Studies on the Cold-Hardiness and Overwintering of
Spodoptera litura F. (Lepidoptera: Noctuidae)
VI. Possible Overwintering Areas Predicted
from Meteorological Data in Japan

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Three criteria necessary for larval overwintering of *Spodoptera litura* were determined from the results of laboratory and field experiments in order to predict the overwintering areas of this insect in Japan. The first criterion is for the daily minimum temperature in winter to be higher than -5°C , which is the lethal low temperature of the larvae. On the other hand, larvae are known to require a daily effective temperature for development (DET) of more than 0.9 degree-days (DD). This necessary DET is decided in accordance with cold intensity and duration of sub-zero temperatures per day. Surplus or deficient DET for long term survival of larvae per day was calculated by subtracting the necessary DET from the actual DET. Consequently, the second criterion is summarized as follows: cumulative surplus DETs $\geq$ cumulative deficient DETs in winter (Dec. 15th to Mar. 15th). The third criterion is for the number of consecutive days with deficient DET to be 30 or less. These three criteria must be met in order for overwintering of *S. litura* larvae to occur. The likely overwintering areas of *S. litura* in Japan were predicted by analyzing temperature data of the Automated Meteorological Data Acquisition System (AMeDAS) on the basis of the three criteria mentioned above.

Key words: overwintering area, *Spodoptera litura*, AMeDAS data, daily effective temperature (DET), lowest daily minimum temperature

INTRODUCTION

Spodoptera litura (FABRICIUS) causes serious widespread damage to many agricultural crops in the areas far south of Central Japan every year. A hypothesis that *S. litura* adult moths immigrate into Japan from overseas every year by long-distance migration has been discussed. However, from our experimental results that the overwintering stage was only the larval stage in warm winters at Tateyama, southern Boso Peninsula (MATSUURA et al., 1992), we suspected that overwintering sites might be located sporadically in warm coastal regions along the Pacific Ocean. It is considered that some adult moths which emerge in spring gradually disperse from the overwintering areas to other northern non-overwintering areas, where they establish new populations and cause widespread damage to many crops. In order to clarify this hypothesis, we have investigated the environmental conditions which

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make it possible for the larvae to overwinter (MATSUURA et al., 1991). As a result, it was determined that larvae can survive for more than 90 days, if they have access to food and are exposed to the daily effective temperature for development (DET) higher than 0.9 degree-days (DD). Further, higher DETs are required as the period of exposure to sub-zero temperatures per day increases. Judging from our results, possible overwintering sites for this insect should be situated in warm areas where all DETs in winter are more than 0.9 DD.

In this study, we have predicted the overwintering areas of *S. litura* in Japan by analyzing temperature data of the Automated Meteorological Data Acquisition System (AMeDAS) based on the DET criteria and the lowest daily minimum temperature determined from laboratory and field experiments.

MATERIALS AND METHODS

Calculation of effective temperatures. The DET of *S. litura* larvae was calculated by the following equation:

$$\text{DET} = 1/24 \cdot \sum_{k=1}^{24} (T_k - 10), \quad (1)$$

where T_k is hourly temperatures higher than 10°C, which is the developmental zero temperature (OKAMOTO and OKADA, 1968; OKADA, 1969; MIYASHITA, 1971).

Actual temperatures at the overwintering habitat of *S. litura* deviate from the temperatures at the AMeDAS stations. When DET was calculated based on the AMeDAS Data, the following equation was used (MATSUURA et al., 1992):

$$\text{DET} = 0.54 + 0.68 \cdot \text{DET}', \quad (2)$$

where DET' is the value calculated from the AMeDAS data using Eq. (1).

The necessary DET for long term (more than 90 days) survival of *S. litura* larvae under fluctuating temperature conditions depended on intensity and duration of sub-zero temperatures per day (MATSUURA et al., 1991). If the daily lowest temperature was above 0°C, the necessary DET was assumed to be 0.9 DD, which is the minimum thermal unit. When the lowest daily temperature was below 0°C, the necessary DET was calculated by the following two cases:

1) If the total hours of temperatures below -2°C was shorter than 5 h per day, the necessary DET was calculated by the following equation (MATSUURA et al., 1991), because -2°C was considered to have the same unfavorable influence on larval survival as 0°C (MATSUURA et al., 1991):

$$\text{necessary DET} = 0.115 + 0.467 X - 0.019 X^2, \quad (3)$$

where X is the hours of sub-zero temperatures per day. However, if X is shorter than 2 h, the necessary DET is 0.9 DD, which is the minimum thermal unit, and if X is longer than 13 h, the necessary DET was assumed to be 3.0 DD, which is nearly the maximum value of the Eq. (3).

2) If the total hours of temperatures below -2°C was longer than 5 h, in which case the necessary DET could not be calculated using Eq. (3), then the necessary DET is assumed to be 3.0 DD.

The surplus or deficient DET for long term survival of the larvae in a day was calcu-

lated by subtracting the necessary DET from the actual DET. We assume that days with surplus DET are thermally sufficient for larval survival, and those with deficient DET insufficient. The surplus and deficient DETs have cumulative effect on long term survival of larvae. The cumulative surplus and deficient DETs in winter were used as the criteria in order to predict the larval overwintering areas.

Experimental procedures. Insects tested were 2nd, 3rd and 4th stadium larvae within 2 days after molting which were reared on an artificial diet (OYAMA and KAMANO, 1976) at 20°C in the laboratory.

There were six treatments to assess the effect of low temperatures on long term survival of larvae, and each treatment consisted of three rearing periods which differed in temperature regime and length (Table 1). The first and the third rearing periods were set for thermal sufficient conditions and the second rearing period for thermal deficient conditions in terms of the necessary DET. The number of larvae and the larval instar examined are shown in Table 1. In the first rearing period of all treatments, larvae were exposed to the same conditions: larvae were reared under alternating temperatures of 13°C for 20 h and 0°C for 4 h (13°C (20 h)–0°C (4 h)) for 15 days. Larvae were then transferred to various thermal deficient conditions of 13°C (16 h)–0°C (8 h), 13°C (12 h)–0°C (12 h) or 9°C (24 h) per day, and maintained under these conditions for 30 (treatments I–III) or 45 days (treatments IV–VI). After this treatment, all larvae were transferred again to the previous thermal sufficient condition of 13°C (20 h)–0°C (4 h) for 45 (treatments I–III) or 30 days (treatments IV–VI). The total rearing period of all treatments was 90 days. Temperature was controlled by a thermo-regulator with a timer, and the photoperiod was 16L–8D for all treatments. Survival of larvae was examined every 5 or 10 days throughout the experimental period of 90 days.

Analyses of the AMeDAS data at the experimental overwintering site. Field experiments on the overwintering possibility of *S. litura* larvae were conducted in three winters (1985–1986, 1986–1987, 1987–1988) at Tateyama (34°59'N, 139°52'E) in the southern Boso Peninsula. AMeDAS data in Tateyama during these three winters were analyzed as follows. DETs from December 15th to March 15th during these winters were calculated by Eqs. (1) and (2). The necessary DETs were calculated by Eq. (3). Surplus or deficient DET was calculated by subtracting the necessary DET from the actual DET, and the respective values were accumulated from Dec. 15th to Mar. 15th. The cumulative deficient DETs were subtracted from the cumulative surplus DETs. This positive or negative value is the most important criterion for predicting the larval overwintering area. In addition, the longest period of consecutive days with deficient DETs and the lowest daily minimum temperature were recorded. These were also important criteria.

Prediction of the overwintering areas in Japan. The temperatures obtained from AMeDAS data at 41 stations located from the Tohoku to the Kyushu districts (shown in Fig. 1) in the winters of 1982–1985 were analyzed in order to predict possible overwintering areas in the field. Overwintering sites were predicted from the following three criteria on the basis of our previous studies (MATSUURA and NAITO, 1991; MATSUURA et al., 1991) and the present study (Table 1):

- 1) the lowest daily minimum temperature $\geq -5^{\circ}\text{C}$, which is the lethal low temperature of larvae (MATSUURA and NAITO, 1991),
- 2) cumulative surplus DET $\geq$ cumulative deficient DET from Dec. 15th to Mar. 15th, and
- 3) consecutive days with deficient DETs ≤ 30 days.

The larvae of *S. litura* can overwinter at sites where these three criteria are met. The first criterion was based on evidence that larvae froze to death by exposure to -5°C , which was an important lethal point (MATSUURA and NAITO, 1991). The reason for the 30 days in the third criterion is explained later.

RESULTS

Cumulative value of surplus and deficient DETs and larval survival period

Table 1 shows the longest survival periods of 2nd, 3rd and 4th stadia larvae in the six treatments. The cumulative value of surplus and deficient DETs in the first rearing period for all treatments was 12 DD, and in the 2nd rearing period they were all negative, ranging from -18 (treatment I) to -67.5 DD (treatment V). In our previous studies (MATSUURA et al., 1991), we described that *S. litura* larvae required a DET of more than 0.9 DD every day to ensure long term survival. Therefore, we assumed that necessary DETs in treatments III and VI for the 2nd rearing period were both 0.9 DD, although sub-zero temperatures were not included in these rearing periods. Actual DETs in these treatments were both zero DD, because the rearing temperatures were also below the developmental zero temperature. In consequence, the cumulative values of surplus and deficient DETs in the second rearing period of treatments III and VI were -27 and -40.5 DD, respectively. In the third rearing period, it was 36 DD for treatments I–III and 24 DD for treatments IV–VI. Total cumulative values of surplus and deficient DETs for these three rearing periods were positive in treatments I–IV and negative in treatments V–VI (Table 1).

Some larvae could survive for more than 90 days regardless of exposure to different degrees of deficient DET-treatments for 30 days in the 2nd rearing period (treatments I–III), when the deficient DET was compensated for by a surplus DET on other days. On the other hand, when the thermal deficient period was extended to 45 days, the survival period decreased to 70–80 days, even though the total cumulative value of surplus and deficient DETs was positive (treatment IV). These results indicated that if the longest period of consecutive days with deficient DET was less than 30 days and the cumulative value of surplus and deficient DETs in winter was positive, *S. litura* larvae could overwinter.

Temperature conditions at the experimental overwintering site

The lowest daily minimum temperature, cumulative value of surplus and deficient DETs and longest period of consecutive days with deficient DET for the three winters (1985–1986, 1986–1987, 1987–1988) at Tateyama are shown along with larval survival in Table 2. The cumulative value of surplus and deficient DETs were 3.4 and 22.7 DD, respectively, in the winters of 1986–1987 and 1987–1988 under which conditions the larvae could overwinter, and -67.8 DD in the unsuccessful winter of 1985–1986. This result indicated that the success or failure in overwintering was related to whether the cumulative value of surplus and deficient DET was positive or negative. The longest period of consecutive days with deficient DET in all three winters was less than 30 days. Thus, having the longest period of consecutive days with deficient DET remain under 30 days was not always a major condition for success of larval overwintering. The lowest daily minimum temperatures in the two successful winters of 1986–1987 (-4.4°C) and 1987–1988 (-3.5°C) were higher than the lethal low temperature of -5°C , and that in the unsuccessful winter of 1985–1986 (-5.1°C) was close to the lethal low temperature.

Table 1. Summary of six experimental treatments and the longest survival period of *S. litura* larvae under these treatments

Treatment No.	Stadium of larvae tested	No. of larvae tested	Rearing conditions ^a			Total DET (degree-days)	Longest survival period (days)
			1st period	2nd period	3rd period		
I	2	50					more than 90
	3	50					more than 90
	4	50				+30	80–85
II	2	50					more than 90
	3	50					85–90
	4	50				+3	more than 90
III	2	50					more than 90
	3	50					more than 90
	4	50				+21	more than 90
IV	3	50				+9	70–80
	4	50					70–80
V	3	50					70–80
	4	50					60–70
VI	3	50					50–60
	4	50				–4.5	70–80

^a The rearing temperature was periodically alternated between 13°C and 0°C for the hours given in parentheses. Surplus or deficient DETs were calculated by Eqs. (1) and (3).

Table 2. Larval overwintering and temperature conditions during three winters at Tateyama

Winter year	Survival rate ^a (%)	Cumulative value of surplus and deficient DETs ^b (degree-days)	Longest period of consecutive days with deficient DET ^b	Lowest daily minimum temperature (°C)
1985–1986	0	−67.8	29	−5.1
1986–1987	2.53	3.4	9	−4.4
1987–1988	17.89	22.7	16	−3.5

^a Results of the overwintering experiments conducted by MATSUURA et al. (1992).

^b Calculated from AMeDAS data from December 15th to March 15th.

Prediction of the overwintering areas in Japan

Table 3 shows the lowest daily minimum temperatures and cumulative values of surplus and deficient DET at 41 AMeDAS stations selected from the Tohoku to the Kyushu districts during the three winters (1982–1983, 1983–1984, 1984–1985). Asterisks indicate stations where the lowest daily minimum temperature was lower than -5°C and the cumulative values were negative throughout the winter. Triangles indicate stations where the lowest daily minimum temperature was occasionally higher than -5°C , whereas the cumulative value was negative. In the non-marked stations, the lowest daily minimum temperature was higher than -5°C all winter.

Kaminaka ($30^{\circ}24'\text{N}$, $130^{\circ}54'\text{E}$) and Naze ($28^{\circ}23'\text{N}$, $129^{\circ}30'\text{E}$), marked with a double circle, had positive cumulative values and had lowest daily minimum temperature of higher than -5°C . Ashizurimisaki ($32^{\circ}43'\text{N}$, $133^{\circ}01'\text{E}$), Aoshima ($31^{\circ}48'\text{N}$, $131^{\circ}28'\text{E}$), Uchinoura ($31^{\circ}16'\text{N}$, $131^{\circ}05'\text{E}$), Kagoshima ($31^{\circ}34'\text{N}$, $130^{\circ}33'\text{E}$), Makurazaki ($31^{\circ}16'\text{N}$, $130^{\circ}18'\text{E}$) and Shionomisaki ($33^{\circ}27'\text{N}$, $135^{\circ}46'\text{E}$), marked with a circle, occasionally had positive cumulative values. At those stations, the lowest daily minimum temperatures were all higher than -5°C . Thus, the criterion of the lowest daily minimum temperature was satisfied in the stations marked with a circle or double circle and the non-marked stations. The criterion for the cumulative value of surplus and deficient DET was satisfied only at stations marked with a double circle: Kaminaka and Naze. However, in warm winters this criterion was satisfied at the stations marked with a circle.

Table 4 shows the longest period of consecutive days with deficient DETs at stations marked with a circle and double circle in Table 3. Stations which had positive cumulative values (indicated with + in Table 3) also had a period of consecutive deficient DET days of less than 30 days. However, the reverse was not true; for instance Kagoshima and Uchinoura in the winter of 1983–1984. The criterion of consecutive days with deficient DET was satisfied at all stations marked with a circle and double circle. The three criteria were always satisfied only in the stations marked with a double circle.

The possible overwintering areas of *S. litura* were predicted as shown in Fig. 1 on the basis of the three criteria (analyses of AMeDAS data) and the results of our previous overwintering experiments. It was inferred that line B was the northern boundary of the annually possible overwintering areas and line A was that of the possible overwintering areas in warm winters only.

Table 3. Lowest daily minimum temperatures and cumulative values of surplus and deficient DETs calculated from AMcDAS data from December 15th to March 15th at 41 stations in Japan

Station No. ^a	Station name	1982–1983		1983–1984		1984–1985	
		Lowest daily minimum temperature	Cumulative value of surplus and deficient DETs	Lowest daily minimum temperature	Cumulative value of surplus and deficient DETs	Lowest daily minimum temperature	Cumulative value of surplus and deficient DETs
1 *	Aomori	−11.1	−226.0	−10.8	−266.0	−10.2	−254.6
2 *	Hachinohe	−11.1	−233.7	−12.7	−271.9	−11.9	−258.7
3 *	Akita	−7.6	−190.4	−8.8	−267.0	−7.8	−240.3
4 *	Morioka	−11.6	−234.4	−14.2	−274.9	−13.4	−240.8
5 *	Kamaishi	−9.5	−219.5	−10.8	−270.0	−10.9	−239.1
6 *	Komayu	−13.2	−249.2	−12.5	−276.0	−10.9	−270.7
7 *	Ishinomaki	−8.4	−197.2	−9.3	−270.9	−9.4	−229.5
8 *	Fukushima	−7.0	−174.1	−8.6	−256.9	−8.4	−191.7
9 *	Onahama	−5.9	−123.7	−7.1	−213.6	−7.8	−136.2
10 *	Nikko	−12.4	−266.6	−18.3	−276.0	−15.4	−272.7
11 *	Nagano	−10.0	−226.2	−10.7	−273.1	−9.9	−242.6
12 *	Takayama	−11.1	−239.4	−16.4	−275.0	−14.9	−247.1
13 *	Chichibu	−8.4	−195.4	−11.5	−269.4	−9.3	−202.6
14 △	Kanazawa	−3.2	−66.8	−6.7	−131.3	−6.0	−83.4
15 *	Tsuchiura	−6.7	−84.0	−7.3	−167.5	−7.3	−105.5
16	Choshi	−3.0	−26.9	−4.1	−68.0	−3.8	−41.5
17 *	Tateyama	−5.8	−22.7	−6.4	−104.9	−6.3	−43.5
18	Miura	−2.2	−17.8	−3.6	−60.9	−2.8	−33.3
19	Oshima	−0.6	−19.8	−2.8	−48.7	−1.5	−29.5
20 △	Shizuoka	−4.7	−17.8	−4.7	−72.0	−5.1	−31.5
21	Omaezaki	−2.4	−19.1	−3.7	−70.7	−2.7	−30.5
22	Irako	−0.9	−27.5	−3.4	−61.0	−2.8	−39.9
23	Yokkaichi	−3.9	−46.2	−4.7	−116.4	−4.3	−69.1
24	Owase	−3.7	−20.0	−3.6	−80.4	−3.7	−36.9
25 ○	Shionomisaki	0	+12.8	−2.2	−36.3	−1.4	−1.7
26	Wakayama	−2.8	−24.3	−3.0	−62.3	−1.8	−33.8
27	Murotomisaki	−1.5	−10.5	−3.0	−53.2	−2.2	−23.5
28 △	Kouchi	−3.2	−27.8	−6.0	−101.9	−4.8	−41.1
29 ○	Ashizurimisaki	+0.3	+32.7	−2.8	−25.7	−2.2	+13.2
30 △	Matsuyama	−3.1	−33.2	−5.2	−73.6	−2.3	−41.8
31 △	Okayama	−4.7	−54.6	−5.0	−118.5	−4.3	−69.2
32 △	Yanai	−4.9	−72.5	−6.5	−141.7	−6.6	−90.1
33	Nagasaki	−2.2	−6.7	−2.1	−40.8	−1.3	−17.7
34	Saga	−3.9	−31.5	−4.3	−87.6	−4.0	−46.6
35 *	Nobeoka	−5.0	−16.2	−5.5	−88.5	−6.2	−34.0
36 ○	Aoshima	−3.2	+18.6	−2.4	−32.3	−4.3	+8.1
37 ○	Uchinoura	−1.3	+60.3	−3.3	−5.5	−2.8	+35.9
38 ○	Kagoshima	−3.7	+30.9	−2.8	−20.4	−2.1	+24.4
39 ○	Makurazaki	−2.3	+41.2	−1.8	−6.4	−0.8	+43.5
40 ◎	Kaminaka	1.5	+75.6	0.4	+12.4	0	+69.1
41 ◎	Naze	7.1	+279.3	6.8	+189.0	6.6	+292.0

^a◎: Possible to overwinter every year. ○: Possible to overwinter only in warm winters.

△: Non-overwintering places due to freezing or deficient DET.

*: Non-overwintering places due to freezing.

Table 4. The longest period of consecutive days with deficient DET calculated from AMeDAS data from December 15th to March 15th

Station No.	Station name	Longest period of consecutive days with deficient DET ^a (days)		
		1982–1983	1983–1984	1984–1985
25	Shionomisaki	12 (+)	36 (–)	34 (–)
29	Ashizurimisaki	7 (+)	35 (–)	15 (+)
36	Aoshima	7 (+)	36 (–)	14 (+)
37	Uchinoura	6 (+)	16 (–)	12 (+)
38	Kagoshima	8 (+)	27 (–)	14 (+)
39	Makurazaki	7 (+)	31 (–)	14 (+)
40	Kaminaka	7 (+)	14 (+)	13 (+)
41	Naze	1 (+)	2 (+)	0 (+)

^a Plus or minus in parentheses indicates surplus or deficiency in cumulative DET necessary for larval overwintering from Dec. 15th to Mar. 15th (see Table 3).

DISCUSSION

From our previous studies thus far (MATSUURA and NAITO, 1991; MATSUURA et al., 1991), lowest daily minimum temperature and daily effective temperature for development (DET) in winter were inferred as the critical factors for larval overwintering of *S. litura* in the field. Larvae required a daily DET of more than 0.9 degree-days (DD) for long term survival (MATSUURA et al., 1991). However, in the present larval rearing experiment under conditions of various alternating temperatures, this DET was not necessary daily if the deficient DET could be compensated for by a surplus DET on other days. Consequently, the DET criterion necessary for larval overwintering is modified as follows: cumulative surplus DET $\geq$ cumulative deficient DET in winter. These experimental results suggest that *S. litura* larvae may be able to overwinter even in places where cold days of less than 0.9 DD occasionally exist in winter, if warm days of more than 0.9 DD exist frequently.

The criteria which allow the larvae to overwinter in the field were a lowest daily minimum temperature $\geq -5^{\circ}\text{C}$, cumulative surplus DET $\geq$ cumulative deficient DET in winter and consecutive days with deficient DET ≤ 30 days. It was necessary for these three criteria to be satisfied. In the overwintering experiments conducted in the southern Boso Peninsula during three winters from 1985 to 1988, larvae could survive in the two warm winters of 1986–1987 and 1987–1988, but failed to survive in the winter of 1986–1987 (MATSUURA et al., 1992). When those three criteria were applied to the results of overwintering experiments using the AMeDAS temperature data in Tateyama, it was recognized that all three criteria were satisfied in the successful overwintering years, but the first and second criteria were not satisfied in the unsuccessful year. There is no inconsistency in our hypothesis that *S. litura* larvae are able to overwinter only in cases where the three above-mentioned criteria are all satisfied.

In the analysis of AMeDAS temperature data from 1982 to 1985 using the three criteria at 41 stations which were randomly sampled, Tateyama was predicted to be a non-overwintering site as well as in the analysis of AMeDAS data of 1985–1986 (Table 3). Consequently, Tateyama is considered to be located on the overwintering boundary area

Fig. 1. Overwintering areas of *S. litura* in Japan predicted on the basis of three criteria by analyses of AMeDAS data (see Tables 3 and 4) and the results of overwintering experiments (see Table 2). Larvae possibly overwinter only in warm winters in the area between lines A and B, and possibly every year on the south side of line B. For the number of localities see Tables 3 and 4.

where *S. litura* larvae cannot usually overwinter but can possibly overwinter in warm winters. The border line of the northern limit of the larval overwintering is shown in Fig. 1 as line A, which was drawn based on the three criteria by analyzing AMeDAS temperature data and the results of overwintering experiments. This line corresponds roughly with the line reported by MIYAI (AFFRC, 1989). The adult moth of *S. litura* are trapped at the earliest

time in spring in places on the south side of his line. It appears that MIYAI's line may suggest the possibly overwintering places of this insect in Japan, as well. Furthermore, an interesting fact is that line A also nearly coincides with the so-called "Honshu Nangansen", running along the coast of the Pacific from Chiba to Wakayama Prefecture (WATANABE, 1952). Honshu Nangansen is well known as the northern border line of the distribution of the southern animals and plants. In the southern coastal areas around Honshu Nangansen, many kinds of food plants of *S. litura* (MIYAHARA, 1977) grow even in winter, for instance, white clover, which is one of the suitable food plants grown sporadically throughout winter in these warmer areas. On the contrary, in northern areas far from this line such as Tsukuba, Ibaraki Prefecture, leaves of this plant are almost withered in winter. The larvae cannot obtain food in these areas and, thus, fail to overwinter. According to HORIKIRI (1964), at station No. 38 in Kagoshima, larvae artificially survived the winters of 1959–1960 and 1960–1961 in Petri dishes under natural conditions. However, we have not found any information on overwintering natural populations of *S. litura* in the field of the overwintering boundary area thus far. A possible reason for this inconsistency may be that the places where the larvae can actually overwinter are restricted to small limited spots by other factors besides air temperature as used in our model such as the presence of food plants, solar radiation or wind velocity (MATSUURA et al., 1991; MATSUURA and NAITO, 1992; KATO, 1939). In consequence, the population density of the overwintering larvae must be very low in the overwintering areas, so that finding them in the field is usually very difficult. We have already demonstrated that *S. litura* larvae needed to maintain a body temperature of more than 10°C to take food (MATSUURA and NAITO, 1992). It is difficult for the larvae to maintain a body temperature of more than 10°C in winter if they cannot directly receive solar radiation in an open field even though air temperatures are higher than 10°C, because wind depletes the latent heat from the larval body. We observed that *S. litura* larvae crawled out from the soil surface under fallen leaves where they stayed at night, and fed on grass receiving solar radiation during the day time in winter (MATSUURA and NAITO, 1992). Further studies on the effects of solar radiation and wind velocity on larval survival in winter are necessary for predicting overwintering places more precisely. We would like to try to incorporate these factors into our prediction model.

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