INTRODUCTION

The fall webworm, *Hyphantria cunea* (Drury) (Lepidoptera: Arctiidae), was originally distributed in North America (Warren and Tadic, 1970) and spread into central Europe and eastern Asia in the 1940s (Warren and Tadic, 1970; Umeya and Itô, 1977). In Japan, this species was first found in Tokyo (35°40′N, 139°46′E) in 1945 (Umeya and Itô, 1977). Since then, this moth has expanded into a range from 32 to 42°N in Japan (Gomi, 1996a, 1997, 2000). Life-history traits are different between the bivoltine and trivoltine populations (Gomi and Takeda, 1996; Gomi, 1997). The critical photoperiod for diapause induction is shorter in the trivoltine population than in the bivoltine population (Gomi and Takeda, 1991, 1996). Temperature dependence of the photoperiodic response is greater in the trivoltine population than in the bivoltine population (Gomi, 1997). The duration of the larval stage is shorter in the trivoltine population than in the bivoltine population (Gomi, 1996b; Gomi and Takeda, 1996).

At present, the life cycle has shifted to a trivoltine one in the southwestern districts of Japan, but has remained bivoltine in the northern districts (Gomi and Takeda, 1990, 1991, 1996). The trivoltine area borders the bivoltine area at around 36°N (Gomi, 1996a, 1997, 2000). Life-history traits are different between the bivoltine and trivoltine populations (Gomi and Takeda, 1996; Gomi, 1997). The critical photoperiod for diapause induction is shorter in the trivoltine population than in the bivoltine population (Gomi and Takeda, 1991, 1996). Temperature dependence of the photoperiodic response is greater in the trivoltine population than in the bivoltine population (Gomi, 1997). The duration of the larval stage is shorter in the trivoltine population than in the bivoltine population (Gomi, 1996b; Gomi and Takeda, 1996).

Two types of *H. cunea* larvae, the six-instar and seven-instar, were reported in Canada (Morris and Fulton, 1970). In Japan, the seven-instar type was predominant during the early stage of invasion (Itô and Miyashita, 1968). Recently, the proportion of
the two instar-types has begun to differ in local populations (Gomi, 1996b; Gomi et al., 2003).

The effects of host plants on the life-history traits, including the larval instar numbers, have been proved for some insects (Gara and Wood, 1989; Ikeda-Kikue and Numata, 1992; Hunter and McNeil, 1997; Casimero et al., 2000). In H. cunea, the life-history traits were investigated using only host plants in the bivoltine population during the early stage of invasion (Itô et al., 1968; Masaki et al., 1968) and with an artificial diet only in the present bivoltine and trivoltine populations (Gomi and Takeda, 1996; Gomi, 1997; Gomi et al., 2003). It is indispensable for the management of the present population of H. cunea to clarify the life-history traits on the host plants. Therefore, in the present study, the effects of diet on the life-history traits were compared between insects reared on an artificial diet and those reared on host plants in a trivoltine population of H. cunea.

MATERIALS AND METHODS

Mid-instar larvae of Hyphantria cunea were collected on Prunus sp., Juglans sp. and Liquidambar styraciflua L. in late September 2000 and 2002 and in mid-June 2001 at the same site in Kobe (34°41’ N, 135°11’ E), Honshu Island, Japan. The larvae were reared on an artificial diet, “Insecta LFS” (Nihon-Nosan-Kogyo, Yokohama), in transparent plastic cups (500 ml) at 25 ± 0.5°C and 16L-8D (16 h-light, 8 h-dark). In 2001, pupae were kept under the same conditions during the larval stage until adult emergence. In 2000 and 2002, almost 100% of the pupae entered diapause and were maintained at 5°C. In the next spring, the pupae were gradually exposed to higher temperatures from 5 to 25°C, and were kept at 25°C until adult emergence.

The adults that emerged within 24 h were paired in the plastic cups for oviposition at 25 ± 0.5°C and 16L-8D. Egg batches were maintained with moist paper towels under the same conditions until hatching. To investigate the developmental traits, larvae hatching in late May 2001 were transferred to the leaves of host plants, either Morus bombycis Koidz. or Populus nigra L., in the cups (500 ml) and were incubated at 18, 20, 22, 23, 25 and 27 ± 0.5°C, 16L-8D. Under these conditions, all individuals averted diapause in the pupal stage. Kobara (1969) categorized M. bombycis as one of the four suitable host species for H. cunea among 12 host plants examined, and P. nigra as a group of host plants that is less suitable than the four species. Therefore, the host plants with different suitability were used in the present study. A few leaves of the host plants cut at the leafstalk were bound in cotton and put in a glass vial (2 ml) filled with water. The leaves were replenished every 1–6 d depending on the larval age and temperature conditions. Days of pupation and adult emergence were recorded. The lower threshold temperature for development and the thermal constant were calculated from the developmental rates at the six temperatures in the larval and pupal stages.

To investigate the seasonal effects of the host plants on the developmental traits, the diets of the larvae hatching in late May and late July 2002 were compared. In the field, larvae of H. cunea aggregate and construct a nest web until the fourth larval instar, and thereafter disperse and live individually. In the present experiment, on the day of molting to the fifth larval instar, the larvae were individually confined to a small plastic cup (200 ml) with a leaf of host plants and kept at 20 ± 0.5°C and 16L-8D. Seventy-five larvae were used in each treatment. Days of molting, pupation and adult emergence were recorded, and the pupae were weighed at 5 d after pupation.

To investigate the effects of diet on the photoperiodic responses controlling diapause induction, larvae hatching in late July and early October 2002 and in late May 2003 were transferred to the artificial diet or a leaf of one of the host plants, and incubated under photoperiodic conditions of 14L-10D, 14.25L-9.75D, 14.5L-9.5D and 14.75L-9.25D at 20 ± 0.5°C and 13.25L-10.75D, 13.5L-10.5D, 13.75L-10.25D, 14L-10D and 14.25L-9.75D at 25 ± 0.5°C. The artificial diet was replenished every 2–5 d depending on the larval age and temperature conditions. Pupae that emerged as adults within 50 and 40 d at 20 and 25°C, respectively, were regarded as non-diapause individuals, and the remaining survivors as diapause pupae (Gomi, 1995). Critical photoperiods were calculated as a photoperiod inducing diapause in 50% of the individuals.

The statistical analyses used in the present study were mentioned in Zar (1999). The incidence of diapause was statistically analyzed at the photoperiod nearest the critical photoperiod at each tempera-
ture, 14.25L-9.75D for 20°C and 13.75L-10.25D for 25°C.

RESULTS

Effects of diet on developmental rate

Developmental periods on the host plants were compared with each other and those on Insecta LFS taken from Gomi et al. (2003) (Table 1). The development time decreased as the temperature increased in the larval and pupal stages with all diets. The developmental rate correlated significantly with the temperatures in these stages with all diets ($r > 0.98$, $p < 0.001$) (Table 2). The development time of the egg stage and the preoviposition period for those fed the artificial diet were used for the calculation of days required for one generation with all diets. The lower threshold temperatures for one generation varied within 0.5°C among the diets. The thermal constant for one generation was about 26 degree-days less with Insecta LFS than with *P. nigra*, and intermediate with *M. bombycis*. These differences in thermal constant were primarily due to differences in the larval stage. On the whole, the lower threshold temperature for development and the thermal constant were not largely different among the diets.

Seasonal effects of host plants on developmental traits

The developmental periods at 20°C and 16L-8D were compared among larvae hatching in May and July 2002 (Table 3). With all diets and hatching times, the larval period was significantly longer for females than for males, and the pupal period was longer for males than for females (Mann-Whitney U-test, $p < 0.05$). The developmental periods were significantly longer for larvae hatching in July and reared on *P. nigra* than for the others of both sexes (Kruskal-Wallis test with nonparametric multiple comparison, $p < 0.05$). Of males, larvae reared on *M. bombycis* showed significantly shorter developmental periods than those fed on the other diets at both hatching times ($p < 0.05$). In the pupal stage, no clear effect was observed for the developmental periods among the diets and between the hatching times.

The proportion of the seven-instar type was significantly higher in females than in males irrespective of the host plants and hatching times (Fisher’s
exact test, \(p<0.05\), except for larvae reared on Insecta LFS (Table 4). The incidence of the seven-instar type was significantly lower for those fed the artificial diet as compared to those fed on the host plants (Tukey-type multiple comparison for proportions, \(p<0.05\), except for male larvae hatching...
in May and reared on *M. bombycis*. When the incidence of the seven-instar type was compared between the two hatching times, seasonal effects of host plants were revealed only for females reared on *P. nigra* \( (p/<0.05) \). Similar seasonal effects were observed for males reared on *P. nigra*, although the difference in the incidence of the seven-instar type was not significant \( (p/0.05) \).

The live pupal weight was significantly greater for females than for males in the six-instar type, irrespective of the diets and hatching times \( (t\text{-test}, p/0.05) \) (Table 5). The female pupae of the seven-instar type were heavier than those of the six-instar type reared on the host plants \( (p/0.05) \). Seasonal effects of pupal weight, significantly different between May and July, were observed for males of the six-instar type and for females of the seven-instar type in *M. bombycis* (ANOVA with Fisher’s PLSD, \( p/0.05) \). In both cases, larvae hatching in May developed into heavier pupae than those hatching in July.

**Effects of diet on diapause induction**

Larvae hatching at different times were reared on different diets under various photoperiod and temperature conditions to investigate the effects of diet on diapause induction (Fig. 1). The critical photoperiods calculated from the photoperiodic responses are shown in Table 6. The seasonal difference of the critical photoperiod in *P. nigra* was 3 min between the two hatching times, July 2002 and May 2003. However, the incidence of diapause under 14.25L-9.75D at 20°C differed significantly between these hatching times (Tukey-type multiple comparison for proportions, \( p/0.05) \). Under this photoperiodic condition, the incidence of diapause on *M. bombycis* was within that reported for those on *P. nigra* and was not significantly different between the host plants \( (p/0.05) \). The differences of the critical photoperiods between the host plants were consequently within 2 min. The incidence of diapause was significantly lower with Insecta LFS than with the host plants at 20°C, 14.25L-9.75D.
DISCUSSION

The present results showed that the effects of diets on the life-history traits of *Hyphantria cunea* were conspicuous for some traits but obscure for others. The thermal constants required for one generation and the lower threshold temperature for development were not largely influenced by the diets. Therefore, the developmental traits obtained from individuals that were reared on Insecta LFS can be directly applicable to a field population. Itô et al. (1968) reported that the thermal constant for one generation was 750–800 degree-days on *Platanus acerifolia* and *Cornus controversa*. This range of thermal constants was higher than that obtained in the present study on *M. bombycis* and *P. nigra*, less than 700 degree-days, although the host plants used differed between the studies. The present results with the host plants confirmed our previous results with Insecta LFS; that is, the developmental period, especially in the larval stage, was shortened with the shift from a bivoltine to a trivoltine life cycle (Gomi, 1996b; Gomi and Takeda, 1996).

In many plants, the concentration of chemicals and the water content in the leaves changed seasonally and affected the development of insects (Slansky, 1993; Speight et al., 1999). The present results showed seasonal effects of host plants on some developmental traits in *H. cunea*. The developmental periods of both sexes on *P. nigra* were longer for larvae hatching in July than in May. The incidence of the seven-instar type was higher for larvae hatching in July than in May, although the difference was not significant for males. The larval period of *H. cunea* is significantly longer for the seven-instar type than for the six-instar type (Gomi et al., 2003). Therefore, on *P. nigra*, the longer developmental period for larvae hatching in July would be caused by the increase in the seven-instar type. A similar tendency was observed for *Helicoverpa armigera* (Casimero et al., 2000), in which the number of larval instars increased with diets that resulted in the larval periods being extended.

Pupae reared on the host plants were heavier for larvae hatching in May than in July, although significant differences were only detected for the males of the six-instar type and females of the seven-instar type reared on *M. bombycis*. In deciduous oak trees, the water content, protein content and concentration of condensed tannin decrease from May to July (Hunter and Schultz, 1995; Speight et al., 1999). Similar seasonal changes in the constituent factors would occur in the leaves of *M. bombycis* and *P. nigra*, which may lead to prolonging the larval period and reducing the pupal weight of *H. cunea* hatching in July. The present results, however, did not completely exclude the possibility that the difference observed between hatching times was caused by differences in the generations of *H. cunea*.

In a tortricid moth, *Choristoneura rosaceana*, the induction of larval diapause is influenced by the host plant species (Hunter and McNeil, 1997). In *H. cunea*, however, the photoperiodic response curves were similar and the differences of the critical photoperiod were small between host plants.
and between the two hatching times with *P. nigra*. The critical photoperiod with Insecta LFS was shorter than that with the host plants. Therefore, the critical photoperiods obtained in the laboratory with Insecta LFS need to be slightly lengthened when applied to field insects. The food quality modified the photoperiodic response for diapause induction and a low-quality diet favored diapause induction and a low-quality diet favored diapause induction in general (Danks, 1987). As for the present results, diapause induction was significantly lower with Insecta LFS than with the host plants. Therefore, the critical photoperiod with Insecta LFS was shorter than that with the host plants.

Therefore, the critical photoperiod with Insecta LFS was significantly lower with Insecta LFS than with the host plants for both sexes, without a marked extension of the larval period. These results suggest that the quality of the artificial diet may be higher for *H. cunea* than that of the host plants.

The Kobe population of *H. cunea* collected in 1989 showed a mean larval period of 38.6 d at 20°C (*N*= 106) when they were reared on Insecta LFS (Gomi and Takeda, 1996). In the present results, the mean larval period with Insecta LFS at 20°C was 38.9 d and was not significantly different from our previous result (Mann-Whitney *U*-test, *p*> 0.7). These results indicate that the larval period in the Kobe population has not changed considerably from 1989 to 2001. In the Kobe population collected in 1987, the critical photoperiod at 20°C was 14 h 23 min with Insecta LFS (Gomi and Takeda, 1990). However, the critical photoperiod of the present results with Insecta LFS was 14 h 10 min. The incidence of diapause at 14.25L:9.75D in our previous study was 78.6% (*N*= 98), and was significantly higher than the present result of 27.4% (Fisher’s exact test, *p* < 0.0001). These results indicate that the critical photoperiod for the Kobe population of *H. cunea* at 20°C has shortened slightly from 1987 to 2001.

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**REFERENCES**


