

Host Utilization by a Sawfly *Strongylogaster osmundae* (Hymenoptera: Tenthredinidae) on Osmund Fern *Osmunda japonica*

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Abstract Voltinism and host plant utilization of the sawfly *Strongylogaster osmundae* were investigated. This species is multivoltine (5 or 6 generations per year) and emerges from late April to July or early August in Kyoto, Japan. Female sawflies deposit eggs on new leaves of the osmund fern, *Osmunda japonica*, and the larvae feed on the leaves. The host plant usually develops new leaves from late April to early May (primary shoots), and intact ferns rarely produce new leaves thereafter. Since the primary shoots are new and only available to the sawfly until the beginning of June at the latest, only the first and second generations can utilize them. The eggs are laid in clusters, and the larvae feed gregariously and frequently defoliate leaves. It is suggested that egg clumping and defoliation by *S. osmundae* is a form of host regulation to maintain its multivoltine life history, since the defoliation by the first and second generations induces compensatory regrowth of the fern, producing food for the third and subsequent generations.

Key Words Host regulation, Insect-plant interaction, *Osmunda japonica*, Positive feedback, Sawfly, Fern, *Strongylogaster osmundae*, Voltinism

Introduction

The number of generations in a year (voltinism) of a phytophagous insect must be constrained by the phenology of the host plant(s) as well as environmental conditions such as temperature and humidity. 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 the 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 tenthredinid sawflies are univoltine. Among 38 species of Japanese Selandriinae (Tenthredinidae), larvae of which feed ferns

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or moss, 26 species (68%) are univoltine (Naito 1971, 1975, Naito pers.com.). The 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 the spring.

Both univoltine and bivoltine (or multivoltine) sawflies, however, sometimes occur on the same host plant (e.g. sawflies on a bracken *Pteridium aquilinum*, Lawton 1976). How do multivoltine species get its food, if new leaves are essential to its diet? 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 pers.com.), 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 completes its multivoltine life history on the fern.

Materials and Methods

Field observations

To elucidate the seasonal fluctuation of population size and voltinism and the pattern of host plant utilization of *S. osmundae* in its habitat, I studied 1) the 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 (Alt. 150-200m; one area was named "JIZO" and another was named "M") and two at Kamigamo (Alt. 130-160m, 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. Dates of the following three growth stages were recorded for each leaf: 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, the date, the pinnule number and the cause of defoliation were recorded. 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.

A similar survey was carried out from 1986 to 1989 in 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 offspring were also used in the experiment on larval growth. All these insects were reared under a constant temperature of 25°C and a photoperiod of 16L8D.

1) Oviposition

In June and July, 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 adult emergence; "young" leaves were leaves which passed the stage OE several days earlier, "aged" leaves were those opened in April more than a month having elapsed after EE. The number of eggs deposited on the young leaves, the aged leaves and the wall of the 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 in the number of eggs and larvae at JIZO area, Ichijoji in 1985 is shown in Fig. 2a. Five generations were observed from late April to the end of July in this area. Emergence of the individuals of each generation was well synchronized. The population size of egg and larval stages reached a maximum in the second generation, and in the subsequent 3 generations it decreased gradually. Table 1 shows the number of eggs of

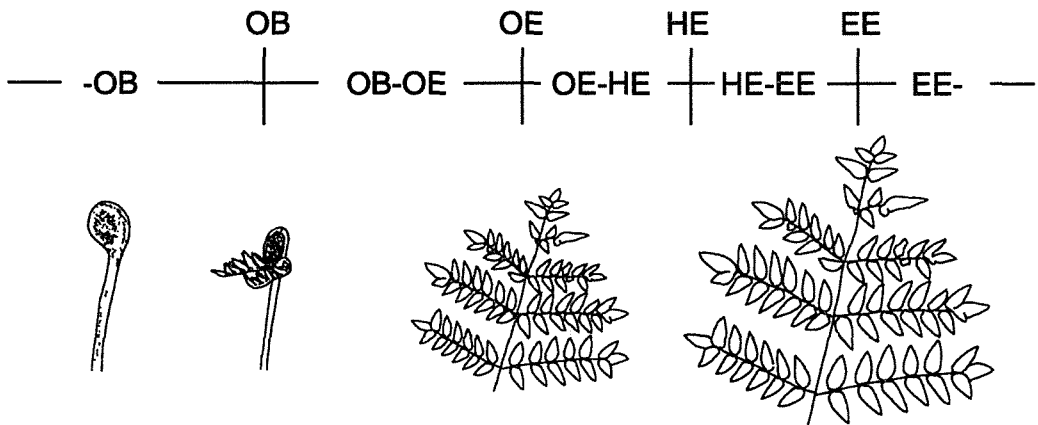


Fig. 1. Growth stages of a leaf of *Osmunda japonica*. The leaf is covered with cottony material before the opening (-OB). OB: beginning of opening, OE: end of opening, EE: end of elongation, HE: the middle day between OE and EE.

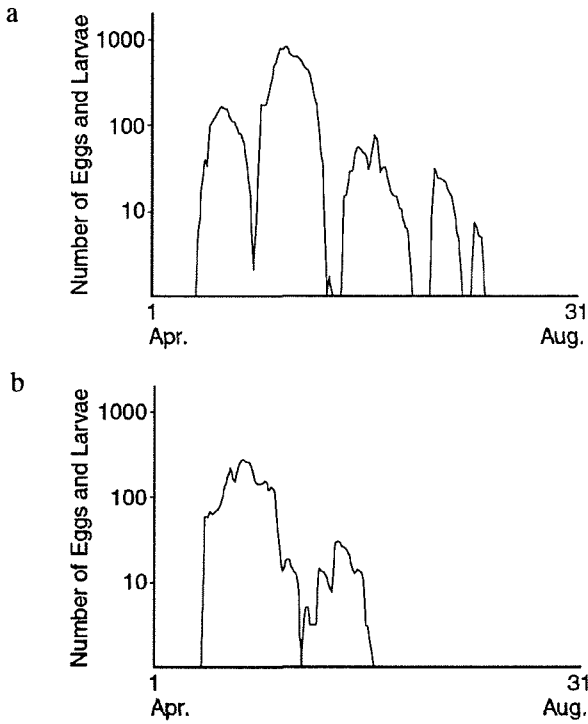


Fig. 2. a: Seasonal fluctuation in the number of eggs and larvae observed on host plant in one study area in Ichijoji in 1985. b: ditto in Kamigamo in 1985.

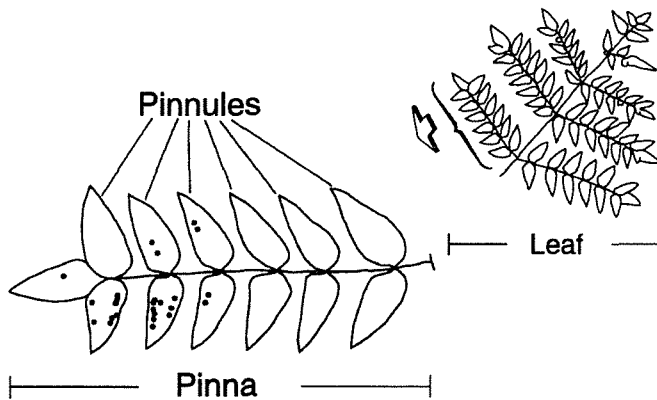


Fig. 3. Distribution of eggs on a leaf deposited by a female of *S. osmundae*. Upper right: A whole leaf. Lower left: A pinna on which eggs were deposited. Each dot indicates an egg.

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

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

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, and population size fluctuated almost the same way every year, though population density differed with the year (Otsuka unpublished).

On the other hand, in Kamigamo, synchronized emergence of the sawfly was not observed and the generations overlapped with each other (Fig. 2b). However, *S. osmundae* was multivoltine in Kamigamo as well, because eggs and larvae were found from April until the end of July or the beginning of August every year. The duration of the eggs and 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* thrust 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, which 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, see also Otsuka 1991). The eggs had a 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 during such 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 stage 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

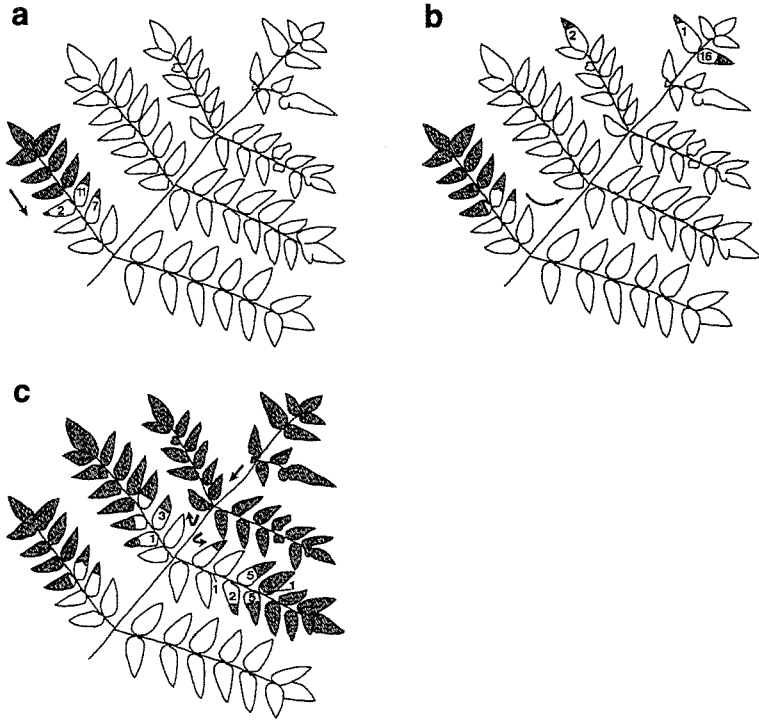


Fig. 4. Typical feeding pattern of *S. osmundae*. a: first instar. b: third and fourth instars. c: fourth and fifth instars. Arrows indicate direction of transfer of the larvae and shaded areas indicate eaten part of the leaf. Numerals indicate the number of larvae on the pinnule.

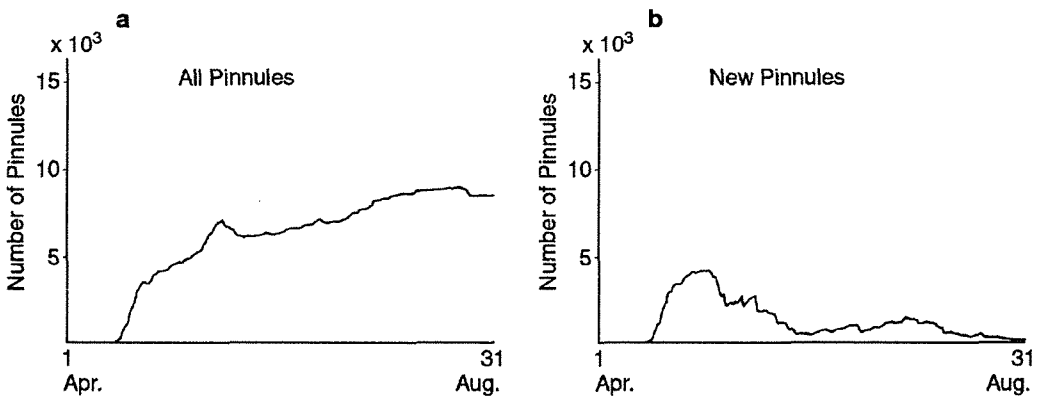


Fig. 5. Seasonal change of pinnules' number at the JIZO area, Ichijoji in 1985. 5a: Total number of pinnules, 5b: Number of pinnules of leaves in the stage between OB and EE.

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

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

of and aging of leaves. Therefore, the number of the pinnules shown in Table 2 is the mean number of pinnules at each of the 5 leaf stages throughout each oviposition period (the period during which 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 of all generations except for the first generation occurred (see also Fig. 5).

4) Resource Supply

Growth stages of a single leaf of *Osmunda japonica* are shown in Fig. 1. The mean duration of leaf opening (i.e. between OB and OE) was 5.3 days in April and 3.3 in July. The mean duration of leaf elongation (i.e. between OE and EE) was 12.2 in April and 9.1 in July.

The seasonal change in 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 latter 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* was in the larval stage (May). New pinnules (stages before EE), however, were abundant only in late 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-

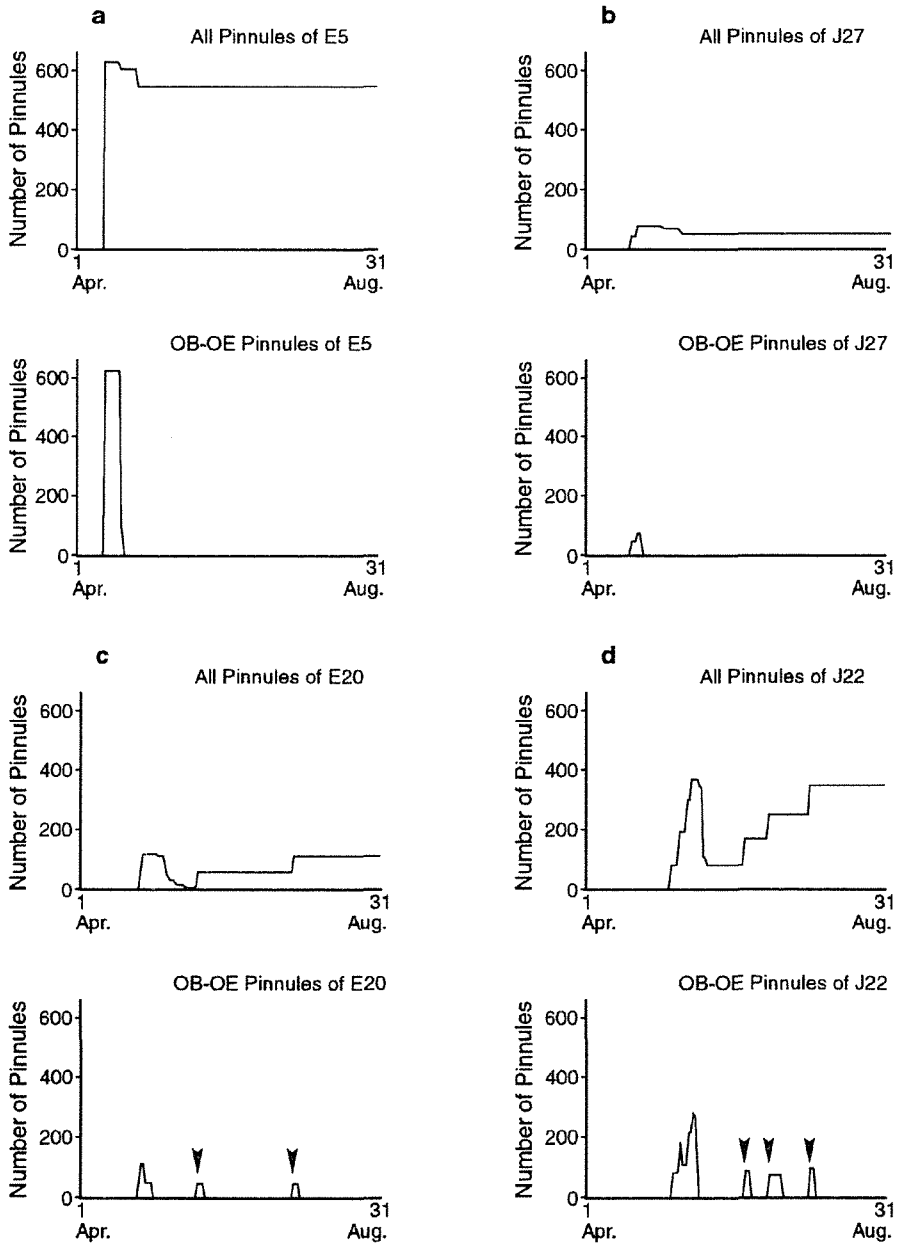


Fig. 6. Seasonal change of the total number of pinnules (upper), number of very new pinnules (OB-OE, lower) of individual plants. a (E5) and c (E20) were observed at Kamigamo and b (J27) and d (J22) were observed at Ichijoji. Each arrow indicates a secondary shoot.

Table 3. Foliage on primary and secondary shoots and defoliation of some individual plants in 1986-1988.

a. MN3 (Ichijoji)					
Year	Primary shoots			Secondary shoots	
	No. of leaves	No. of pinnules	No. of pinnules defoliated	No. of leaves	No. of pinnules
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 leaves	No. of pinnules	No. of pinnules defoliated	No. of leaves	No. of pinnules
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 leaves	No. of pinnules	No. of pinnules defoliated	No. of leaves	No. of pinnules
1986	5	512	278	2	149
1987	5	533	0	0	0
1988	4	417	7	0	0

Table 4. Causes 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 humans (Japanese eat shoots of *O. japonica*) or accidentally by the observer. Others were mostly due to senescence of leaves in late August.

Intact	Cause of defoliation					Total	Total
	<i>S. o.</i>	<i>S. s.</i>	Herbivores	<i>Homo</i>	Others		
9116	5053	28	87	745	1013	6926	16042

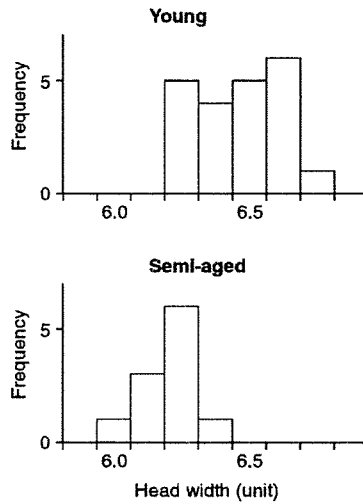


Fig. 7. Head width of adult female *S. osmundae* reared in laboratory. Upper: grew on young leaves. Lower: grew on semi-aged leaves. Head width was measured with a micrometer on eyepiece of a binocular (1 unit = 0.246 mm).

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 & d) and others did not (Fig. 6a & b). Most of the secondary shoots were observed on such plants that experienced heavy defoliation (Fig. 6c & d, upper). The same individual plant which shot secondarily in 1986 did not show secondary shooting when it did not experience heavy defoliation (Table 3).

Causes and amount of the pinnule disappearance of the primary shoots at JIZO area until the end of August 1986 are shown in Table 4. The main cause of defoliation was feeding by *S. osmundae*. The higher the population of *S. osmundae*, the higher the incidence of secondary shooting.

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.

2) Larval Growth

Few of the 25 first-instar larvae ate the aged leaves and died before the last instar. All larvae reared with young or semi-aged leaves attained the adult stage (N=42 and N=11, respectively). The larvae that ate semi-aged leaves became females and they had a 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-Whitney's U-test, see Fig. 7).

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 (Fig. 7). Since a female thrusts her saw into the leaf for oviposition, old leaves would be too tough to be pierced. Like 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) and eggs laid on the plastic container wall did not hatch. This would be another reason why females oviposit on young leaves which are 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 in the amount of its food resources.

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 are 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), the 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 pers. com.). Most sawflies of this genus are univoltine and feed on new leaves of ferns in the spring. Host plants of bi- or multivoltine *Strongylogaster* other than *S. osmundae* shoot not only in the spring but also in the summer (Naito pers. com.). These facts shows that egg clustering and larval aggregation of this sawfly are unique and that they play an important role in inducing the unusual shooting of the host plant.

Defoliation by phytophagous insects often occurs during the outbreak of their populations (e.g. cinnabar moth *Tyria jacobaeae*, Dempster 1971, Myers & Campbell 1976, Dempster & 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.

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 a much larger amount of food resource than the temporal amount of leaves of food plants (e.g. Coughenour *et al.* 1985a, b; McNaughton 1976, 1979, 1983, 1984, 1985). Unlike herbivorous mammals in Serengeti, sawflies that cause defoliation can not utilize the compensatory growth by themselves, but their offspring do eat.

A univoltine stem-galling sawfly, *Euura lasiopsis* shows host regulation like *S. osmundae*. Its galls 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. lasiopsis* keeps the willow young and susceptible to the galling (Craig *et al.* 1986). The main difference between the *E. lasiopsis* and *S. osmundae* is that *S. osmundae* seems to be unable to maintain its multivoltinism without defoliating its host plant, while *E. lasiopsis* can utilize more or less old willows without that host resource regulation. Host regulation by *S. osmundae* may be the same as that by *E. lasiopsis*, because 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*.

In conclusion, *S. osmundae* seems to defoliate its host plants and forces them to shoot secondarily in later seasons, and the subsequent generation(s) utilizes these shoots as a food resource.

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