on the leaf (Fig. 3). The eggs had long oval shape when they were deposited and became rounder thereafter. The first instar larvae ate the leaf tissue on which they hatched (Fig. 4a). After eating almost all of the pinna, the larvae (usually third and/or fourth instar) moved to the top pinna of the leaf (Fig. 4b). Thus larval aggregation was often observed on the top of the leaf. The larvae ate the leaf downward and often ate over the whole leaf (Fig. 4c, by the fourth and/or fifth instar larvae). Then, the larvae moved to other leaves of the same individual host plant, or transferred to leaves of other individual host plants. They did not show aggregation while such

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leaf-to-leaf migration.

3) Preference for leaf age.   Table 2   shows the amount of
host plant (shown by the number of pinnules), frequency of the
oviposition (the number of egg masses) and the number of eggs on
each stages of leaves. *S. osmundae* deposited eggs on new leaves.
The number of pinnules of the leaves at each developmental stage
changed day by day because of the new emergence of and aging of
the leaves. Therefore, number of the pinnules shown in Table 2
is the mean pinnule number of each of the 5 leaf stages
throughout each oviposition period (the period while I could find
newly deposited egg masses) of each generation.   All eggs were
deposited on new leaves (before EE; all except EE- in Table 2.),
while most leaves were old (EE-) when oviposition except for the
first generation occurred (see also Fig. 5).

4) Resource supply.   Growth stages of a single leaf of
Osmunda japonica were shown in Fig. 1.   Mean duration of leaf
opening (i.e. between OB and OE) was 5.3 days in April and 3.3
in July. Mean duration of leaf elongation (i.e. between OE and
EE) was 12.2 in April and 9.1 in July.

Seasonal change of the number of pinnules of the host plant
at JIZO area in 1985 is shown in Fig. 5a. The number of pinnules
increased rapidly from the later half of April to the beginning
of May and remained almost the same level throughout the active
season of *S. osmundae* (until August); though it slightly
decreased while the second generation of *S. osmundae* were in the
larval stage (May). New pinnules (stages before EE), however,

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were abundant only in later April and May and rather rare thereafter (Fig. 5b).

Fig. 6 shows the total number of pinnules (upper) and the number of very new (OB-OE) pinnules (lower) of four individual ferns. In spring, a plant shot all leaves together (primary shooting). After the primary shooting, some plants produced one or more leaves (secondary shoots, Fig. 6c and 6d) and others did not (Fig. 6a and 6b). Most of secondary shoots were observed on such plants that experienced heavy defoliation (Table 3, Fig. 6c and 6d. upper). The same individual plant which shot secondarily in 1986 did not show secondary shooting when it did not experience heavy defoliation (Table 4).

Causes and amount of the pinnule disappearance of the primary shoots at JIZO area until the end of August 1986 are shown in Table 5. The main cause of defoliation was feeding by *S. osmundae*. The more *S. osmundae* occurred, the more secondary shooting were observed (Kendall's Tau = 0.819, p<0.0001, Fig. 7).

Laboratory experiments

1) Oviposition. The seven females laid all eggs on young leaves (mean: 41.3, SD: 20.4) and none on aged ones. Five females kept with only aged leaves deposited no eggs on the leaves; a female deposited about 20 eggs on the wall of the plastic container but no eggs hatched.

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2) Larval growth. Few of 25 first instar larvae ate the aged leaves and none survived until the last instar. All larvae reared with young or semi-aged leaves attained the adult stage (N=42 and N=11, respectively). Those ate semi-aged leaves became females and they had significantly smaller head width (1.54±0.03 mm, N=11) than females which fed on young leaves (1.59±0.02 mm, N=21, p<0.001, Mann-Whiteney's U- test. see Fig. 8).

Discussion

Females deposited eggs on new leaves but not on old leaves with few exceptions, even when only old leaves were presented to them. Old leaves are not good for larval growth. A female thrusts her saw into the leaf for oviposition, therefore, old leaves would be too tough to be pierced. As well as the eggs of the other congeneric sawflies, this sawfly's eggs absorbed water from the leaf tissue and their volume increased after oviposition. Water absorption appeared indispensable for the egg development, for no eggs hatched when the leaf withered (Otsuka unpublished observation) and eggs laid on the plastic container wall did not hatch. This would be another factor that females oviposit on young leaves which abundant in earlier seasons, although the host plant is abundant throughout the active season of this sawfly. The seasonal change in the number of eggs and larvae well matches the seasonal change of the amount of its food

resource.

The first and the second generations of this sawfly eat the leaves of primary shoots. On the other hand, the third and subsequent generations depend on the secondary shoots, which frequently develop on the ferns having experienced heavy defoliation by *S. osmundae*. This means that the third and subsequent generations depend on the compensatory response of the host plants to defoliation caused by the earlier generations.

It seems important to point out that this sawfly applies a tactics for effective harvest, i.e. local heavy defoliation. Eggs are deposited on the host plant as egg masses and the larvae feed gregariously, thus certain plants damaged greatly and compensatory shooting is induced successfully. These unique features of *S. osmundae* form a contrast with a univoltine congeneric species, *S. secunda*. In *S. secunda*, which also feeds on the osmund fern, the size of an egg mass is small (usually 3 to 7 eggs, Otsuka unpublished), the larvae do not form aggregation (Okutani 1959), population density of *S. secunda* is low (Otsuka unpublished), and feeding load on the fern is not heavy enough to cause the compensatory regrowth of the host plant.

No other *Strongylogaster* sawflies deposit eggs in clusters or show larval aggregation (Okutani 1959, Naito personal communication). Most sawflies of this genus is univoltine and feed on new leaves of ferns in the spring. Host plants of bi- or multivoltine *Strongylogaster* other than *S. osmundae* shoot not

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only in the spring but also in the summer (Naito personal communication). These facts shows that egg clustering and larval aggregation of this sawfly are unique and that they play important role in inducing unusual shooting of the host plant.

Defoliation by phytophagous insects often occur during the outbreak of their populations (e.g. cinnabar moth *Tyria jacobaeae*, Dempster 1971, Myers and Campbell 1976, Dempster and Lakhani 1979; larch bud moth *Zeiraphera diniana*, Baltensweiler, et al. 1977; diprionid sawflies, Jahn et al. 1980, Tachibana et al. 1988). Heavy damage on each individual osmund fern by *S. osmundae* is not a result of a population outbreak but occurs even in low density population because of its mode of egg laying and larval aggregatory feeding habit. This works as an indispensable resource regulator for multivoltinism of this sawfly.

The defoliation-compensatory regrowth interaction between *S. osmundae*, and the host fern resembles that between large herbivorous mammals and graminoid plants in Serengeti in Africa, where grazing by large herbivores triggers compensatory regrowth of grassland plants, so that they can utilize much larger amount of food resource than the temporal amount of leaf of food plants (e.g. Coughenour et. al. 1985a, 1985b, McNaughton 1976, 1979, 1983, 1984, 1985). Unlike herbivorous mammals in Serengeti, sawflies that defoliated can not utilize the compensatory growth by themselves, but their offspring do eat.

A univoltine stem-galling sawfly, *Euura lasiolpis* shows host regulation similar to that by *S. osmundae*. Its galls

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significantly reduce the production in reproductive buds (Sacchi et al. 1988). Normally, the willow tree becomes less susceptible to galling with age, but heavy galling by *E. lasiolpis* keeps the willow young and susceptible to the galling (Craig et al. 1986). The main difference between the *E. lasiolpis* and *S. osmundae* is that *S. osmundae* can not maintain its multivoltinism without defoliating its host plant, while *E. lasiolpis* can utilize more or less old willows without that host resource regulation. *S. osmundae* may have the same host regulation as that of *E. lasiolpis*, for small and younger plants of *O. japonica* are easily defoliated by the larvae and tend to be eaten again by the subsequent generation(s) of *S. osmundae*.

As a summary, *S. osmundae* defoliates its host plants and forces them to shoot secondarily in later seasons, and utilizes these shoots as the food resource of the subsequent generation(s). This host regulation is unique in the following 2 points. Firstly, this host regulation alters the phenology of the host plant and let it shoot after spring. Secondly, the regulation does not increase on-time population size of the sawfly but increases the number of generations per year.

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Table 1. Number of eggs at two areas (JIZO and M) in Ichijoji.

Year	Area	Generations				
		1st	2nd	3rd	4th	5th
1985	JIZO	251	1291	123	31	6
	M	125	895	54	21	0
1986	JIZO	280	263	70	71	31
	M	72	108	42	12	0
1987	JIZO	37	11	0	0	0
	M	23	6	9	0	0
1988	JIZO	36	61	58	52	13
	M	0	0	0	0	0

Table 2. Number of the pinnules (average) at each stage of leaf development and number of egg masses and total eggs deposited on them at JIZO area, Ichijoji in 1985. See Fig. 1 for definition of the stages. "+" means that a small number of eggs might be missed because of difficulty in counting (a. and b.) or because of delay in finding egg masses (c.).

a. First generation

Stage of leaf	No. of pinnules	No. of egg masses	Total no. of eggs
-OB	–	16	209+
OB-OE	1000.7	5	32
OE-HE	90.6	1	10
HE-EE	6.1	0	0
EE-	0.0	0	0

b. Second generation

Stage of leaf	No. of pinnules	No. of egg masses	Total no. of eggs
-OB	–	6	45
OB-OE	825.7	28	824
OE-HE	739.4	14	328
HE-EE	1343.3	6	94
EE-	2607.3	0	0

Continued

Table 2. Page 2

c. Third generation

Stage of leaf	No. of pinnules	No. of egg masses	Total no. of eggs
-OB	-	2	21+
OB-OE	195.9	1	9
OE-HE	227.8	5	86
HE-EE	161.5	2	15
EE-	5897.5	0	0

d. Fourth generation

Stage of leaf	No. of pinnules	No. of egg masses	Total no. of eggs
-OB	-	0	0
OB-OE	373.3	0	0
OE-HE	417.0	2	22
HE-EE	267.3	2	9+
EE-	6400.3	0	0

Table 3. Rate of defoliation on the primary shootings and amount of primary and secondary shootings of the host plant, *Osmunda japonica* at Ichijoji (4 areas) in 1985.

rate of defoliation	No. of plant	mean no. of primary		mean no. of secondary		secondary pinnules / primary pinnules
		leaf	pinnule	leaf	pinnule	
0 ~ 0.33	42	2.14	161.6	0.48	29.3	0.18
0.33 ~ 0.67	14	2.71	221.3	1.57	92.9	0.42
0.67 ~ 1	19	2.47	169.2	1.89	124.6	0.74

Table 4. Amount of primary and secondary shootings and defoliation of some individual plants in different years.

a. MN3 (Ichijoji)

Year	Primary shoots			Secondary shoots	
	No. of leaf	No. of pinnule	No. of pinnules defoliated	No. of leaf	No. of pinnule
1986	3	87	79	2	91
1987	2	97	50	1	48
1988	3	200	0	0	0

b. MN5 (Ichijoji)

Year	Primary shoots			Secondary shoots	
	No. of leaf	No. of pinnule	No. of pinnules defoliated	No. of leaf	No. of pinnule
1986	3	69	54	2	83
1987	3	119	0	0	0
1988	2	117	0	0	0

c. M2R (Ichijoji)

Year	Primary shoots			Secondary shoots	
	No. of leaf	No. of pinnule	No. of pinnules defoliated	No. of leaf	No. of pinnule
1986	5	512	278	2	149
1987	5	533	0	0	0
1988	4	417	7	0	0

Table 5. Causes and amount of decrease in pinnules at JIZO, Ichijoji in 1986. *S. o.* and *S. s.*: Eaten by *S. osmundae* and *S. secunda*, respectively. Herbivores: Eaten by the other herbivores. *Homo*: taken by human (Japanese eat shootings of *O. japonica*) or by mistake of the observer. Most of Other was senescence of leaves in late August.

Intact	Factors of defoliation						Total
	S. o.	*S. s.*	Herbivores	*Homo*	Other	Total	
9116	5053	28	87	745	1013	6926	16042

Figure legends

Fig. 1.   Growth stages of a leaf of *Osmunda japonica*.   The leaf
          is covered with cottony material before the opening (-OB).
          OB: beginning of opening, OE: end of opening, EE: end of
          elongation, HE: the middle day between OE and EE.

Fig. 2. Seasonal fluctuation in the number of eggs and larvae
          observed on host plant at Ichijoji in 1985.

Fig. 3. Distribution of eggs on a leaf deposit by a female of *S.*
          osmundae.   Upper right: A whole leaf.   Lower left: A pinna
          on which eggs were deposited.   Each dot indicates an egg.

Fig. 4. Typical feeding pattern of *S. osmundae*.   a: first instar.
          b: third and fourth instar.   c: fourth and fifth instar.
          Arrows indicate direction of transfer of the larvae and
          shaded areas indicate eaten part of the leaf.   Numerals
          indicate the number of larvae on the pinnule.

Fig. 5. Seasonal change of pinnules' number at the JIZO area,
          Ichijoji in 1985.   5a: Total number of pinnules,   5b: Number
          of pinnules of leaves in the stage between OB and EE.

Fig. 6. Seasonal change of the total number of pinnules (upper),
          number of very new pinnules (OB-OE, lower) of individual

plants. a (E5) and c (E20) were observed at Kamigamo and b (J27) and d (J22)were observed at Ichijoji. Each arrow indicates a secondary shoot.

Fig. 7. The number (density) of *S. osmundae* early in the season and the amount of secondary shooting. PPN: Number of pinnules of primary shootings. EN: Total number of eggs of the first and second generations. SPN: Number of pinnules of secondary shootings.

Fig. 8. Head width of adult female *S. osmundae* reared in laboratory. Upper: grew on young leaves. Lower: grew on semi-aged leaves. Head width was measured with a micrometer on eyepiece of a binocular (1 unit = 0.246 mm)

Fig. 1

OB — OB — OB-OE — OE — OE-HE — HE — HE-EE — EE — EE-

Fig. 2

No. of Eggs and Larvae in JIZO

1000 —
100 —
10 —

1
APR

31
AUG

Fig. 3

PINNA

PINNULES

LEAF

Fig. 4a

a

2

11

7

Fig. 4b

b

Fig. 4c

C

Fig. 5a

$\times 10^3$ a

No. of Pinnules in JIZO

15

10

5
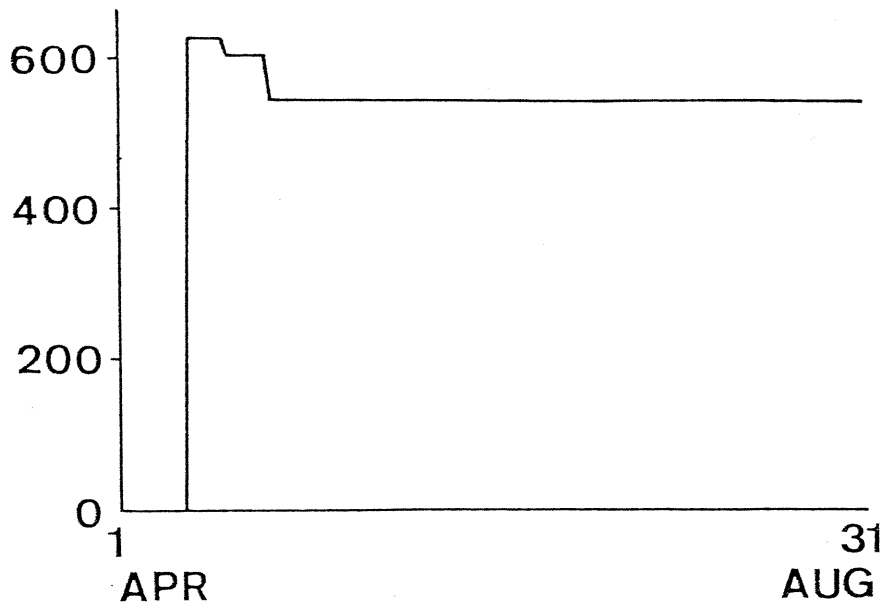
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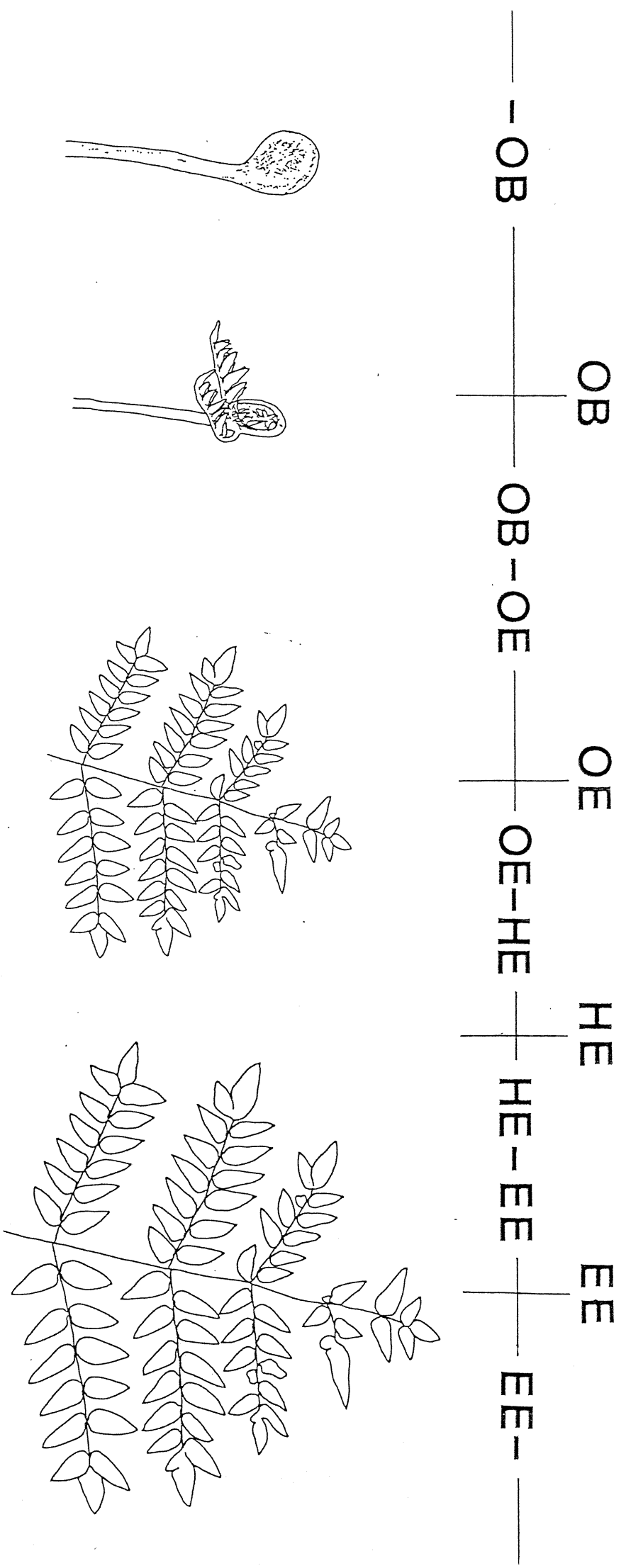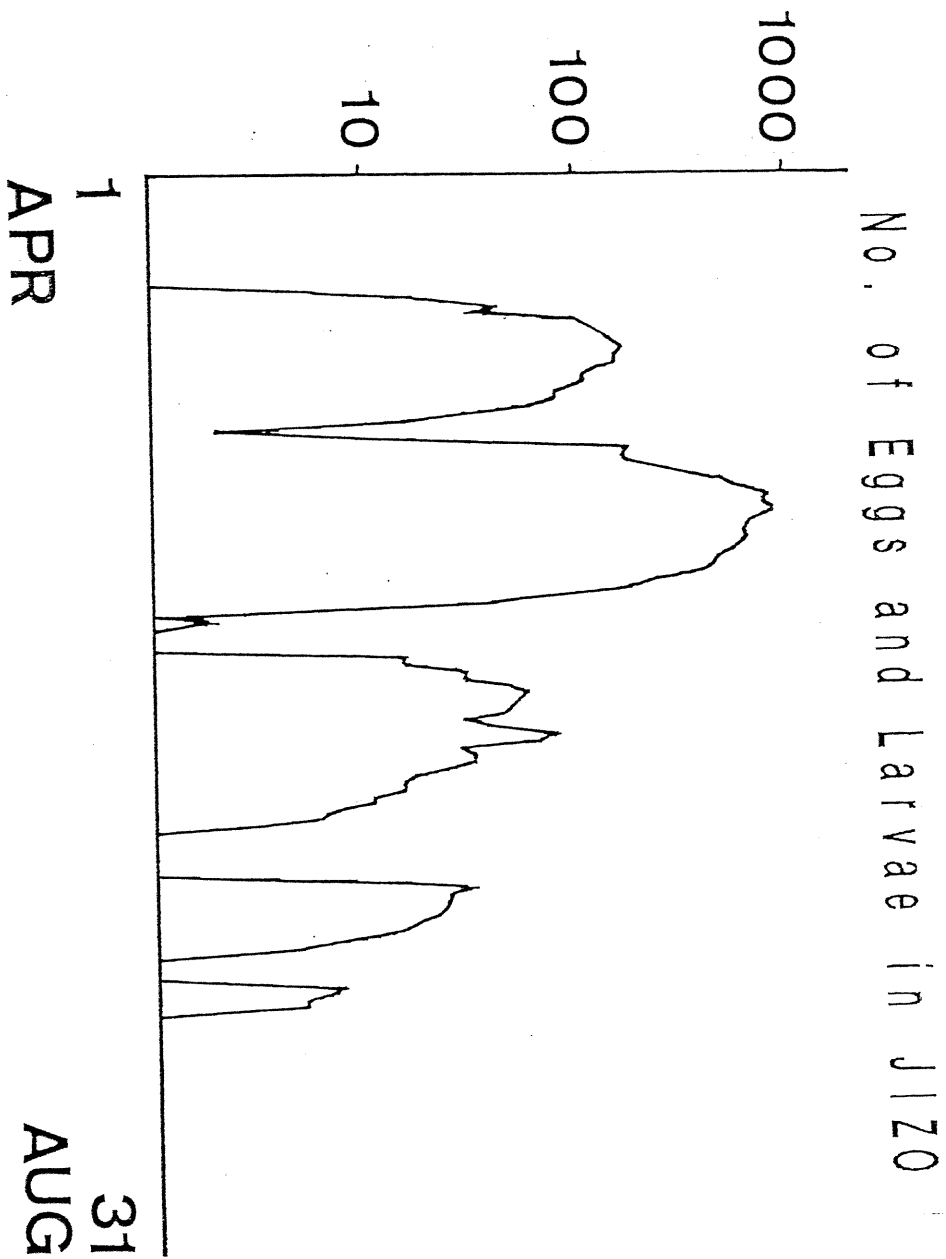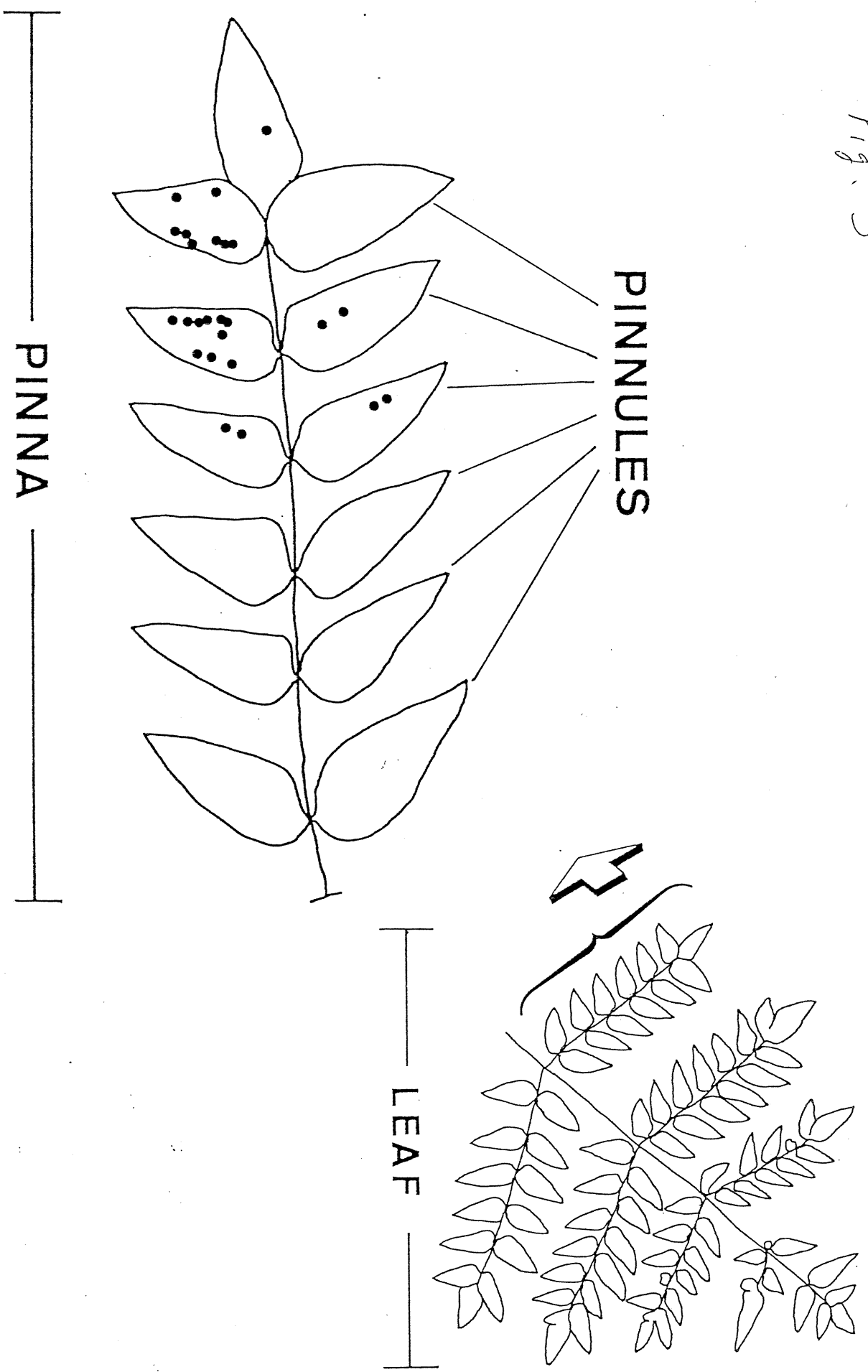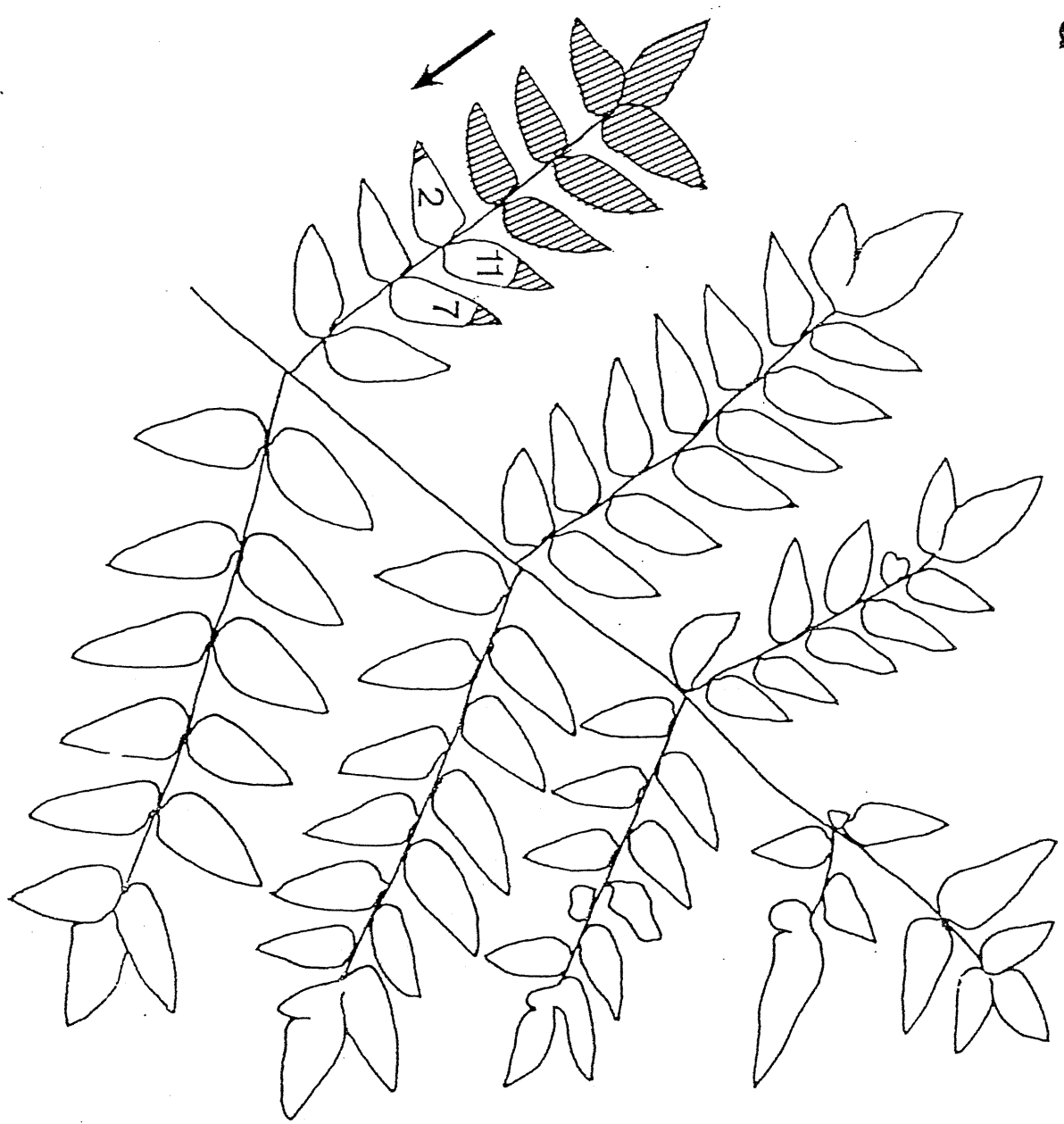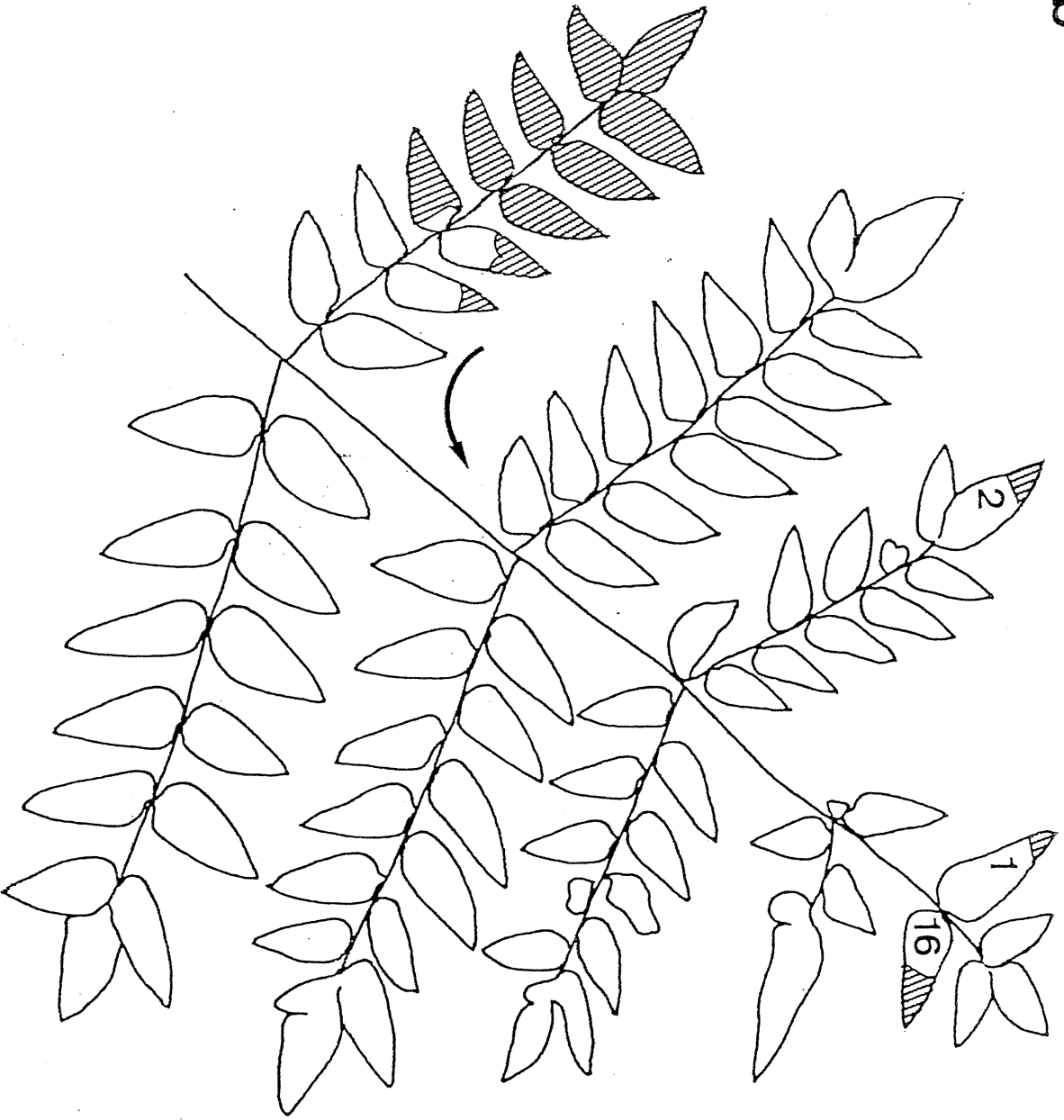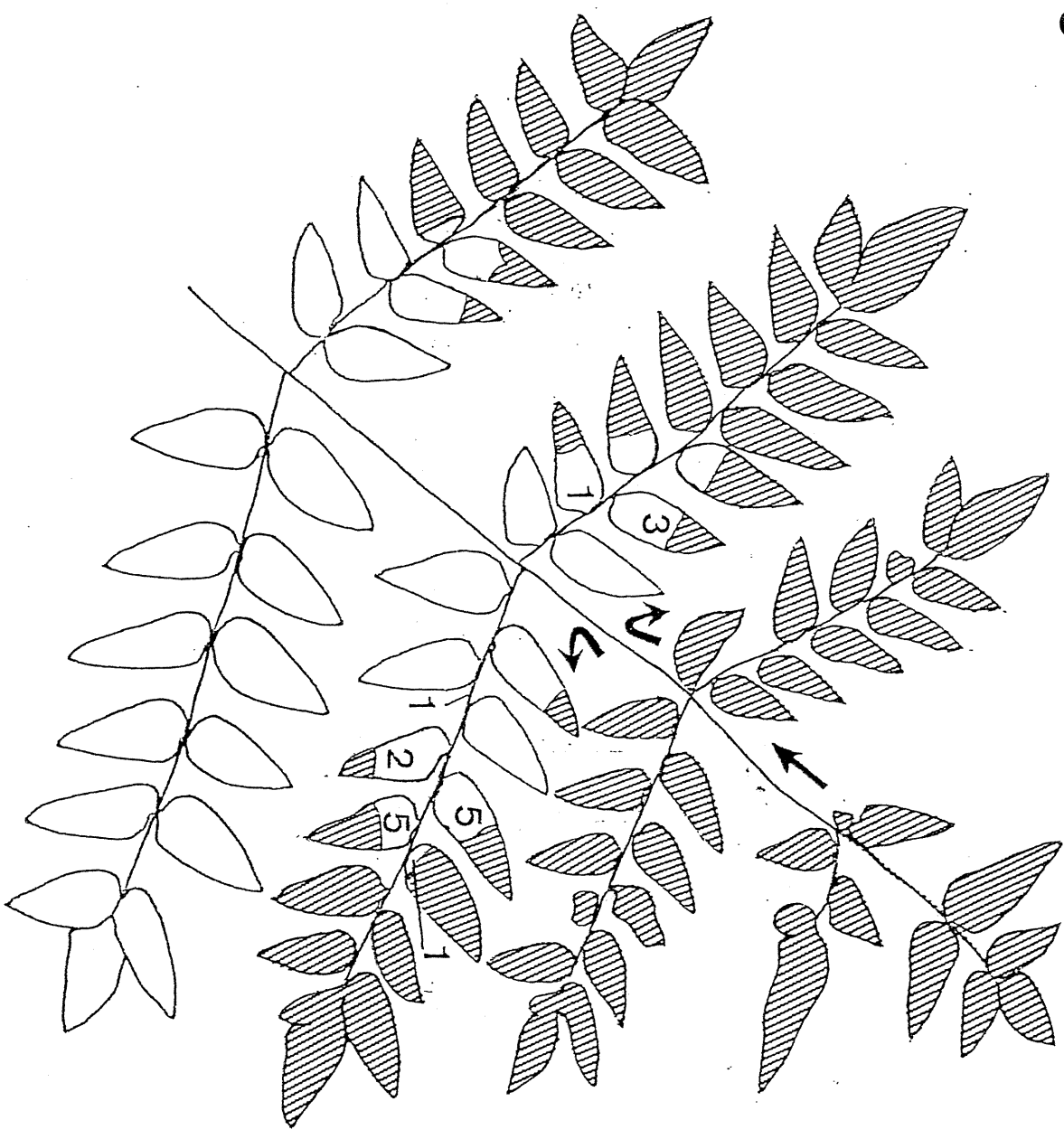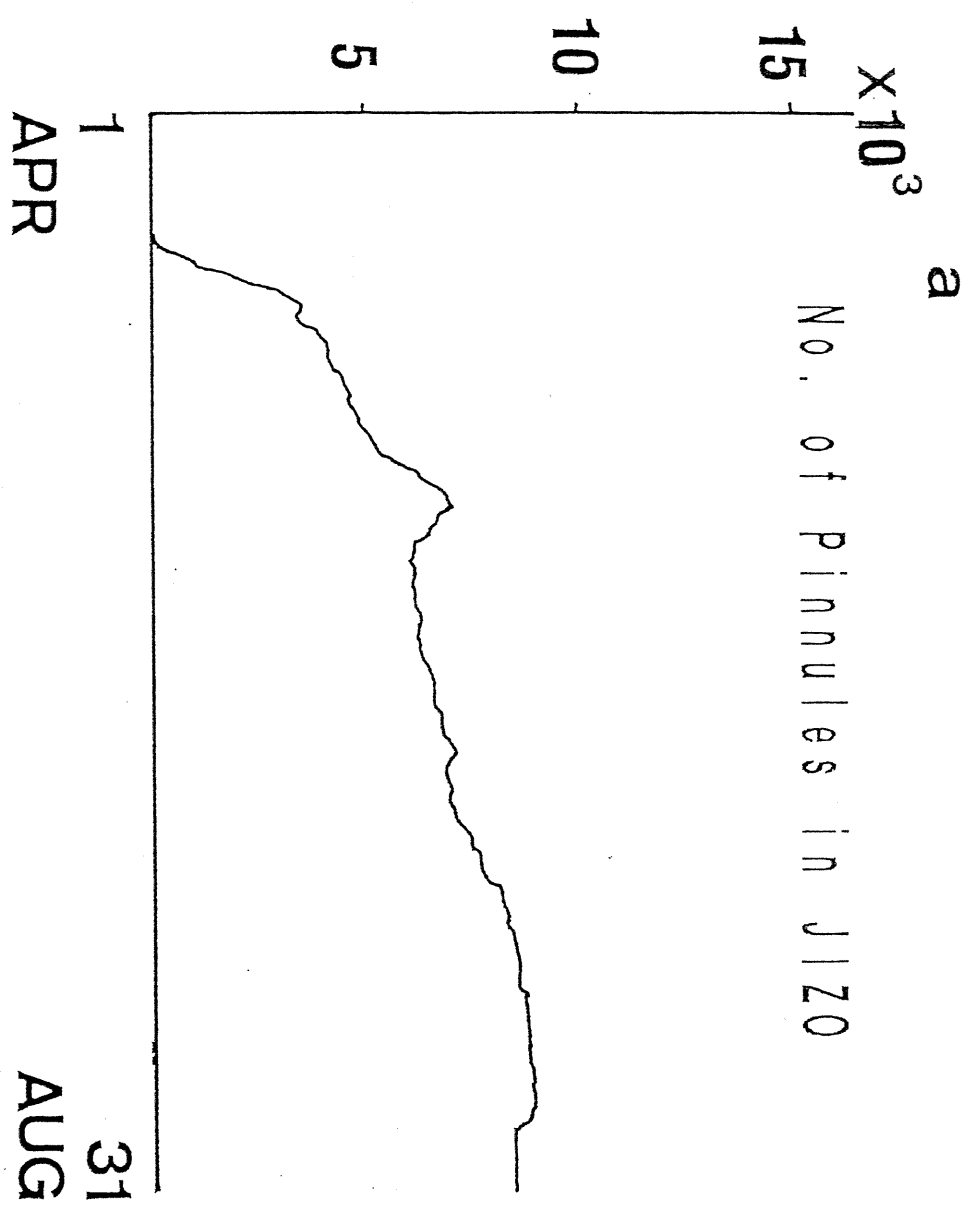
Fig 5 b

b   No. of New Pinnles in JIZO
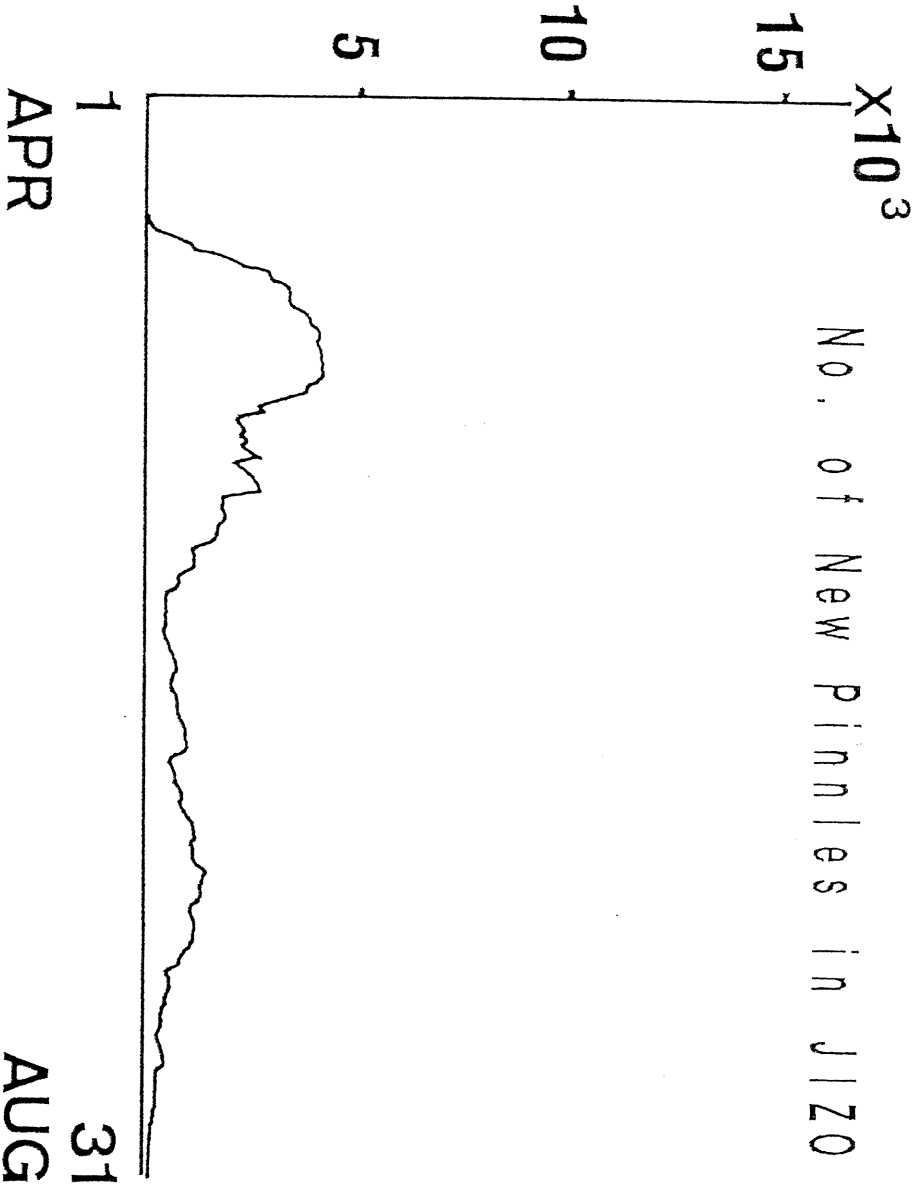
Fig. 6a

a

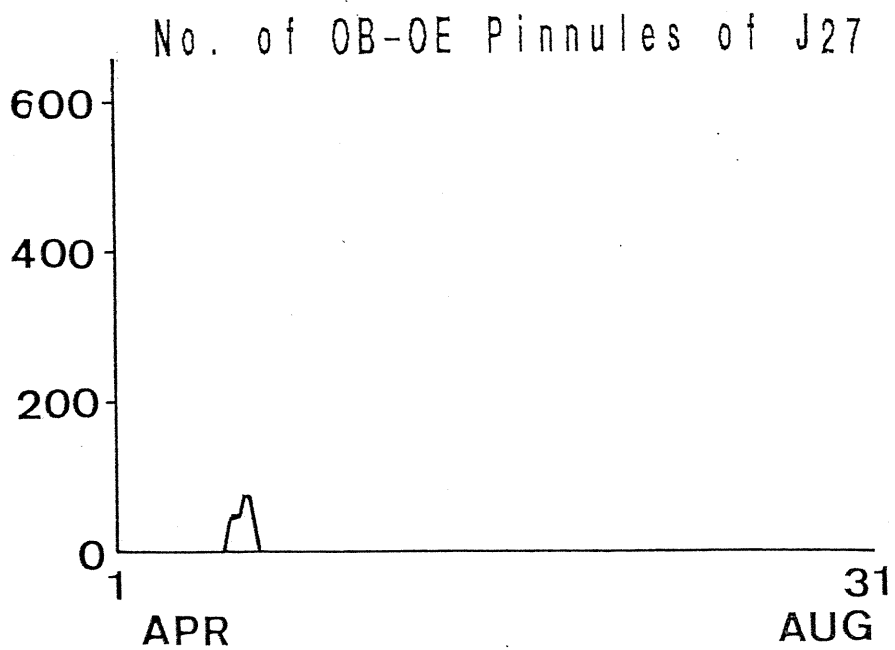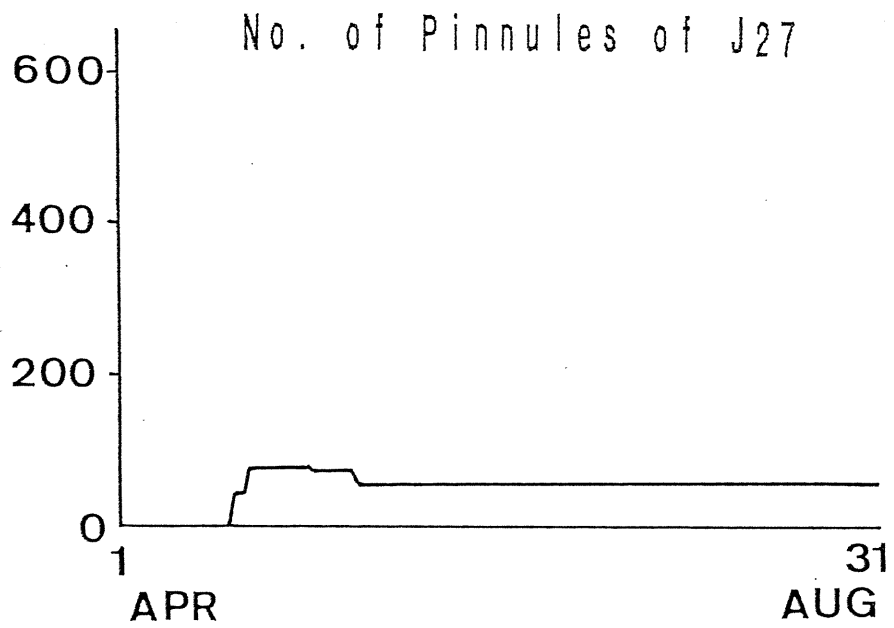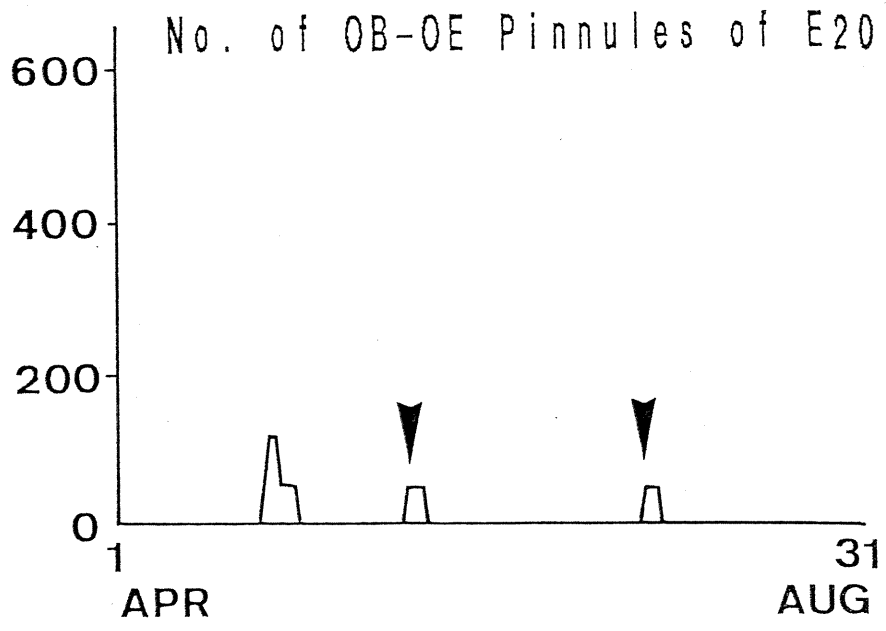No. of Pinnules of E5

No. of OB-OE Pinnules of E5
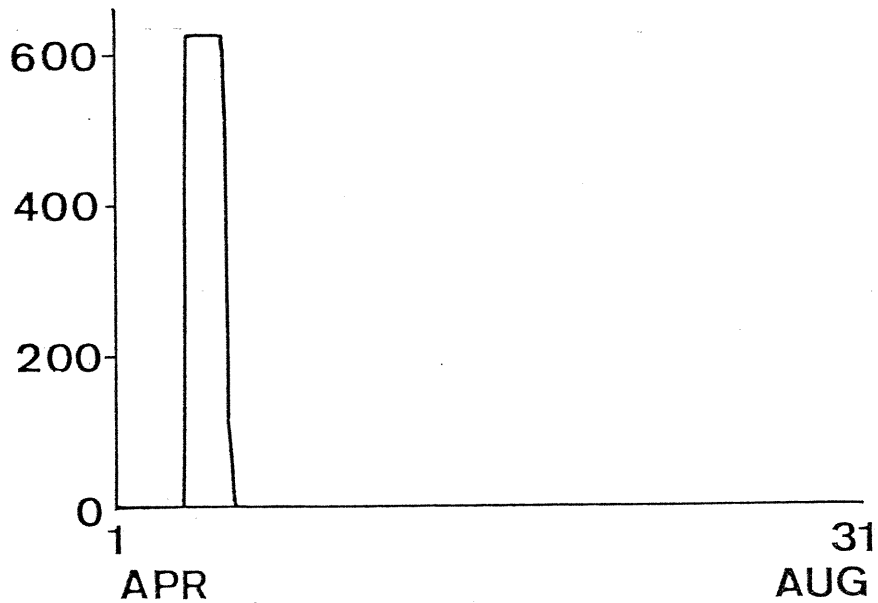
Fig. 66
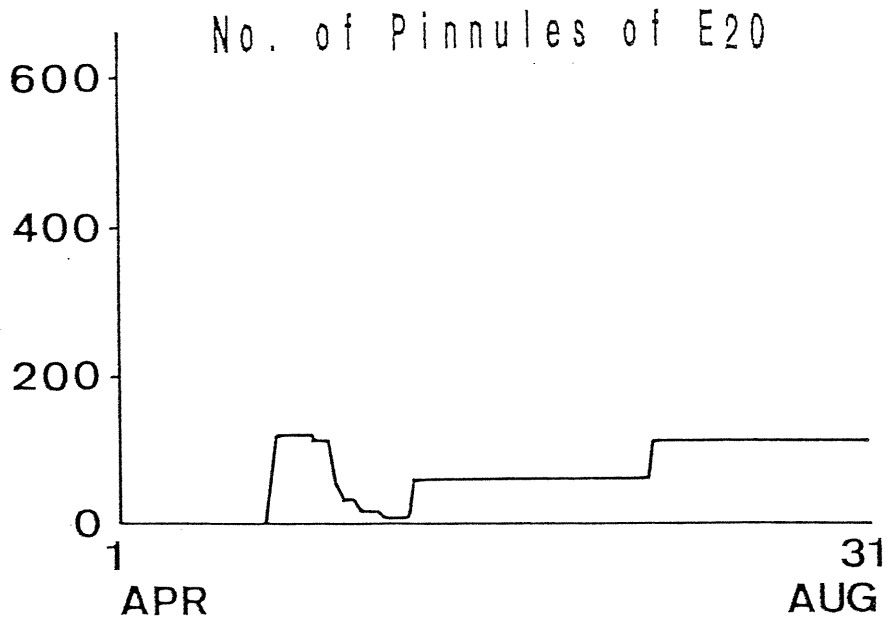
b

No. of Pinnules of J27

No. of OB-OE Pinnules of J27

Fig 6 c

C

No. of Pinnules of E20

600

400

200

0

1   31
APR   AUG

No. of OB-OE Pinnules of E20

600

400

200

0

1   31
APR   AUG

Fig 6 d

d

No. of Pinnules of J22

No. of OB-OE Pinnules of J22

Fig 7

Fig 8
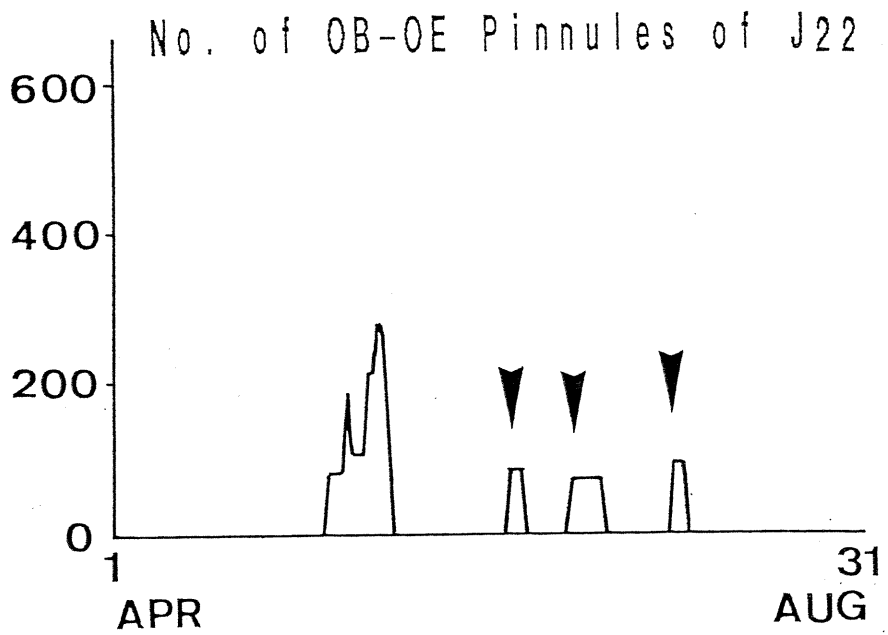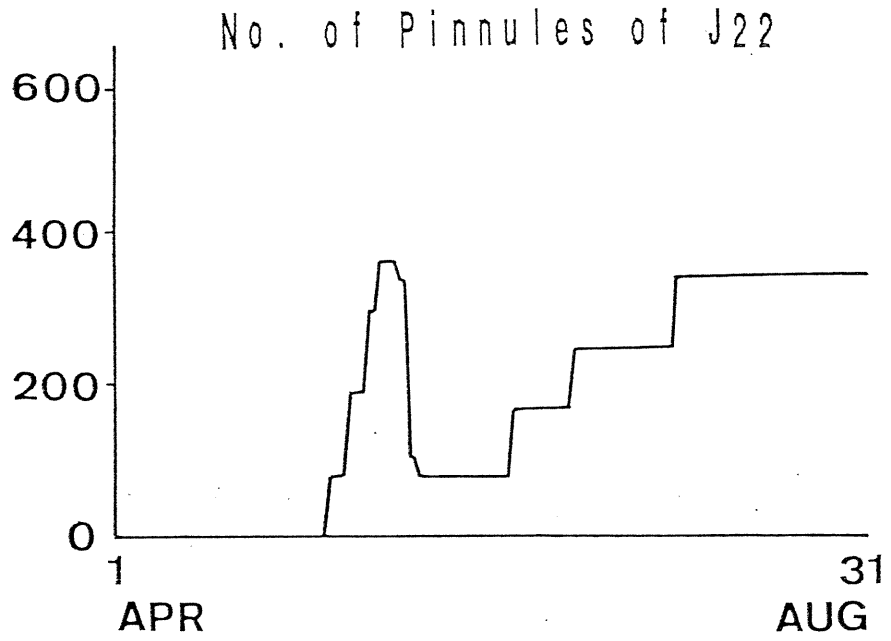
Young
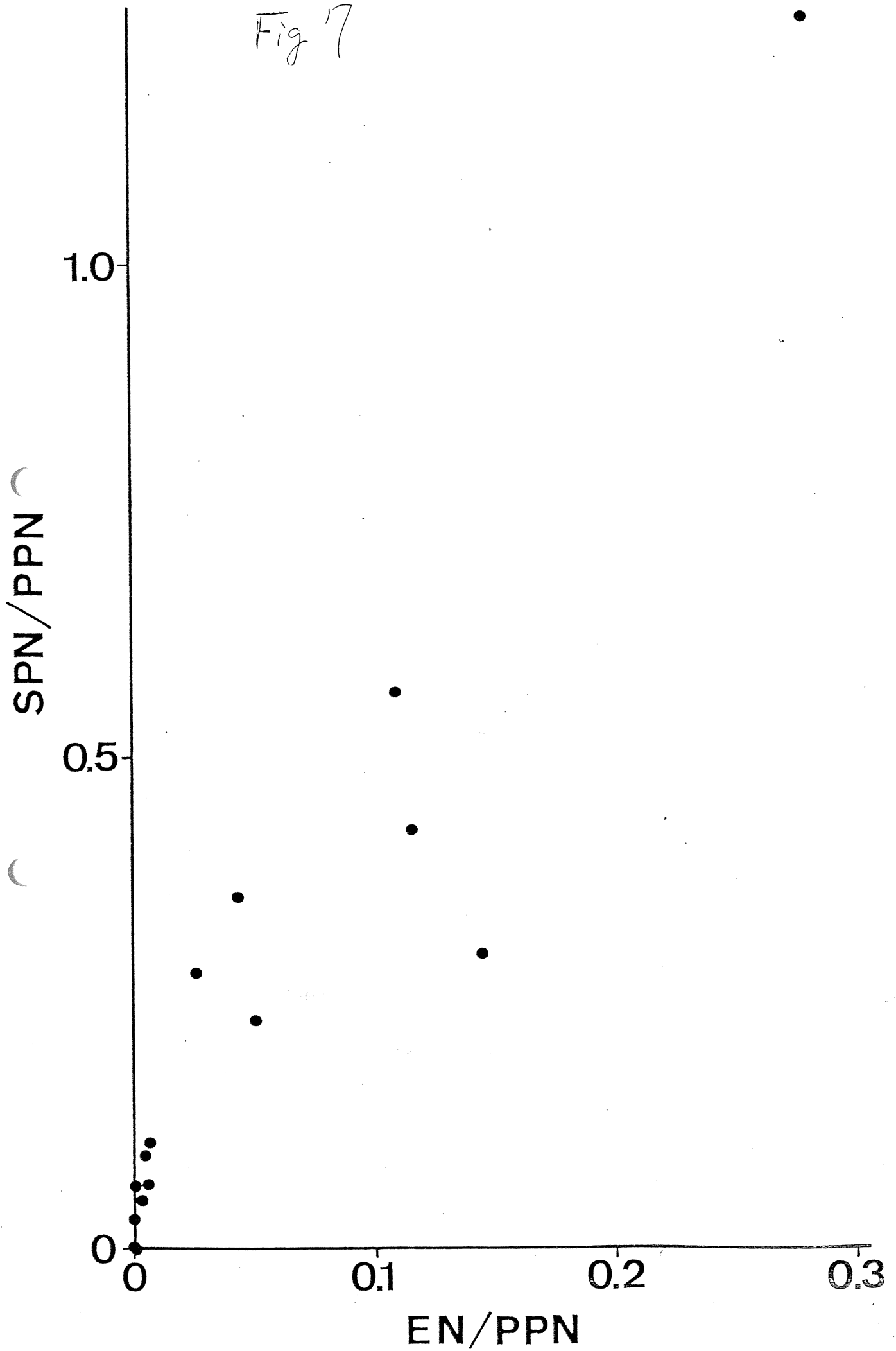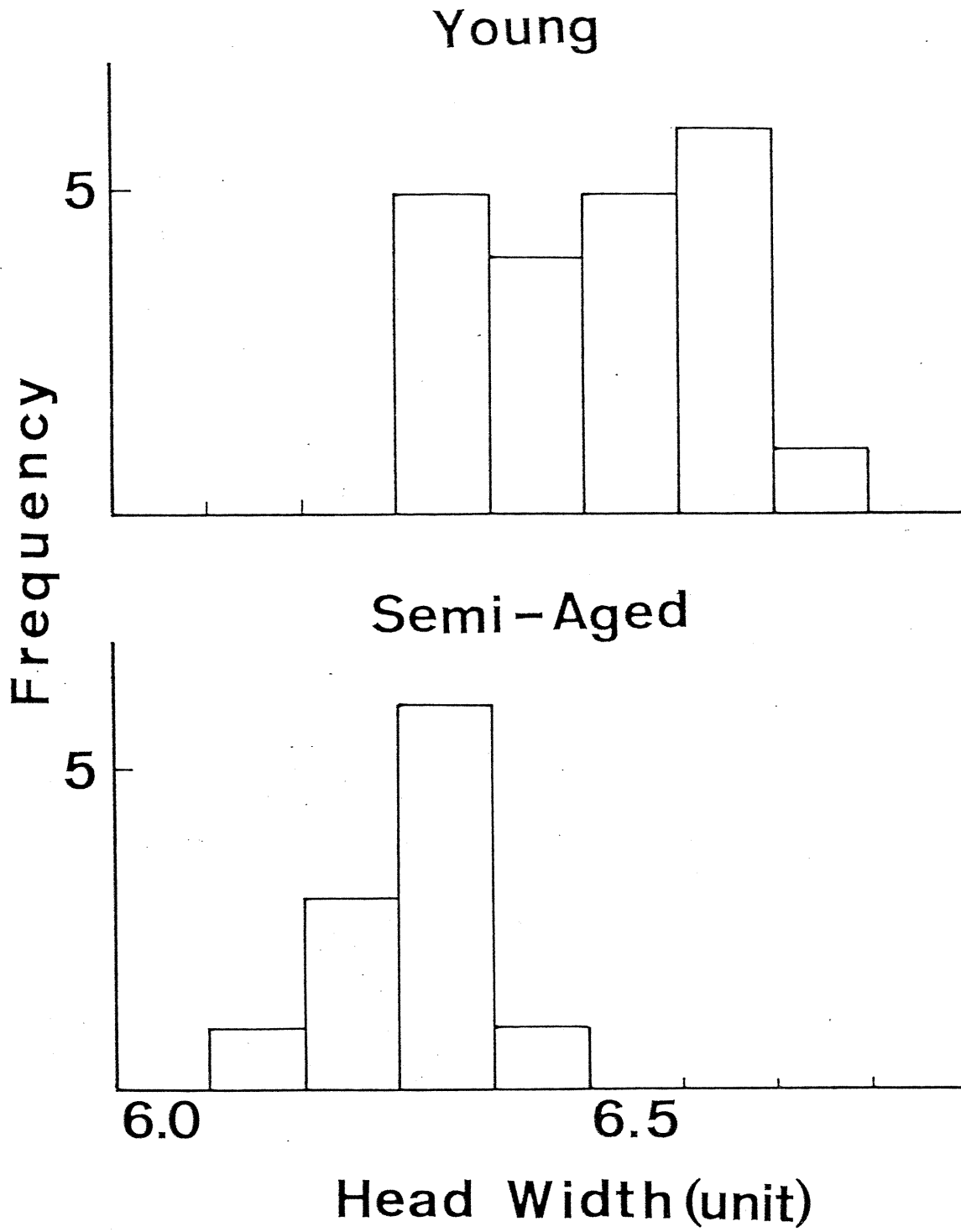
Semi-Aged

Frequency

5

5

6.0　　　　　　6.5

Head Width (unit)

Life History Polymorphism of a Sawfly, *Strongylogaster osmundae*

Forms an "Installment Savings of Prepupae"

(Hymenoptera, Tenthredinidae)

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18 Text pages
 5 Tables
 4 Figures

Abstract   Timing and rate of prepupal diapause of a
multivoltine sawfly, *Strongylogaster osmundae* were investigated
using insects collected from outdoors and ones reared in
laboratory.   Fifth (last) instar larvae of first to third
generations were collected from two localities in Kyoto City,
Kamigamo (first generation) and Ichijoji (second and third
generations), and reared at the constant temperature of 25°C in
1985.   In 1989, fourth and fifth instar larvae of the first to
the last (fifth) generations were collected from both of the two
populations except for the third generation of the Ichijoji
population.   They were reared under temperature and photoperiod
similar to outdoors.   Almost all individuals of the first
generation emerged as adults without diapause, while the second
and subsequent generations showed fractional (often 30 - 60 %)
diapause in the prepupal stage.   The photoperiodism of this
sawfly were studied under constant temperature of 25°C on various
generations in 1985, 1986 and 1988.   Photoperiodic response was
varied among generations.   The first generation showed very low
rate of diapause both under short day (13L11D) and long day
(16L8D).   Rate of diapause of the second and subsequent
generations was high under short day (up to 13L) and low under
long day (16L or longer).   Under 14L10D and 15L9D, they showed
fractional diapause similar to that observed in the second and
subsequent generations in the outdoor conditions.   Under such
photoperiodic regime, diapause rate of the third generation was
higher than that of the second generation.   Although observable

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population size (i.e. number of eggs and larvae on host plants) decreased after the second generation (Otsuka in prep. (1)), the number of diapausing prepupae (i.e. overwintering generation of the next year) increased by generations. Almost all of the diapausing prepupae metamorphosed in the next spring. This accumulation of diapausing prepupae and synchronous metamorphosis in the next spring was named "Installment savings of prepupae".

Many phytophagous insects repeat reproduction while the temperature is high enough to complete their life cycle, so that the number of generations outdoors is often equal to that calculated using total effective temperature accumulation (Danilevskii 1961; Tauber et al. 1986). An osmund fern (*Osmunda japonica*) feeding sawfly (Okutani 1967), *Strongylogaster osmundae* (Takeuchi), is not the case. *S. osmundae* is multivoltine and repeats 5 or 6 generations from late April to July or early August (Otsuka in prep. (1)). Therefore *S. osmundae* ceases reproduction even when the temperature is high enough to complete another or more generations.

S. osmundae shows rather unusual seasonal fluctuation of population density. Its population size of egg and larval stage reached maximum in the second generation, and in the subsequent 3 or 4 generations, it decreased gradually coinciding with the decrease of food resource (Otsuka in prep. (1)). The number of eggs and larvae of the last generation is about 1/10 of that of the first generation (Otsuka in prep. (1)). It seems that such a local population may be extinct, for some part of the last generation should die during overwintering. This study revealed that some part of the second and subsequent generations enter diapause (fractional diapause) and that they form an "installment savings of prepupae", that is in some sense similar to "seed bank", for overwintering generation.

Materials and methods

Diapause rate of outdoor populations.

Preliminary experiments were carried out in 1985. Specimens were collected at Kamigamo (Kamigamo Experimental Forest Station, Kyoto University) and Ichijoji, in Kyoto City (latitude; ca. 35°N). The altitude is 150 - 200 m and 130 - 160 m, respectively. Fifth (last) instar larvae of the first generation were collected from Kamigamo and fifth instar larvae of the second and third generations were collected from Ichijoji. Since the generations of *S. osmundae* did not overlap each other at Ichijoji (Otsuka in prep. (1), see also upper part of Fig. 4), it was easy to distinguish each generation from others. On the other hand, generations in Kamigamo were overlapped. Then I collected 5th instar larvae from Kamigamo when the fifth instar larvae are observed at Ichijoji except for the animals that are shown as 1* in Table 1. I collected them when the larvae of the first generation at Ichijoji had already dispersed, and some eggs and early instar larvae of the second generation were found on the host plant. The emergence of the first generation at Kamigamo was earlier than at Ichijoji. Thus, it was not sure that the insects shown as "1*" in table 1 really belonged to the first generation. The captured larvae were reared in the laboratory at 25°C and were exposed to photoperiods of 14L10D (1st generation), 15L9D (2nd generation), and 16L8D (3rd generation), respectively. These photoperiods simulated the

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outdoor day-length at the time of collection.

In 1989, the fourth and the fifth instar larvae of each of the first to fifth generations, except for the third generation from Ichijoji, were collected from the above two localities and reared in the laboratory of Kyoto University (altitude ca. 70 m) under the condition of temperature and photoperiod similar to outdoors. Dr. Sakurai gave me eggs and larvae collected from Toyooka, Nagano Prefecture (ca. 36.5°N). They seemed to belong to the second generation, because when they were collected, larvae of the second generation were observed at Ichijoji. They were reared in the laboratory under the conditions of temperature and photoperiod similar to outdoors.

The larvae were reared in plastic containers (ca. 200cc, 7-9 insects per container). A cake of moistened cellulose powder was provided in each container as the site for pupation. In nature, the last instar larvae of *S. osmundae* makes a small chamber in decayed wood and becomes prepupae in it (Okutani 1959). The larvae utilized the cellulose cakes in the same manner as decayed wood and showed low mortality. One to 2 weeks after adult eclosion, the cellulose-powder cakes were broken and examined for counting the remaining animals. The living prepupae were regarded as diapausing, and dead pupae and dead adults, as well as emerged individuals, were counted as not diapausing. No living pupae were found when I examined the animals.

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Photoperiodic response.

Photoperiodism of *S. osmundae* was investigated in 1985 (second, third and fifth generations), 1986 (second to fourth generations) and 1988 (first to third generations) on Ichijoji and/or Kamigamo population(s). In 1985 and 1986, fifth instar larvae were collected from outdoors and reared in the laboratory at 25°C under photoperiod that simulated that of outdoor day length as mentioned in *"Diapause rates of outdoor populations* in 1985". Fourth and fifth instar larvae were captured and reared in the laboratory under temperature and photoperiod similar to outdoors in 1988. When the adult sawflies emerged, females were forced to deposit eggs of the next generation which were used in the experiment. For the first generation in 1988, adult females which emerged after overwintering were collected from Kamigamo and were forced to deposit eggs of the first generation. The eggs were reared at 25°C and exposed to various photoperiodic regimes: from 10L11D to 16L8D in 1985 and 1986, 13L11D and 16L8D for the first generation and from 5L19D to 24L for the second and third generations in 1988. The judgment of diapausing or not was the same as that used in *"Diapause rates of outdoor populations"*. As in other hymenopterans, fertilized (diploid) eggs develop into females and unfertilized (haploid) eggs into males. Since this sawfly did not copulate in a small cage in the laboratory, all the animals used in this series of experiments were males except for the first generation.

Fate of prepupae in diapause

Diapausing prepupae (N=281; 51 of Ichijoji population and 231 of Kamigamo population) were put in a small cage outdoors in Kyoto University during autumn and winter in 1989. They were collected from the two localities in the egg and the larval stages and entered diapause under the condition similar to outdoors. They were examined whether pupated or not on 29 April, 1990.

Results

None of the prepupae which I regarded as diapausing pupated within the same year except one individual of group 1* in Table 1 which pupated and became adult.

Diapause rate of outdoor populations.

The larvae quit feeding one or two days after collected from outdoors and became prepupae. Adult emergence occurred in 7 to 10 days after collection under 25°C, or 1 to 2 weeks under the same conditions as outdoors.

Tables 1 to 3 describe the rate of diapause of the outdoor populations. No individual of the first generation diapaused except for the 3 individuals of Kamigamo shown as group 1* in 1985 (Table 1). On the other hand, some portion of the second and subsequent generations entered diapause. Not all individuals

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entered diapause even in the last generation (such as the fifth generation of Ichijoji and Kamigamo 1989 populations). Rate of diapause increased by generations in Ichijoji population but not decreased in Kamigamo population (Tables 1 and 2). Thus rate of diapause were different between the two populations in the second, fourth and fifth generation ($p < 0.01$ Fisher's exact probability test).

Photoperiodic response.

Figures 1 to 3 show the results of the experiment on photoperiodism of this sawfly. The first generation (1988 Fig. 3a) showed very low rate of diapause in both short (13L11D) and long (16L8D) day.

Results for all the generations examined in 1985 and 1986 (the second and subsequent generations) indicated that the rate of diapause was high under the short-day and low under the long-day conditions (Figs. 1 and 2). Some portion (not all) of the individuals diapaused especially under photoperiods of 14L10D and 15L9D (fractional diapause). In such cases, fractional diapause was observed in a clutch of one female. In spite of the different rearing condition of the mothers, the results of the experiments in 1988 were almost the same as those in 1985 and 1986. They showed high diapause rate under a photoperiodic condition of 13L11D or shorter and low rate under a 16L8D or longer photoperiod. The photoperiodic response of the Kamigamo and Ichijoji populations was same in the third generation in 1985

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(Fig. 1b).

Rate of diapause under photoperiods of 13L11D, 14L10D and 15L9D in the second and third generations were compared in Tables 4a (Kamigamo 1985), 4b (Ichijoji 1986) and 4c (Ichijoji 1988). The third generation diapaused with significantly higher rate than the second generation under 13L11D (1985), 14L10D (1985) and 15L9D (all the three years) (Fisher's exact probability test).

Fate of prepupae in diapause

Most of successfully hibernated prepupae of the both two populations terminated diapause and pupated in April 1990 (Table 5). Among the prepupae which did not pupated until 29 April, all the 2 prepupae of the Ichijoji population died within 1990. Three out of the 7 prepupae of the Kamigamo population pupated within 1990 and three died until December 1990. Thus, only one of the 281 prepupae diapaused until the end of next year.

Discussion

All individuals of the first generation of *S. osmundae* which were collected from outdoors became adults except for a few individuals of Kamigamo 1985 population. It was not sure whether the insects shown as "generation 1*" in Table 1 really belonged to the first generation (see Materials and methods). The tendency of not entering diapause of the first generation was

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confirmed by the experiments. They did not diapause even under a short photoperiod of 13L11D which induced diapause at a higher rate in all the second and subsequent generations (Figs. 1 to 3). Some eggs and first instar larvae were captured in Kochi Prefecture and reared under the condition of 25°C and the photoperiods of 13L11D and 16L8D following a continuous light condition during transportation in 1987. In spite of this unnatural condition, all 28 individuals emerged as adult sawfly without entering diapause. The same tendency is common to the first generation (i.e. the progeny of overwintered generation) of other multivoltine insects (e.g. nymphalid butterfly *Polygonia c-aureum*, Hidaka and Takahashi 1967; flesh fly *Sarcophaga bullata*, Henrich and Denlinger 1982). To assure a low rate of diapause of the first generation may be necessary to keep multivoltinism.

The second and subsequent generations of outdoor populations showed fractional diapause: a part of the population entered diapause and the others became adults. Photoperiodic response curves of many insects rises very steeply as the passed through critical photoperiod (Danilevskii 1961; Tauber et al. 1986). This sawfly did not show such steep curve. Fractional diapause occurred under photoperiods of 14L10D and 15L9D, which outdoor population of *S. osmundae* really experience. The longest day-length that this sawfly experiences in Kyoto is about 15.5 h around the summer solstice, when the third generation is observed outdoors. The last (usually fifth) generation seems to be

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exposed to the shortest day-length of about 13.5 h in the end of July. Therefore, the results of the experiments on the photoperiodic response of this sawfly well agree with the occurrence of fractional diapause of outdoor populations. It is unknown why not all of the last generation entered diapause.

Although fractional diapause is often observed (e.g. rice leaf bug *Trigonotylus coelestialum*, Kudo 1988) especially on the second last generation of bi- or multivoltine insects (e.g. Agromyzid fly *Agromyza oryzae*, Okamoto 1968; ichneumonid parasitoid wasp *Agrothereutes minousubae*, Shiotsu and Arakawa 1982), occurrence of fractional diapause over many generations seems to be rare. A noctuid moth, *Naranga aenescens*, shows similar fractional diapause in its second to forth generations (Okamoto 1968). Its population size of adult stage is largest in the first generation (Okamoto 1968).

In the present sawfly, the third generation almost always showed a higher rate of diapause than the second generation under 13L11D, 14L10D, and 15L9D. On the other hand, the third generation experiences a longer photoperiod, and this seems to lead to similar incidence of diapause in the second and the third generations of the outdoor populations. Determination of diapause should be affected by the former generation or generations, because the photoperiodic response varied with generations despite the larvae were subjected to the same condition from the egg stage. Parental effects on diapause induction are reported in many insects (e.g. nymphalid butterfly

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Polygonia c-aureum, Hidaka and Takahashi 1967, silkworm *Bombyx mori*, Kogure 1933; rice leaf bug *Trigonotylus coelestialium*, Kudo 1989; Pteromalid wasp *Nasonia vitripeanns*, Saunders 1965a, 1965b). Utilization of the information about the environments during the parental generation in addition to that during the insect's own may be advantageous to know the timing of reproduction or diapause.

It is unknown why the diapause rates of the third generation in outdoor populations from Kamigamo and Ichijoji were different each other, in spite of their same photoperiodic response and of their similar distribution with respect to altitude and latitude.

The phenology of *S. osmundae* is schematically drawn in Fig. 4. The upper part of Fig. 4 shows the seasonal change of the number of eggs and larvae at Ichijoji in 1985 (Otsuka in prep. (1) Fig. 1). The population size determined from the numbers of eggs and larvae on the host plants decreases by generations after the peak in the second generation. And, this gradual decrease may lead this local population to extinction. However, the population size of the diapausing individuals, although I could not count because of their dispersal prior to prepupation, should increase by generations. Because a part of the second and the subsequent generations enter diapause which is not terminated before the next spring. Therefore, many diapausing prepupae have been accumulated in the later period of the active season, which will give a sufficient number of insects of the first generation in the next spring.

Since many generations of this species show fractional diapause incidence, prepupae of various generations form an overwintering generation. This phenomenon is similar to the soil 'seed bank' of annual weeds in which seeds of a variety of ages are likely to occur together (Begon et al. 1990 p.141). Takahashi (1977a) found analogous 'egg bank' of tadpole shrimps. Such 'egg bank' is reported in a fresh water copepod *Diaptomus sanguineus* (De Stasio 1989). Takahashi (1977b) considered such seed or egg bank reduces the risk of extinction. The 'prepupal bank' of *S. osmundae* remains only until next spring and almost all the prepupae terminated diapause and pupated after overwintering, while 'seed bank' has dormant seeds the whole year. Therefore, "installment savings of prepupae" should be suitable for the accumulation of diapausing prepupae of *S. osmundae*.

The function of the habit of fractional diapause for the population and why fractional diapause have evolved are different problems. To establish a seed bank is advantageous when the environment changes unpredictably (Cohen 1966, 1967, 1968). On the other hand, fractional diapause evolves when the carrying capacity decreases in the bivoltine insects (Sota 1988). Population size of the egg and larval stage of *Strongylogaster osmundae* decreased by generations coincident with the decrease of food resource (i.e. new leaves, Otsuka in prep. (1)). Therefore, a condition similar to that assumed in the model by Sota (1988), such as decreasing in food resources, might occur in the second

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and subsequent generations in this sawfly. Further analysis and discussion will be carried out in another paper.

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Table 1. Rate of diapause of outdoor populations in 1985. 1*; Fifth instar larvae were collected from Kamigamo when the larvae of first generation had already dispersed and eggs and early instar larvae of the second generation were observed at Ichijoji. The third generation showed higher rate of diapause than the second generation (p<0.01 by Fisher's exact probability test).

Gene-ration	Population	Number of individuals	Number of diapause (%)
1	Kamigamo	30	0 (0)
1*	Kamigamo	10	3 (30)
2	Ichijoji	84	30 (36)
3	Ichijoji	42	25 (60)

Table 2. Rate of diapause of outdoor populations in 1989.

a. Ichijoji population.

Number of ration	individuals	diapause (%)*
1	22	0 (0)a
2	39	3 (8)a
3	0	-
4	53	17 (32)b
5	8	7 (88)c

*: Rates followed by the same letter within collumn were not significantly different at the p<0.01 by Fisher's exact probability test.

b. Kamigamo population

Gene- ration	Number of individuals	Number of diapause (%)**
1	55	0 (0)A
2	93	52 (56)B
3	29	12 (41)B
4	130	18 (14)C
5	55	10 (18)C

**: Rates of the 3rd and 5th generaions and those followed by the same letter within column were not significantly different at the p<0.01 by Fisher's exact probability test.

Table 3. Rate of diapause of outdoor population of the second
generation in Toyooka, Nagano 1989 population. The generation
was estimated referring to that of Ichijoji, Kyoto.

Gene-	Number of	Number of
ration	individuals	diapause (%)
2	189	92 (49)

Table 4. Rate of diapause under the photoperiods of 13L11D, 14L10D and 15L9D of the second and third generations. p; result of Fisher's exact probability test. Numerals in parentheses are numbers of insects examined.

a. Kamigamo 1985 population

Gene-ration	Diapause rate under 13L11D	Diapause rate under 14L10D	Diapause rate under 15L9D
2	.57 (79)	.44 (63)	.09 (23)
3	.99 (194)	1.00 (13)	.59 (75)
	p<0.001	p<0.001	p<0.001

b. Ichijoji 1986 population

Gene-ration	Diapause rate under 13L11D	Diapause rate under 14L10D	Diapause rate under 15L9D
2	.95 (37)	.85 (33)	.47 (30)
3	1.00 (15)	–	1.00 (16)
	p>>0.05	–	p<0.001

c. Ichijoji 1988 population

Gene-ration	Diapause rate under 13L11D	Diapause rate under 14L10D	Diapause rate under 15L9D
2	1.00 (37)	.69 (39)	.21 (58)
3	.89 (35)	.77 (30)	.53 (45)
	p>>0.05	P>>0.05	p<0.001

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Table 5 Fate of overwintered prepupae

Population	No. of dead	No. of metamorphosed	No. of prepupae	Total No.
Ichijoji	4	45	2	51
Kamigamo	7	216	7	231

Figure legends

Fig. 1.   Photoperiodic response of *S. osmundae* in 1985 (1a: Second generation,   1b: Third generation,   1c: Fifth generation).   Circles and triangles indicate Kamigamo and Ichijoji population, respectively.   Numerals near the points indicate the number of insects examined.
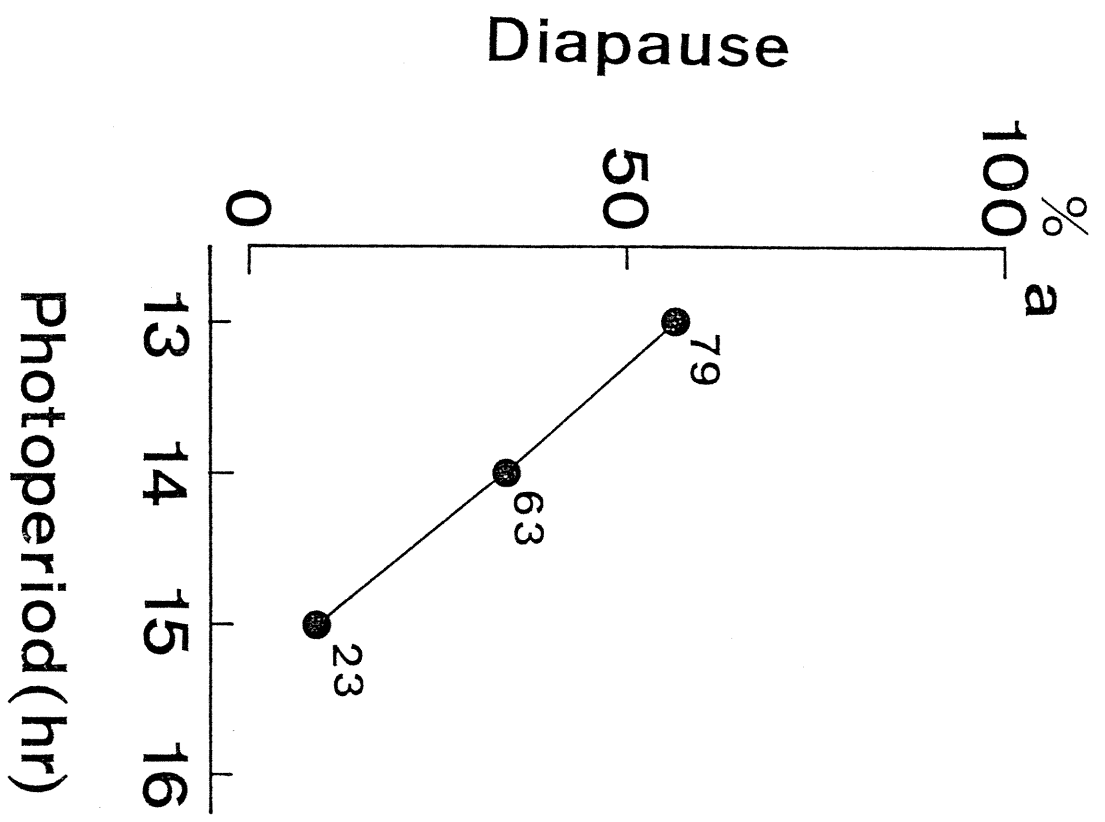
Fig. 2.   ditto 1986   (2a: Second generation, 2b: Third generation, 2c: Fourth generation).   All animals belonged to the Ichijoji population.   Numerals near the points are the number of insects examined.

Fig. 3.   ditto 1988 (3a: First generation, 3b: Second generation, 3c: Third generation).   All animals belonged to the Ichijoji population.   Numerals near the points are the number of insects examined.
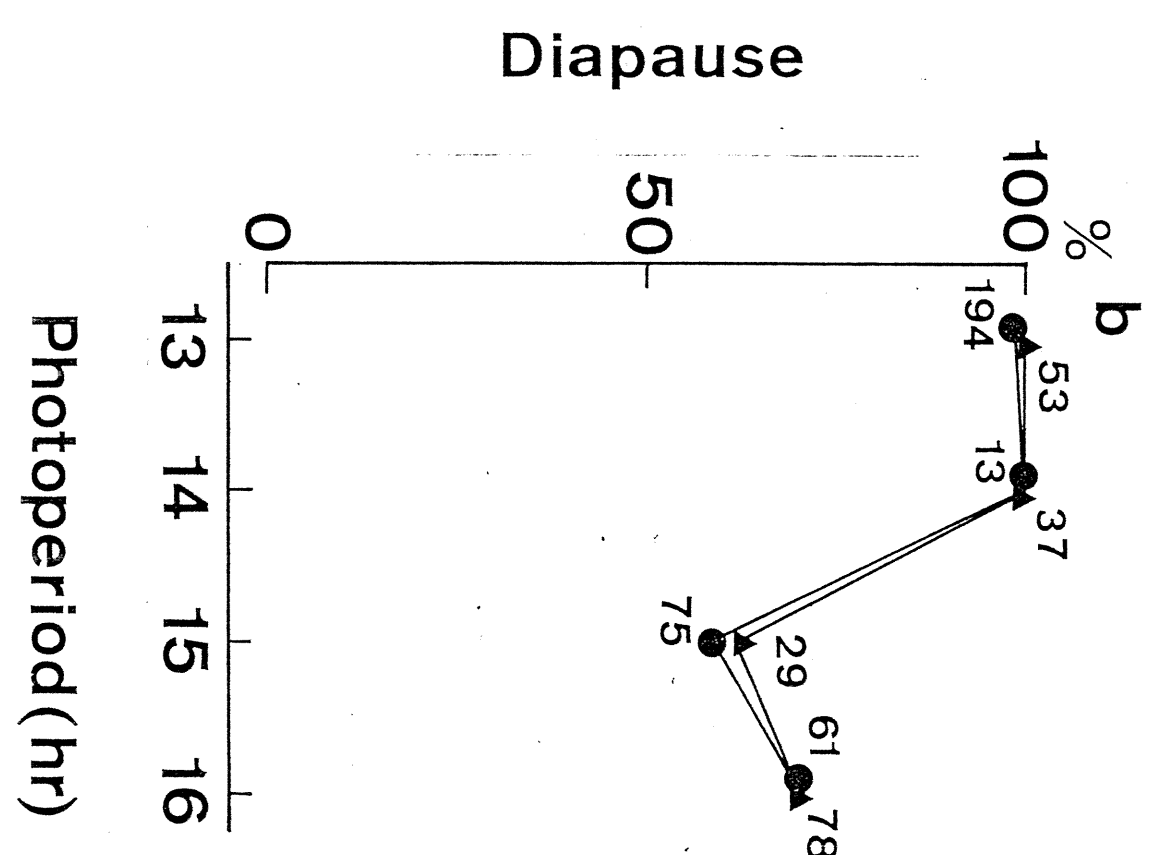
Fig. 4.   Schematic drawing of phenology of *S. osmundae*.   Upper: seasonal change of the above ground population size (number of eggs and larvae).   Lower: population   in diapause (prepupae).   The upward arrow and the downward arrows indicate terminating and entering diapause, respectively.
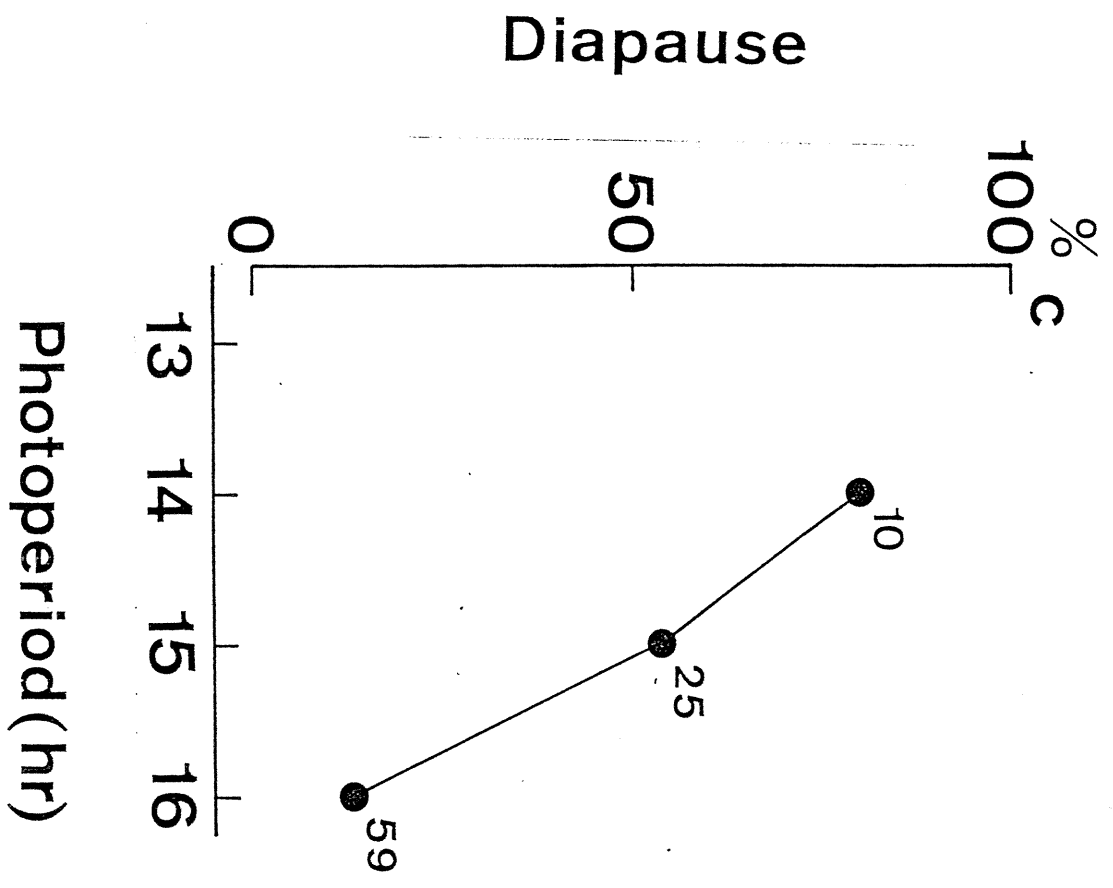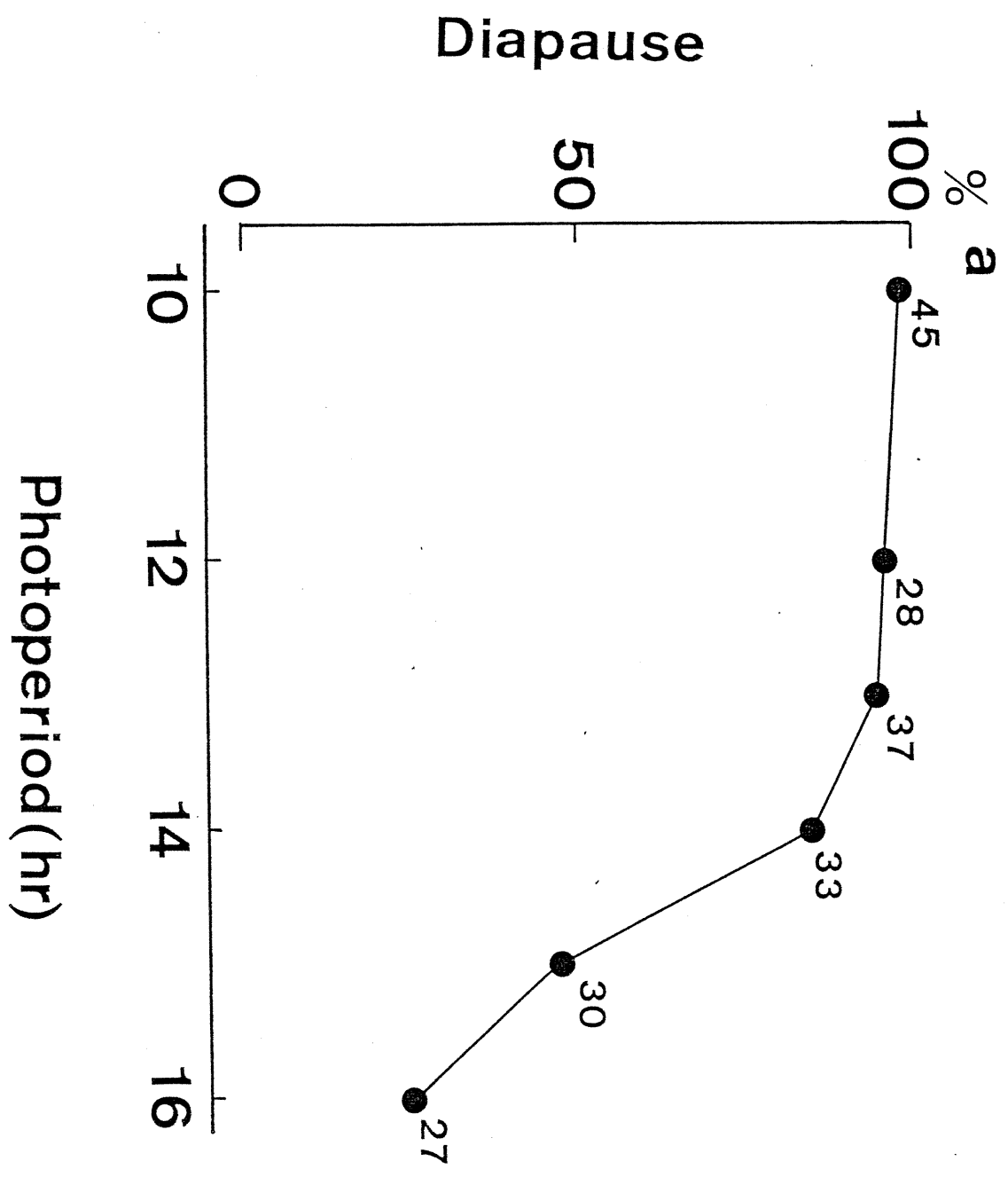
Fig. 1a
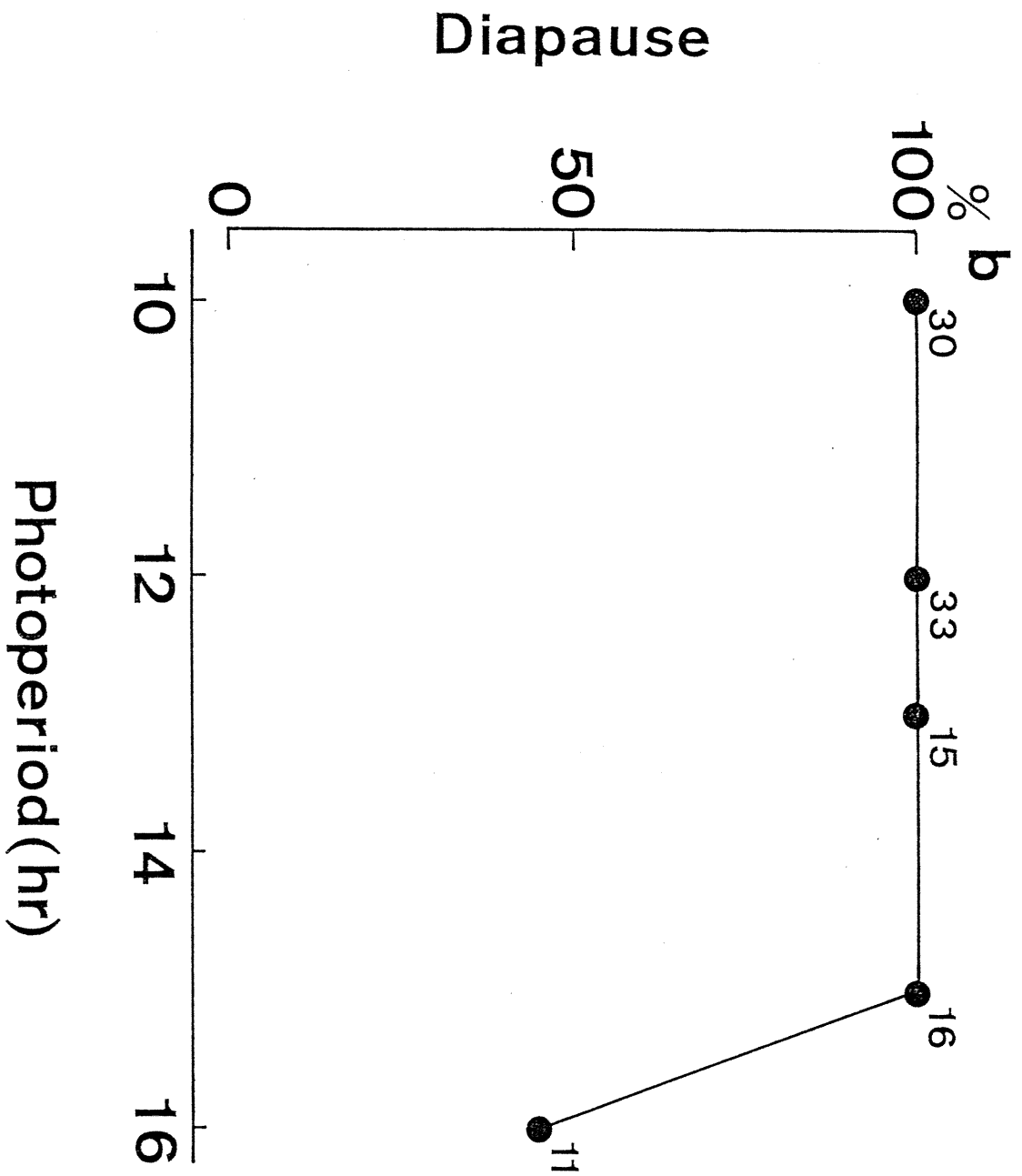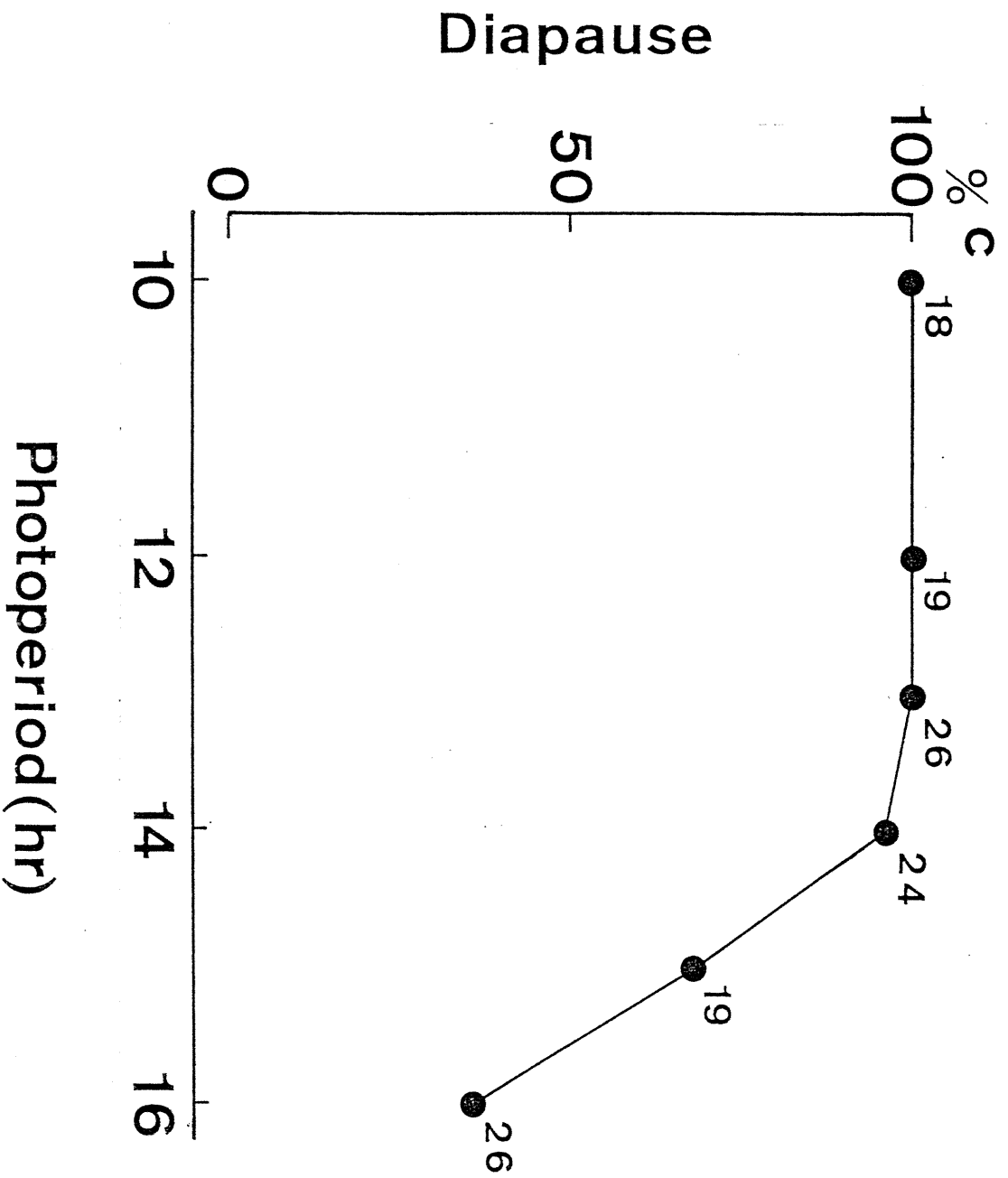
Fig. 1 b

Diapause

% b

Photoperiod (hr)

Fig. 1c

Diapause

% C

100

50

0

Photoperiod (hr)

13 14 15 16

10

25

59

Diapause

%
a

Photoperiod (hr)

45
28
37
33
30
27

Fig. 2b

2c Fig. 2c

Diapause

% C

100

50

0

Photoperiod(hr)

10   12   14   16

18
19
26
24
19
26

Fig. 3a

%
a

100
50
0

13 14 15 16

16
21

Fig. 3b

Fig. 3c

Fig. 4

No. of Eggs and Larvae

1000

100

10

4.1

9.1

DIAPAUSE (pre pupa)
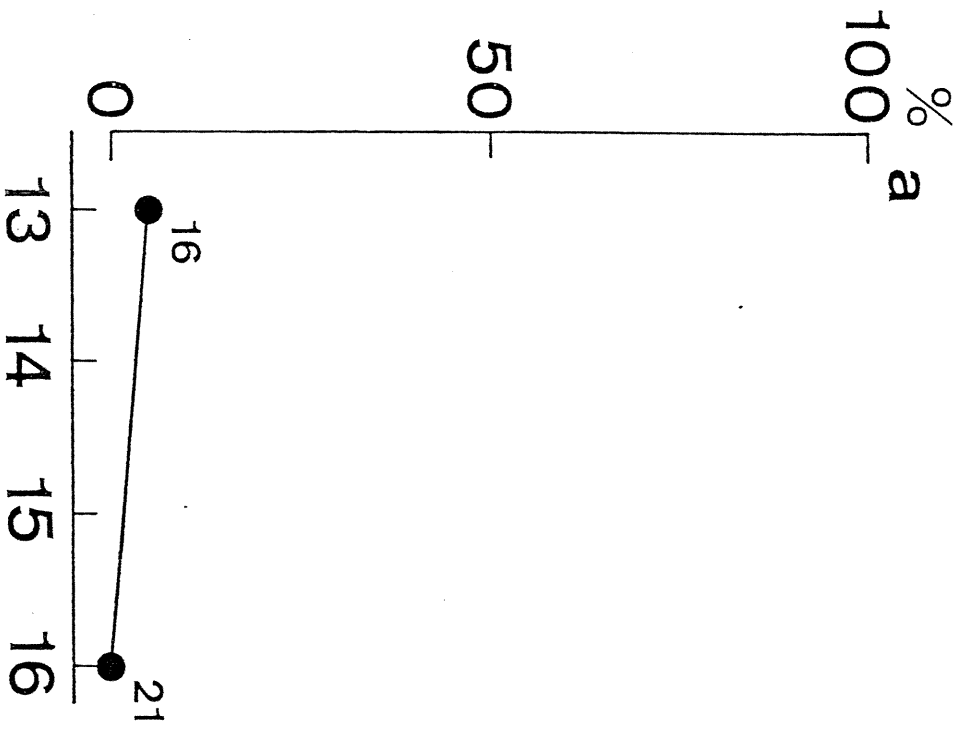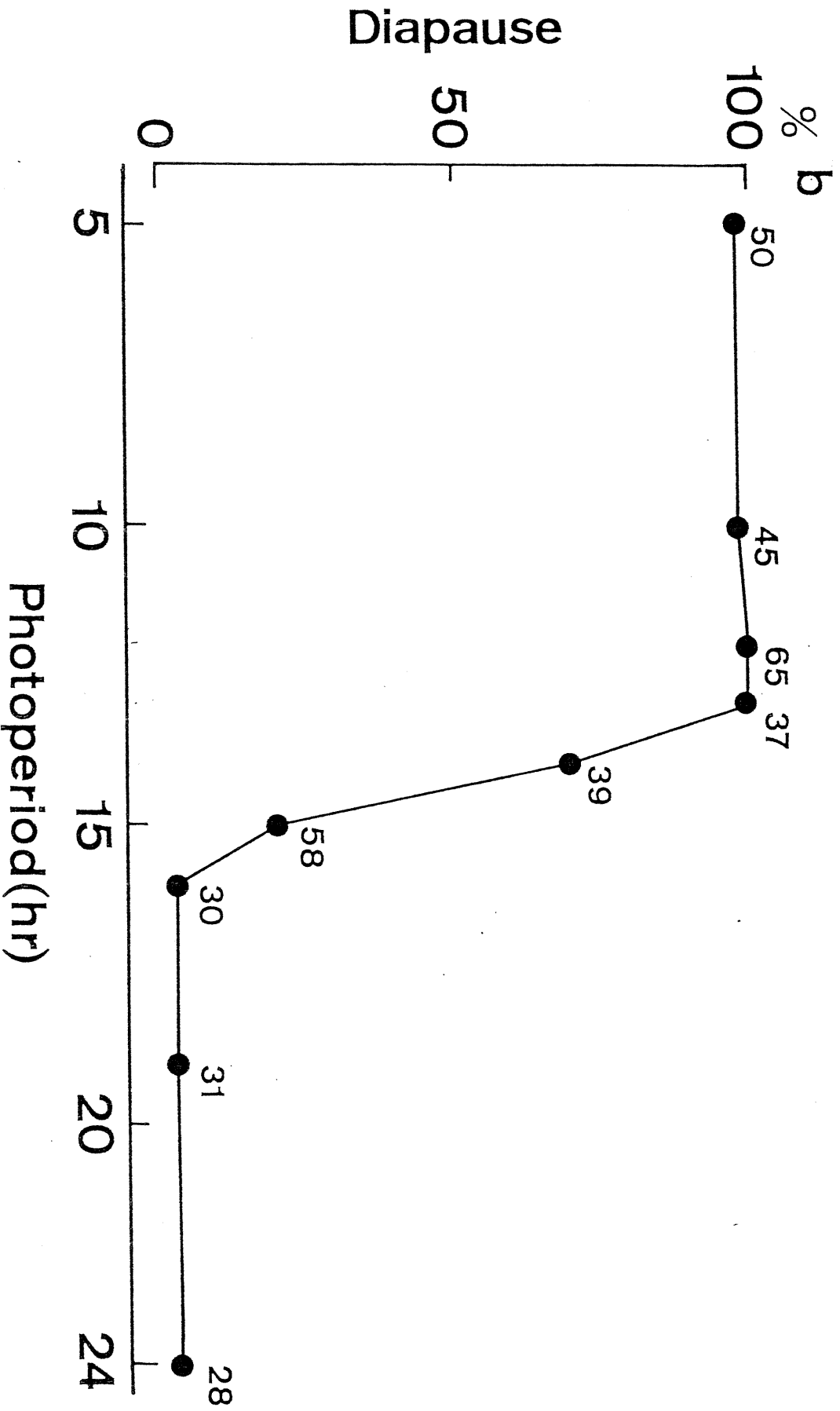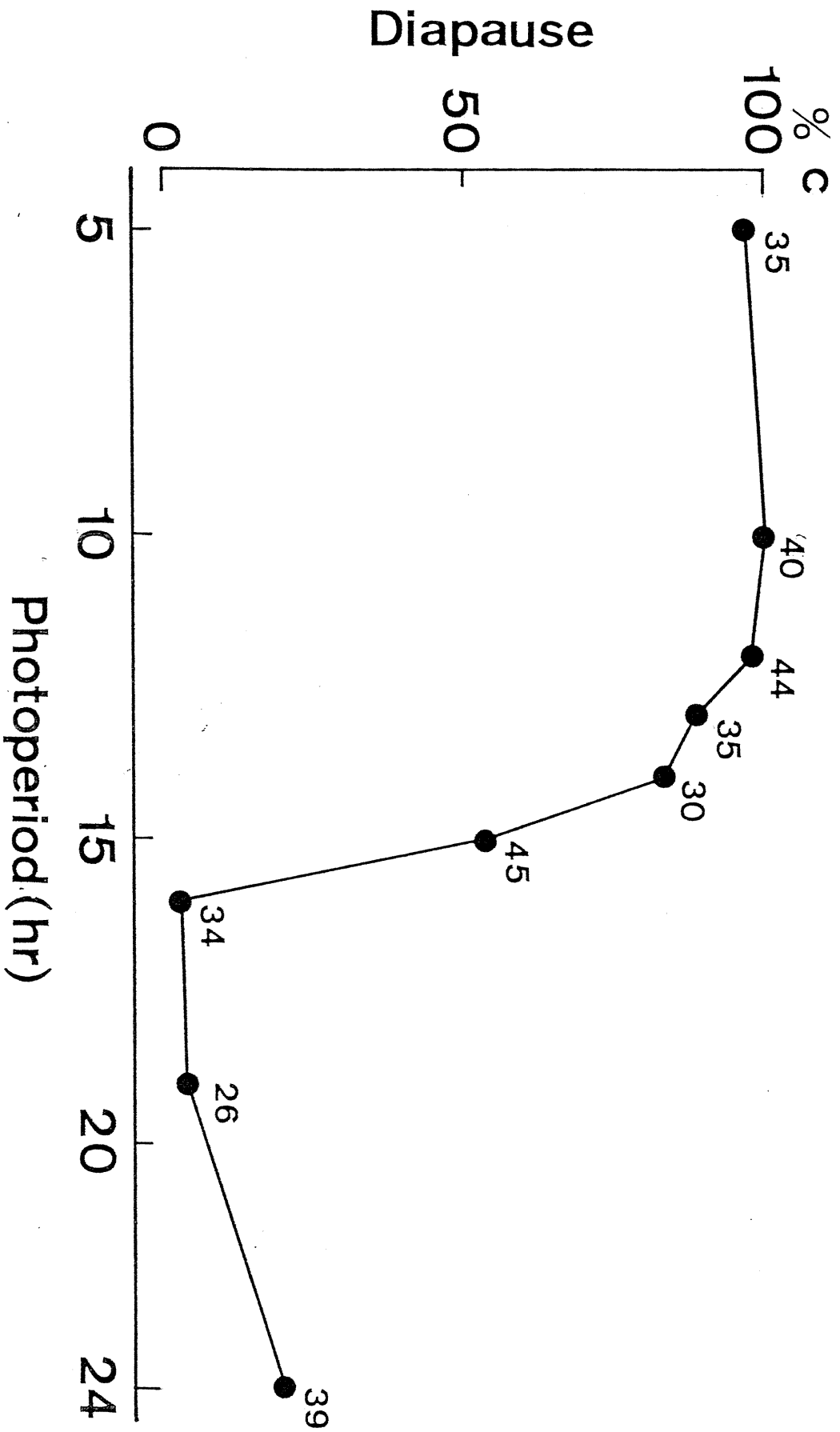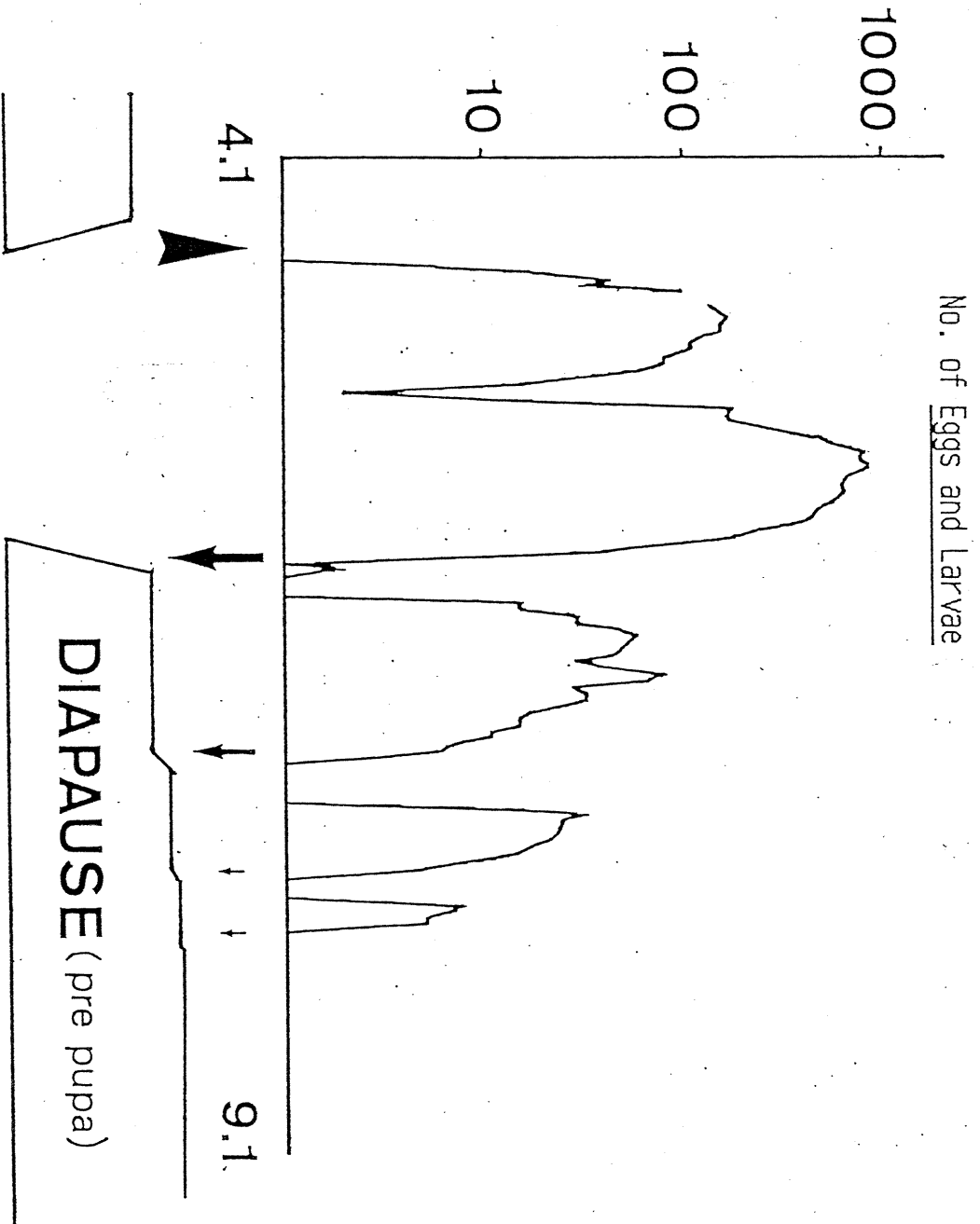
Resource availability and life history polymorphism of a sawfly,

Strongylogaster osmundae: Model and field data

(Hymenoptera: Tenthredinidae)

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21 Text pages
 4 Tables
 6 Figures

Abstract   *Strongylogaster osmundae* is multivoltine (5 or 6 generations; from late April to July). In the second generation, its population density of the egg and larval stages reaches maximum, then it decreases gradually in the subsequent 3 to 4 generations. In the second and subsequent generations of the two populations of *S. osmundae*, a fraction of a population enter diapause until next spring while others produced the next generation (fractional diapause).

The condition that favored the evolution of this life history polymorphism was investigated using a model, field experiment and field observation. Density dependent population regulation was assumed in the model. The model predicted that fractional diapause evolves when the equilibrium population density decreases seasonally. The asumptions and prediction of the model were compared with the field data qualitatively. Firstly, a field experiment was carried out to test whether carrying capacity reduced outdoors or not. Almost the same numbers of adult sawflies of the first (May) and the second generation (June) were released in the field, and the number of their offsprings (i.e. the second and third generations) were counted. The third generation showed a much smaller number of eggs and last instar larvae, and a lower survival rate during the larval stage than the second generation. This seemed to be caused by food shortage. This result indicated a reduction of carrying capacity after the second generation in the field. Secondly, the model predicted that the rate of diapause in ESS

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is stable if the rate of reduction of the carrying capacity is stable. Amount of available food resource for the third and subsequent generations (secondary shots) was used for the carrying capacity of the later generations. It was almost proportional to the population density of earlier two generations. Thus, fractional diapause of *S. osmundae* might have evolved without ability of estimation of population density or resource amount. Thirdly, fractional diapause was observed in a population where the number of the second generation is smaller than the first generation. Thus all the results of field experiment and the field data supported the model. Though it does not seem that density dependence plays important role in determining population density, especially that of the earlier generations, it must have played an important role in evolution of "installment savings" of this sawfly.

A sawfly, *Strongylogaster osmundae*, alters the phenology of its host fern, *Osmunda japonica*, by feeding out in order to maintain its mutivoltine life history. The population density of eggs and larvae reached a peak in the second generation, and thereafter it decreased gradually as if the local population was going to be extinct (Otsuka in prep. (1)). A part (not all) of the second and subsequent generations enter diapause (fractional diapause). Then the diapausing insects formed "installment savings" which is similar to a seed bank (Begon et al. 1990) of annual weeds (Otsuka in prep. (2)).

Establishment and maintenance of a seed bank or an egg bank (Takahashi 1977a, De Stasio 1989) would be advantageous in situations where the environment changes unpredictably (Cohen 1966, 1967, 1968, Templeton and Levin 1979). Seed/egg bank becomes an important buffer against local extinction (Takahashi 1977b). The installment savings of prepupae in *S. osmundae* might have evolved under a similar condition to those which favor the seed/egg banks.

Fractional diapause is predicted also by the model under the conception of an evolutionarily stable strategy (ESS) (Maynard Smith 1982), too. Sota, through his mathematical model on bivoltine insects (Sota 1988), predicted that fractional diapause in the first generation evolves when the carrying capacity decreases. Population density of the egg and larval stage of *S. osmundae* decreased by generations. And the amount of new leaves is smaller in the later generations than those in the earlier

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generations (Otsuka in prep. (1)). Therefore, similar conditions to that assumed in Sota's model, such as decreasing food resources, might have occurred in the second and subsequent generations in this sawfly.

Unpredictable changes of environmental conditions and decreasing of carrying capacity can co-occur. However, if the population density or the pattern of population dynamics is stable, the latter would have more important role in the evolution of the installment savings of prepupae. A simple ESS model that predicts installment savings of population was made. This model was tested qualitatively with a field experiment and some field data.

Model

I assumed an asexual insect and made a model similar to the model of Sota (1988). To simplify, its reproduction curve was assumed as shown in Fig. 1. That has a large rate of increase and strong density-dependent regulation. Then population size of the next generation is constant and equal to the carrying capacity. I assumed that survival rate of diapausing animals until next year is constant and independent of when an insect enter diapause. Thus, fitness is able to be measured by the number of diapausing insects.

A. Bivoltine Insect

All insects of the second generation enter diapause. Let N_1 and N_2 be the equilibrium population sizes of the first and the second generation, respectively. Then fitness (i.e. the number of diapausing individuals it produces) of an insect which enter diapause after the first generation becomes

$$1 \qquad (itself)$$

and fitness of an insect which does not enter diapause after the first generation is

$$N_2/p_t N_1$$

Where p_t ($0 \leq p_t \leq 1$) is the rate of not-diapause insects of the first generation. Thus the condition for univoltine and bivoltine to be ESS should be

$$N_2 = 0$$

and

$$N_2 \geq N_1$$

respectively. Therefore, the condition for p_1 (rate of not-diapause insects of the first generation: $0 < p_1 < 1$) to be an ESS is

$$0 < N_2 < N_1 \qquad\qquad (1)$$

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This condition is consistent with the conditions which favor fractional diapause in Sota's model. Under this condition, we get

$$p_1 = N_2/N_1 \qquad\qquad (2)$$

Equation (2) means that p_1 (rate of not-diapause) is constant independent of the population size (N_1 and N_2) so far as N_2/N_1 is constant. Under such conditions, fractional diapause with a stable p_1 can evolve without the evolution of the ability to estimate population size density carrying capacity. Schematic drawing of seasonal change of the population size and occurrence of diapause is shown in Fig. 2.

B. Multivoltine insect

The model presented above can be applied to the multivoltine insects. Let N_i and p_i to be the population size and the rate of not-diapause in ESS, respectively, in the i th generation.

Change N_1 and N_2 into N_i and N_{i+1}, respectively. Then we get the condition that favors fractional diapause and the rate of not-diapausing insects in the i th generation. They are

$$0 < N_{i+1} < N_i \qquad\qquad (3)$$

and

$$p_i = N_{i+1}/N_i \qquad\qquad (4)$$

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respectively. As predicted in the case of bivoltine insect, P_i is stable if N_{i+1}/N_i is stable. Consider the seasonal change of population size like *Strongylogaster osmundae* in 1985 at Ichijoji,

$$N_1 < N_2, \quad N_2 > N_3 > N_4 > N_5, \quad N_6 = 0$$

where N_1, N_2, N_3, N_4, and N_5 are the population sizes of the first to fifth generation, respectively. Obviously, all the animals of the fifth generation should enter diapause and all the animals of the first generation should not enter diapause. A part and not all of each second to fourth generation should enter diapause. A summarized scheme of seasonal changes of the population size and diapause is shown in Fig. 3.

Tests

Appropriateness of the model was tested on the following three points. 1) Reduction of carrying capacity, 2) Stability in the change of carrying capacity, and 3) Does fractional diapause occur in the first generation where $N_1 > N_2$?

1) Reduction of carrying capacity - A field experiment.
Is the carrying capacity in the third generation smaller

than that of the second generation (i.e. $N_2 > N_3$)? The most important assumption of the model is the regulation of the population density with density dependent process. The population density and the amount of resource (new leaves) of the second generation was larger than the third generation. These facts appear that the assumption of the model ($N_2 > N_3$) is really occurs. However, N_i is carrying capacity. Whether decreasing of population density reflected decrease of carrying capacity or not is still unknown. Observed population density might have been much smaller than equibrium. Does such reduction of carrying capacity really occur outdoors?

Method

The experiment was carried out in 1989 at a small area named "JIZO" at Kyoto. JIZO area included about 30 individuals of *Osmunda japonica*, and it was a part of Ichijoji population (Otsuka in prep. 1). Within the area, many eggs and larvae of *S. osmundae* were observed in 1985 and 1986 (e.g. in 1985, 209 and 1291 eggs in the first and second generation, respectively) , its population density decreased by years (Otsuka in prep (1)). In 1989, no eggs and larvae of the first generation were found at JIZO area, though a few eggs and larvae were found nearby.

I released 108 males and 103 female adult sawflies from 4 to 15 May, and 110 males and 108 females from 4 to 19 June, when eggs of the second generation and the third generation respectively were observed in other areas at Ichijoji.

Therefore, almost all eggs and larvae observed in JIZO area can be regarded as the offspring of the adult sawflies that I had released.

Field survey was done every day. The method was same as that in Otsuka (in prep. (1)), excepted that all the last instar larvae were captured. They were reared in the laboratory (Alt. ca. 70 m) under the temperature and photoperiodic conditions similar to outdoors. The larvae found near JIZO area (about one tenth number of those in JIZO area) were also captured. Thus second generation was removed from JIZO area and its surroundings. Therefore the second generation derived from released sawflies would not have affected the number of the third generation.

Wet weight of the prepupae of the third generation which were captured in JIZO area were measured in order to know the effects of leaf age on the growth of larvae. The larvae which mixed with other larvae from leaves of different ages were omitted. Wet weight of prepupae those were reared with new leaves in the laboratory was compared with that of above ones.

Result

The third generation showed smaller number of eggs and larvae than the second generation (Table 1). Survival rate during larval stage was significantly smaller in the third generation (Table 1, p<0.01 Fisher's exact probability test). Some egg masses were deposited on old leaves (after the end of

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elongation, stage EE- in Otsuka in prep. (1)) especially in the third generation (Table 2). In the third generation, some of the eggs deposited on old leaves withered gradually and did not hatch. Even if hatched, some of them died in the first instar without showing any trace of feeding on leaves (Table 3). This gradual egg withering and failure in feeding occurred on the old leaves which emerged in April.

Unusual mortal cases which seemed to be caused by high density were observed in the third generation: 1) Cannibalism: Eggs or first instar larvae of an egg mass were all eaten by conspecific larvae together with pinnules. The larvae which ate conspecifics had been deposited on the same leaf several days before the sufferer had. Such cannibalism was observed in three cases where a total 43 individuals from 3 egg masses were sacrificed. 2) Three egg masses (48 eggs) were deposited on a single small new leaf. When they entered into second and third instars, they ate up the whole leaf and started move out. Not more than 3 out of 45 larvae reached other leaves and grew up to the last instar, but the remaining disappeared. Such high mortality while leaf-to-leaf movement was not observed on the fourth and fifth instar larvae, for they seemed to have enough mobility (Otsuka unpublished).

Table 4 shows the effect of leaf age on weight of the prepupae and the result of Mann Whitney's U-test. Prepupae which fed on new leaves until fifth instar (all of them were males) got heavier weight (mean: 14.6 mg) than male prepupae which fed old

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leaves since first instar (12.0 mg). The former was also heavier than those fed old leaves since fourth instar (12.3 mg) and as heavy as those fed on new leaves in the laboratory (both 14.8 mg). Female prepupae which fed on old leaves since first instar and those fed on old leaves since fourth instar were about 20 mg. They were lighter than those fed on new leaves in the laboratory (heavier than 25 mg).

2) Stability in the change of carrying capacity.

Is is often assumed in the models on the conceptional framework of ESS that all individuals know everything. In the above model, an ESS need ability of estimate N_{i+1}/N_i when it fluctuates year by year. It seems difficult for a sawfly to estimate population density and carrying capacity for the next generation. However, my model predicts that fractional diapause can evolve without ability of estimation if the decreasing rate of carrying capacity (N_{i+1}/N_i) is stable. Does such stable decreasing in carrying capacity really occur outdoors?

Method

The resource for *S. osmundae* is new leaves (Otsuka in prep. (1)). The result of the field experiment suggests that the amount of new leaves might have limited the population density of the third generation. The third and subsequent generations cannot utilize leaves which emerged in the spring (primary

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shoots), because these shoots have already become old. The later generations (i.e. the third and subsequent generations) must depend on the secondary shoots which are compensation for defoliation caused by the earlier (the first and second) generations (Otsuka in prep (1)). Thus, the carrying capacity of the later generations is the amount of the secondary shoots. Therefore, the stability in the change of carrying capacity can be tested by determining whether or not the amount of the secondary shoots is proportional to the population size of the earlier generations. Correlation between the egg number of the earlier two generations and the amount of secondary shoots in each of two areas of Ichijoji (1986 to 1988) and Kamigamo (1985 to 1988) were examined using the data of Otsuka in prep. (1).

Result

Correlation between the density of eggs of the earlier two generations and the amount of secondary shoots per the amount of primary shoots is shown in Fig. 5. Their relationship appears stable, even though the population density of the earlier two generations varied widely. The amount of secondary shoots is almost proportional to the population size of the sawfly's earlier two generations (SPN/PPN = 3.672 NE/PPN + 0.0556, r=0.919).

3) Does fractional diapause occur in the first generation

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where $N_1 > N_2$?

The rate of diapause of the first generation was zero in both Ichijoji and Kamigamo (Otsuka in prep. (2)). Population density was larger in the second generation than in the first generation (Otsuka in prep. (1)). These facts are consistent with the prediction of the model ($p_i=0$ when $N_{i+1}>N_i$, i=1). Fractional diapause should occur in the first generation ($0<p_1<1$) if the population density in the first generation is larger than the second generation.

Method

Preliminary observation showed in a local population at Kumogahata, Kyoto (Fig. 4), the density of egg and larval stage reached a peak in the first generation. Field survey was carried out every three days in 1990 at an area in Kumogahata, by the same methods as Otsuka (in prep. (1)). Some eggs were captured near the area and reared in the laboratory under temperature and photoperiodic condition similar to outdoor condition of Kyoto University. The rearing method and the criterion of diapause were the same as those used in Otsuka (in prep. (2)).

Result

In Kumogahata, population of the sawfly in egg and larval stage fluctuated seasonally as shown in Fig. 6b. The seasonal fluctuation of the amount of new leaves is shown in Fig. 6a. Three generations were observed. The number of the fist

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generation was the largest of the three. The first generation emerged a little later than the emergence of the leaves of the host plant, while the emergence of the first generation of Ichijoji population was well synchronized with the emergence of leaves (Otsuka in prep. (1) Figs 2 and 5). The larvae of the second generation appeared when new leaves of primary shoots had already decreased.

Among 339 individuals of the first generation captured at Kumogahata, 129 (38 %) entered diapause.

Discussion

Sawflies released in June reproduced less successfully than those released in May, though almost the same number of adult sawflies were released at the same place (JIZO, Ichijoji) in May and June (Table 1).

Female *S. osmundae* usually deposits eggs on new leaves (Otsuka in prep. (1)). Amount of new leaves (number of pinnules) in the third generation was less than one twentieth of that in the second generation (Table 2). The small amount of new leaves in June might haave caused fewer eggs of the third generation and its higher ratio of the egg masses on old leaves (Tables 1 and 2). Higher mortality was observed on the eggs and larvae on old leaves. Further, smaller prepupae were produced by larvae which fed on old leaves only (Table 4). Multiple egg

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masses on a single leaf often resulted in death of eggs and/or larvae through failure in inter-plants movement or cannibalism.

A low rate of reproductive success of the sawflies released in June was induced by the following three factors: 1) shortage of good oviposition site (i.e. new leaves), 2) low quality of food plant, and 3) high density during the egg and larval stages. Thus, the experiment proved that the reduction of carrying capacity, the most important assumption of the model, actually occur in the field. Further, number of eggs and larvae observed at JIZO area in this experiment was not much larger than that observed at JIZO in 1985. Thus the result also suggests that reproductive success would have been much lower if there were many of not-diapause sawflies in the second generation.

Test 2) shows that carrying capacity of the third and subsequent generations (amount of secondary shoots) is proportional to the population size of the earlier generations (Fig. 5). This is a natural result, since the secondary shooting is induced by defoliation by the earlier generations. This result strongly suggests that decreasing pattern of the carrying capacity is stable. Thus, it seems that fractional diapause can evolve even though each sawfly cannot estimate population density or carrying capacity of the next generation.

Test 3) revealed that the prediction of the model well agrees with the occurrence of fractional diapause in the Kumogahata population. For, the number of eggs and larvae and the amount of new leaves were largest in the first generation

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$(N_1 > N_2)$. It seems that later emergence of the first generation caused the emergence of the second generation after the peak of the amount of new leaves. Why the emergence of the first generation did not synchronized with the beginning of shooting is unknown.

Therefore, all three tests supported my model. Further, the result of Test 2 suggests that unpredictable environmental changes, that favors establishment of a seed bank, might not have played large role in the evolution of "installment savings" of prepupae of this sawfly.

Density dependence and fractional diapause is also observed in some herbivorous ladybeetles. Some of female lady beetles quit oviposition and de-mature their ovaries and overwinter. This fractional diapause occurs when the density is high (Nakamura, 1976, 1977, Ohgushi 1986). Hibernation in adult stage enables these lady beetles to assess food resource for the next generation and to enter diapause even after deposition of some eggs. On the other hand, *S. osmundae* can not have such flexibility, for they enter diapause when they are prepupae.

This low flexibility may cause genetic variation among populations. It seems that there is genetic difference between the Kumogahata population and the other two populations. Since fractional diapause occurred in the first generation of Kumogahata population under semi-outdoor conditions, while the first generation of the other two populations seldom entered diapause even under short-day conditions.

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Whether density dependent processes occur frequently in nature or not is vigorously debated in this decade (eg. Stilling 1987, 1988, Hassell et al. 1989, Brown 1989). However, important problem is not frequency of density dependence but whether or not it plays an important role in population dynamics (Itô 1990) and its effects on the evolution of the traits of each species. Though density dependence does not seem to determine the population density of this sawfly (eg. Fig. 5), density dependence must have played an important role in the evolution of life history polymorphism (fractional diapause in many generations) of *S. osmundae*.

Acknowledgments

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Table 1. No. of Eggs, hatch rate, No. of larvae and survival rate in JIZO, 1989 (Field Experiment). #: already hatched when they were found. *a: rate of hatch. *b: survival rate during larval stage. Larval survival rate was higher in the second generation (p<0.01 Fisher's exact probability test).

	Second generation	Third generation
Egg	2004	554
Hatch (*a)	1391 (0.69)	363 (0.66)
1. instar#	128	71
Total 1. instar	1519	434
5. instar (*b)	925 (0.61)	89 (0.21)

Table 2. Ages of leaves and Number of Egg masses deposited. (1989 Field experiment). New: Before the end of leaf elongation (i.e. OB-OE, OE-HE and HE-EE in Otsuka in prep. (1)). Old: after the end of leaf elongation

Stage of leaf	2nd generation		3rd generation	
	No. of pinnules	No. of egg masses	No. of pinnules	No. of egg masses
New	7922.2	70	316.2	11
Old	2909.2	30	9135.8	19

Table 3. Fate of some egg masses which were deposited on old leaves. EE: End of leaf elongation

Leaf code	Date of EE	Date of Oviposition	No. of eggs	No. of 1.ins	No. of 2.ins	No. of 5. ins
J1-4	12 MAY	16 JUN	22	0	0	0
J5-3	10 MAY	12 JUN	5	3	0	0
J20-6	9 MAY	15 JUN	18	10	4	1

Table 4. Age of food leaves and the growth of the sawflies (wet weight of prepupae, mg). New: prepupae which ate new leaves only. New-old: prepupae which transfered from new leaves to old ones when they wer 4th instar. Old: prepupae which ate old leaves only.

a. Males.

	Field experiment (third generation)			On new leaves	
	New	New-old	Old	20°C	25°C
N	7	7	28	60	54
Mean*	14.6a	12.3b	12.0b	14.8a	14.8a
SD	1.4	1.4	0.9	1.3	1.4

*: Means followed by the same letter within a line were not significantly different at the $p < 0.01$ by Mann-Whitney's U test.

b. Females.

	Field experiment (third generation)			On new leaves	
	New	New-old	Old	20°C	25°C
N	0	21	45	50	40
Mean**	–	20.7A	20.2A	25.1B	25.4B
SD	–	1.0	1.8	1.4	2.2

**: Means followed by the same letter within a line were not significantly different at the $p < 0.01$ by Mann-Whitney's U test.

Figure legends

Fig. 1. Reproduction curve assumed in the models.

Fig. 2. Schematic drawing of the fractional bivoltine insect. t; time, N_1 and N_2; Number of individuals of the first and the second generation, respectively. D and ND; diapausing fraction and not-diapausing fraction of each generation, respectively

Fig. 3. Schematic drawing of the multivoltine insect with similar population dynamics as *S. osmundae*. See text and Fig. 2 for abbreviations.

Fig. 4. Map of Northern part of Kyoto City. Only 200m contour line is drawn. I; Ichijoji, Ka; Kamigamo, Ku; Kumogahata. Square indicates Kyoto University.

Fig. 5. Correlation between the total egg density of the earlier two generations and the amount of secondary shoots. The data are same as used in Fig. 7 of Otsuka in prep. (1). PPN; Number of pinnules of primary shootings. EN; Total number of eggs of the first and second generation. SPN; Number of pinnules of secondary shootings. SPN/PPN = 0.0556 + 3.672 NE/PPN (r=0.919)

Fig. 6. a. Seasonal fluctuation of amount of new leaves (i.e. number of new pinnules). b. Number of eggs and larvae of Kumogahata 1990 population.
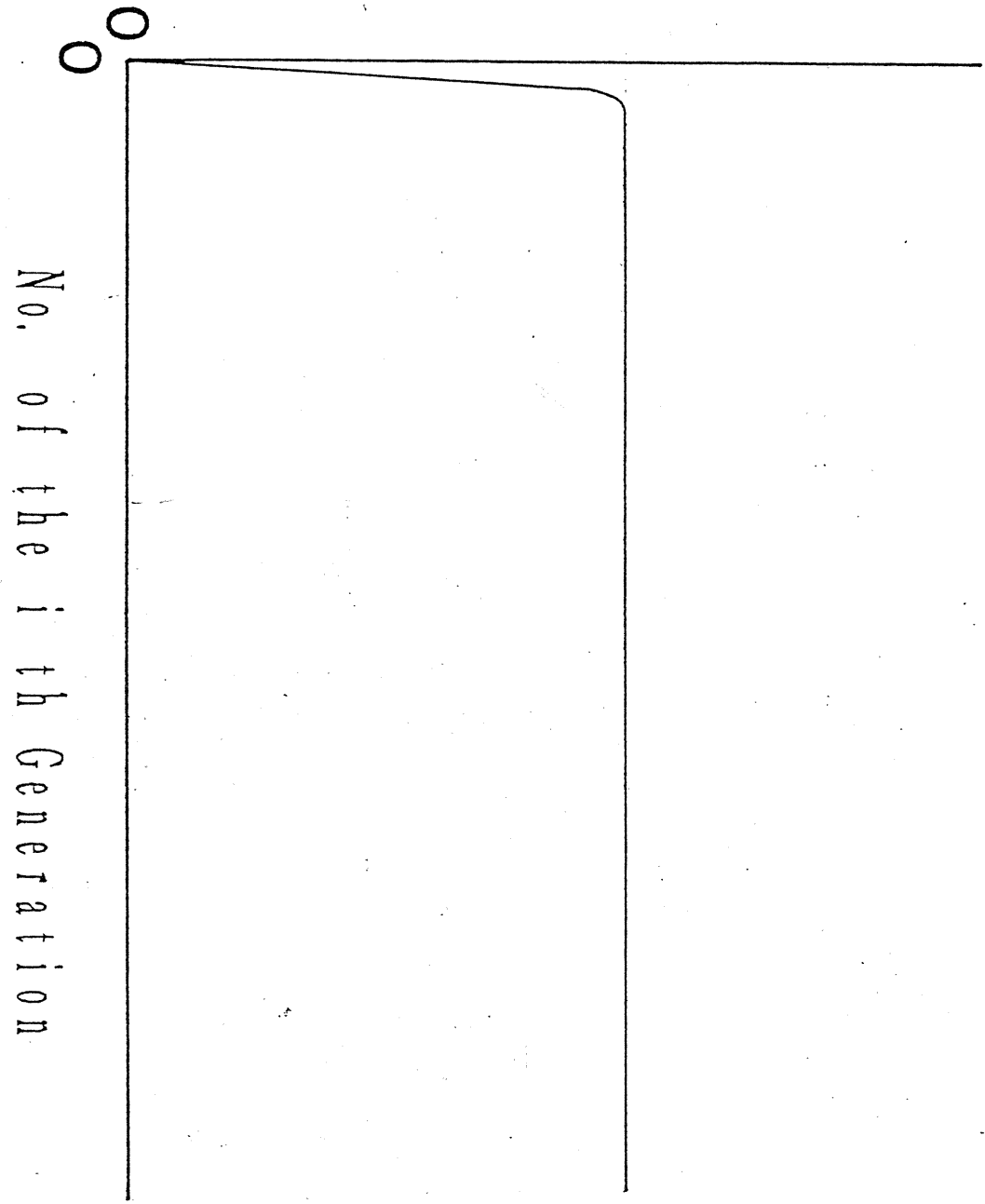

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Fig. 1

No. of the i+1 th Generation

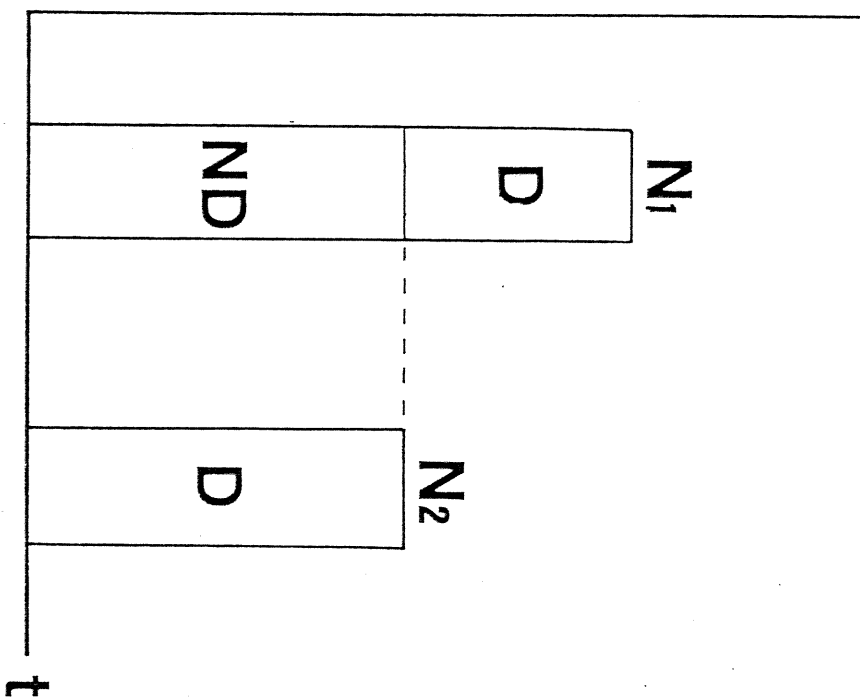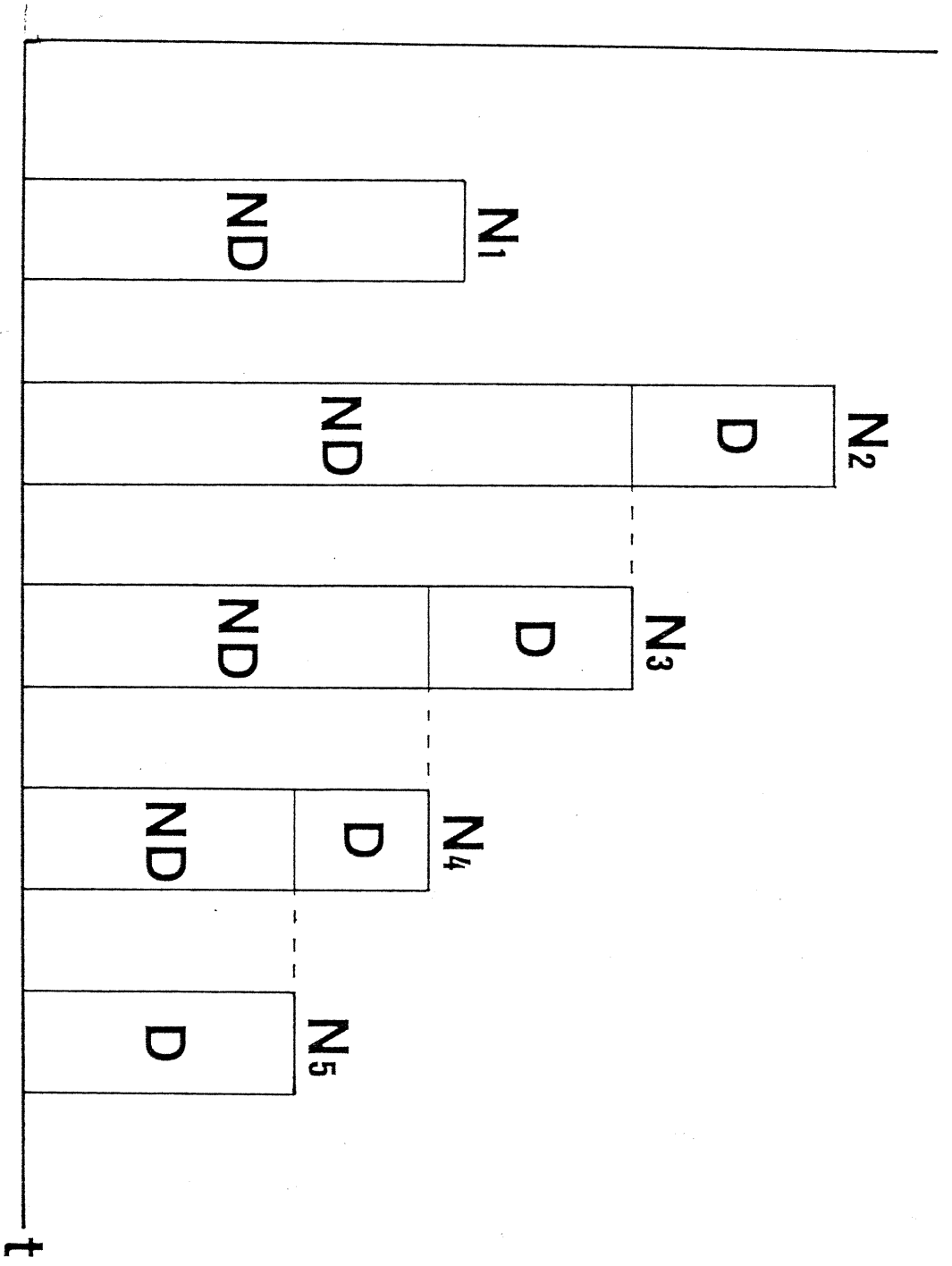No. of the i th Generation

Fig. 2

Fig. 3

Fig. 4

200
m

1 km

Ku

Ka

I

200m

Fig.5

Fig 6

a

x10³

No. of New Pinnles

15

10

5

0

4.1   8.31

b

No. of Eggs and Larvae

1000

100

10

4.1   8.31