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Comparisons of cocoon density and survival processes of the blue-striped nettle grub moth *Parasa lepida* (Cramer) between deciduous and evergreen trees

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Abstract

We studied population dynamics of the blue-striped nettle grub moth *Parasa lepida* (Cramer), in terms of cocoon density over four years from 2004 to 2007 at the campus of The University of Shiga Prefecture, Hikone, western Japan on a wide range of host trees including both deciduous trees (36 spp. of 282 individual trees) and evergreen trees (15 spp. of 122 individual trees). Detailed survival processes were examined by tracking developmental stages both on the deciduous Chinese tallow tree *Triadica sebifera* (L.) Small (Euphorbiaceae) and an evergreen oak *Quercus myrsinaefolia* Blume (Fagaceae) to identify factors responsible for the population dynamics and the host utilization patterns. The density of cocoons was significantly higher in deciduous hosts than in evergreen hosts in the first generation, but this tendency disappeared in the second generation. Life table analyses revealed there was a higher cocoon density in deciduous *T. sebifera* than in evergreen *Q. myrsinaefolia* in the first generation but detected the opposite tendency in the second generation. These generation specific trends were attributable to the greater egg density and the higher survival rate during the larval stage in the first generation, and to density-dependent occurrence of larval death due to nuclear polyhedrosis virus (NPV) in the second generation on *T. sebifera*.

Key words : *Parasa lepida* (Cramer), Population dynamics, Life table, Host plant, Deciduous tree, Evergreen tree

Introduction

The blue-striped nettle grub moth *Parasa lepida* (Cramer) (Lepidoptera: Limacodidae) is an invasive pest originally distributed widely in the tropics and subtropics, such as southern China, south-east Asia, India, and central-south Africa (Hirashima, 1989; Zhang, 1994). Invasion of *P. lepida* was first recorded in Kagoshima in 1921 but it was rare until the 1960s (Miyata 1981). Ever since the end of the 1970s outbreaks have occurred frequently in western Japan (Miyata, 1981) together with rapid northward expansion of the distribution range, now reaching to northern Kanto (Nakano, 2003). During the 1980s *P. lepida* established a pest status, seriously defoliating cherry trees, persimmons and various trees on the streets and city gardens in urban areas (Oda and

Hattori, 1981). Moreover, larvae of *P. lepida*, being armoured with sharp spines, are annoying.

P. lepida is highly polyphagous. For instance Robinson *et al.* (2001) listed 78 species belonging to 35 families, such as Leguminosae, Arecaceae, and Euphorbiaceae, as the host plants in India and Southeast Asia. Moreover, *P. lepida* is a notorious pest of fruit trees, damaging coconuts, coffee, mango and cacao in Indonesia (Kalshoven, 1981) and mango particularly in India (Kapoor *et al.*, 1985; Jeyabalan and Murugan, 1996). Extreme polyphagy was also documented in Japan. Yamazaki *et al.* (1994) revealed the presence of cocoons on 194 trees of 85 species belonging to 34 families among a total of 463 trees of 166 species belonging to 48 families growing in the Botanical Garden of Kyoto University, Kyoto, western Japan. By tracking cocoon density of *P. lepida* for 51

tree species over three years in Hikone, western Japan, Nishida *et al.* (2006) reported the host utilization as follows: 1) The cocoon was observed on 26 tree species (66.7 %) among 39 common tree species, 2) The cocoon density was relatively high in the Japanese red maple *Acer pycnanthum*, the Japanese maple *A. palmatum* var. *matsumurae* (Aceraceae), an evergreen oak *Quercus myrsinaefolia* (Fagaceae), and the Chinese tallow tree *Triadica sebifera* (Euphorbiaceae), 3) Plant phylogeny may play a minor role in determining the cocoon density, and 4) In the first generation the cocoon density was higher among deciduous species than among evergreen species.

In this study we report the host utilization of *P. lepida* by comparing the cocoon density between deciduous and evergreen hosts, together with detailed survival processes of all the developmental stages on deciduous *T. sebifera* and evergreen *Q. myrsinaefolia*. By examining these data we discuss factors affecting host-related differences in the cocoon density of *P. lepida*.

Materials and Methods

The study area

We performed field censuses at the campus of The University of Shiga Prefecture (USP) (N35° 17', E 136° 15'), located in the southern suburbs of Hikone city, western Japan. The campus of USP was constructed in 1995, with 70 species of trees planted in the 30 ha area. The campus was similar to a large scale city park, with a large number of *P. lepida* cocoons observed on the tree trunks.

Census of cocoon density

We chose a total of 51 tree species comprising 404 individual trees (36 species of 282 deciduous trees and 15 species of 122 evergreen trees) among approximately 70 tree species planted in the campus. The deciduous trees included *T. sebifera*, Yoshino cherry *Prunus X yedoensis*, and Japanese zelkova *Zelkova serrata* and the evergreen trees included *Q. myrsinaefolia*, *Q. glauca*, and Camphor laurel *Cinnamomum camphora*. The census started from the first generation in 2004 and ended at the second generation in 2007, over 8 generations during the four years. In principle we conducted the censuses on 10 trees for each tree species except when the maximum number of tree species was less than 10. The censuses were performed once a week during the periods from

the start to the end of cocoon spinning, from late July to early September in the first generation and from middle September to early November in the second generation. On the grounds that *P. lepida* pupates exclusively in the lower parts of tree trunks, we counted the number of cocoons on tree trunks less than 2.5 m in height for each census tree. Cocoons being formed on substratum annexed to a census tree were included in the data of the census tree. To avoid double counting, each cocoon was marked with a felt pen after being counted.

Life table

Life tables of *P. lepida* were constructed for both *T. sebifera* (deciduous tree) and *Q. myrsinaefolia* (evergreen tree) by pooling data of each tree species over 6 generations from the first generation in 2005 to the second generation in 2007. Both host species were selected because of the relatively high cocoon densities and the abundance of trees that can ensure large sample sizes.

The numbers of census trees were 10 in 2005 and 13 in 2006 and 2007 for each tree species. The height and diameter of the census trees were similar for *T. sebifera* and *Q. myrsinaefolia* with a tree height of 3.6-6.2 m and 3.0-5.6m, respectively, and a tree diameter of 9-20 cm and 8-17 cm at 20 cm above the ground, respectively. The census periods covered whole developmental stages from the beginning of the adult emergence to the last formation of the cocoon, from middle May to early September in the first generation and from early August to early November in the second generation. During the census periods all the leaves of the census trees were checked for the number of eggs and egg batches every other day. Each egg batch was individually marked by attaching a label nearby and thereafter mortality factors, such as hatching failure, predation, parasitoids and so on, were checked. If a group of newly hatched larvae was found, nearby leaves were examined intensively for the presence of the egg batch from which the larvae derived to count the egg batch size, the number of hatched larvae, and the number of parasitized eggs. Young instars are very conspicuous because they are gregarious with very noticeable feeding scars on leaves. The cocoons were checked using the same methods described in the previous section.

Comparison of life table data between the two host plants

Survival processes were compared between *T.*

sebifera and *Q. myrsinaefolia* for each generation and year. The cocoon density of a given generation or year was determined as follows.

$$C = E \times L/E \times C/L = E \times S(E) \times S(L) \quad (1)$$

Here, C, E, and L denote the density of cocoons, eggs, and hatched larvae, respectively, whereas S(E) and S(L) denote the survival rate during the egg and larval stages, respectively. Consequently, the relative cocoon density on *T. sebifera* to that on *Q. myrsinaefolia* was given as

$$C_a/C_b = E_a/E_b \times S(E)_a/S(E)_b \times S(L)_a/S(L)_b \quad (2)$$

Here, a and b, respectively, indicate *T. sebifera* and *Q. myrsinaefolia*. Then Equation (2) can be expressed by taking the common logarithm.

$$\log C_a - \log C_b = (\log E_a - \log E_b) + (\log S(E)_a - \log S(E)_b) + (\log S(L)_a - \log S(L)_b) \quad (3)$$

Equation (3) means that in terms of the common logarithm, the difference in the cocoon density between the two host plants is expressed as the sum of between-plant differences in the following three life stage components; egg density (E), egg survival (S(E)), and larval survival (S(L)). Then we tried to detect the key stage that accounted most for the host-related differences in cocoon density by comparing C, E, S(E), and S(L) plotted on a common logarithm basis.

Results and Discussion

Cocoon density on the deciduous and evergreen trees

Fig. 1 shows the cocoon density on the deciduous and evergreen hosts for 8 generations over four years.

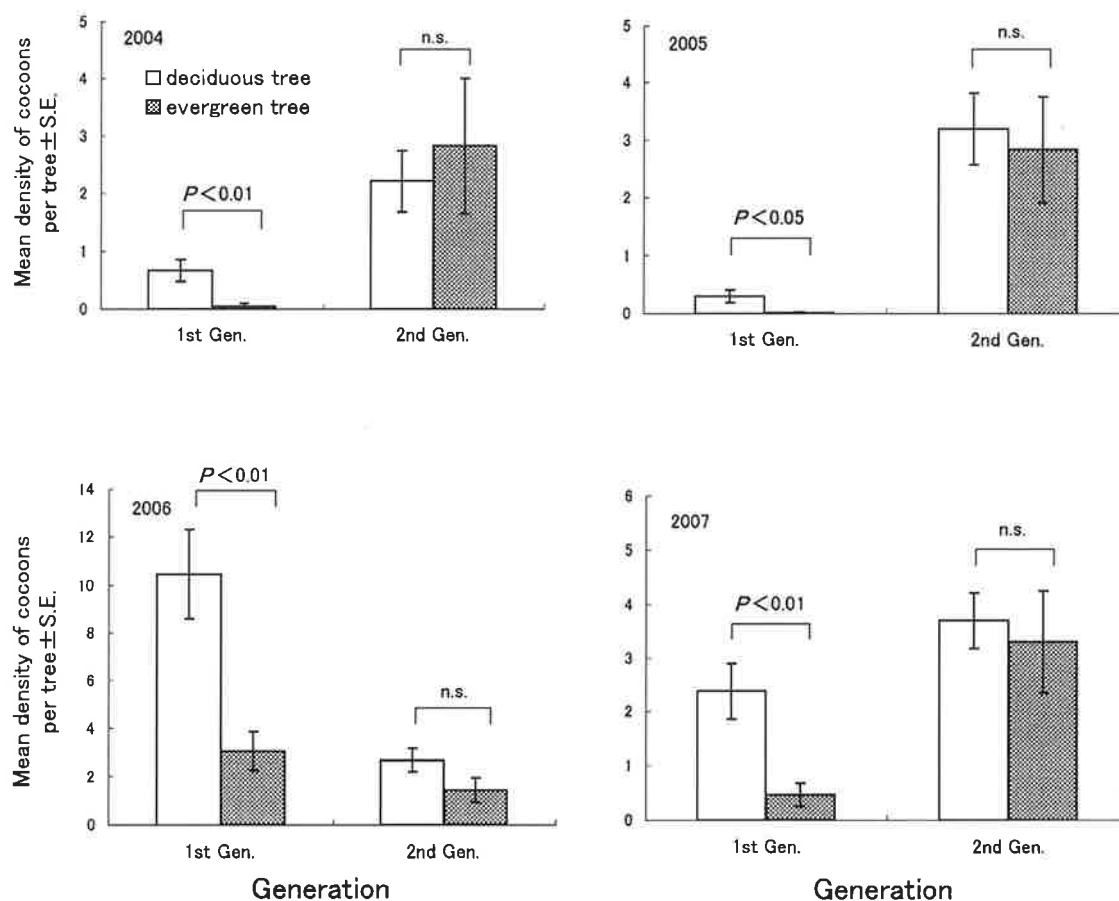


Fig. 1 Comparisons of the mean cocoon (*Parasa lepida*) density per tree (\pm S.E.) between deciduous and evergreen trees from 2004 to 2007. Open bars and gray bars indicate mean densities in deciduous and evergreen trees, respectively. The differences in cocoon density between the host trees were tested using Welch's *t* test. n. s.: not significant.

In the first generation of 2004, the cocoon density per tree was higher in the deciduous trees (0.67 ± 0.19 ; $m \pm se$) than in the evergreen trees (0.05 ± 0.05) (Welch's *t* test: $P < 0.01$). By contrast, in the second generation no significant difference in cocoon density was detected (2.21 ± 0.52 and 2.87 ± 1.87 for the deciduous and evergreen trees, respectively, Welch's *t* test: $P = 0.63$).

The same seasonal trend was observed consistently throughout the study period up to 2007 (Fig. 1).

Life tables of the first generation in deciduous *Triadica sebifera* and evergreen *Quercus myrsinaefolia*

Life tables of the first generation during 2005–2007 were compared between deciduous *T. sebifera* and evergreen *Q. myrsinaefolia* (Table 1). In 2005 the total egg density was 3.6 times higher in *T. sebifera* than in

Q. myrsinaefolia, with 844 eggs and 235 eggs, respectively. The tendency was the same in 2006 and 2007, with 3.2 times and 7.3 times more eggs in *T. sebifera* than in *Q. myrsinaefolia*.

As the egg mortality agent, *Trichogramma dendrolimi* Matsumura, an egg parasitoid, was identified as the egg mortality agent by rearing parasitized eggs in the laboratory. The parasitized eggs were readily identified due to the darkened coloration. *T. dendrolimi* was also described as an egg parasitoid of another Limacodidae moth, the small blackish cochlid *Scopelodes contractus* Walker (Oda and Hattori, 1981). The mortality rate due to *T. dendrolimi*, fluctuating from 2.3% up to 36.6% on *T. sebifera*, did not exhibit consistent host-related tendencies though all the between-host differences were statistically significant ($P < 0.0001$ in 2005, 2006 and 2007, Fisher's exact test).

Table 1a. Life tables of the first generation of *P. lepida* on *T. sebifera* and *Q. myrsinaefolia* in 2005.

| Host plant | <i>T. sebifera</i> | | | | <i>Q. Myrsinaefolia</i> | | | |
|------------|--------------------|--|----------------------|-----------------------------|---------------------------------|--|----------------------|-----------------------------|
| | Age class | No. of alive at beginning of X Nx (lx) | Factors of Mx MxF | No. of dying during X Mx | Mortality rate (%) Mx/Nx*100 | No. of alive at beginning of X Nx (lx) | Factors of Mx MxF | No. of dying during X Mx |
| Egg | 844 (1000) | | 309 | 36.6 | 235 (1000) | | 25 | 10.6 |
| | | parasitoid unknown and miscellaneous | 57 | 6.8 | | parasitoid unknown and miscellaneous | 12 | 5.1 |
| Larva | 478 (566.4) | | 422 | 88.3 | 198 (842.6) | | 193 | 97.5 |
| | | unknown and miscellaneous | | | | unknown and miscellaneous | | |
| Cocoon | 57 (67.5) | | | | 5 (21.3) | | | |

Table 1b. Life tables of the first generation of *P. lepida* on *T. sebifera* and *Q. myrsinaefolia* in 2006.

| Host plant | <i>T. sebifera</i> | | | | <i>Q. Myrsinaefolia</i> | | | |
|------------|--------------------|--|----------------------|-----------------------------|---------------------------------|--|----------------------|-----------------------------|
| | Age class | No. of alive at beginning of X Nx (lx) | Factors of Mx MxF | No. of dying during X Mx | Mortality rate (%) Mx/Nx*100 | No. of alive at beginning of X Nx (lx) | Factors of Mx MxF | No. of dying during X Mx |
| Egg | 3722 (1000) | | 85 | 2.3 | 1172 (1000) | | 70 | 6.0 |
| | | parasitoid unknown and miscellaneous | 459 | 12.3 | | parasitoid unknown and miscellaneous | 71 | 6.1 |
| Larva | 3178 (853.8) | | 2374 | 74.7 | 1031 (879.7) | | 838 | 81.3 |
| | | unknown and miscellaneous | | | | unknown and miscellaneous | | |
| Cocoon | 804 (216.0) | | | | 193 (164.7) | | | |

Table 1c. Life tables of the first generation of *P. lepida* on *T. sebifera* and *Q. myrsinaefolia* in 2007.

| Host plant | <i>T. sebifera</i> | | | | <i>Q. Myrsinaefolia</i> | | | |
|------------|--------------------|--|----------------------|-----------------------------|---------------------------------|--|----------------------|-----------------------------|
| | Age class | No. of alive at beginning of X Nx (lx) | Factors of Mx MxF | No. of dying during X Mx | Mortality rate (%) Mx/Nx*100 | No. of alive at beginning of X Nx (lx) | Factors of Mx MxF | No. of dying during X Mx |
| Egg | 3437 (1000) | | 421 | 12.2 | 472 (1000) | | 24 | 5.1 |
| | | parasitoid unknown and miscellaneous | 906 | 26.4 | | parasitoid unknown and miscellaneous | 77 | 16.3 |
| Larva | 2110 (613.9) | | 1862 | 88.2 | 371 (786.0) | | 329 | 88.7 |
| | | unknown and miscellaneous | | | | unknown and miscellaneous | | |
| Cocoon | 248 (72.2) | | | | 42 (89.0) | | | |

A few cases of egg predation by *Harmonia axyridis* (Pallas), a common ladybeetle, were included as other miscellaneous deaths. Egg mortality was 43.4%, 14.6%, and 38.6% on *T. sebifera*, respectively, in 2005, 2006 and 2007, which was greater than the corresponding mortality on *Q. myrsinaefolia*, 15.7%, 12.0% and 21.4% ($P < 0.0001$, $P < 0.05$ and $P < 0.0001$, Fisher's exact test). Mortality agents during larval stages were poorly identified except for a small amount of predation by spiders, a ladybeetle (*H. axyridis*), and a mantis (*Hierodula patellifera* (Serville)) and by disease. Thus all larval mortality was treated as miscellaneous. Larval mortality was greater on *Q. myrsinaefolia* both in 2005 and 2006 than on *T. sebifera* but was not statistically significantly different in 2007 ($P < 0.0001$, $P < 0.001$ and $P = 0.86$, in 2005, 2006 and 2007, respectively, Fisher's exact test).

A total of 57, 804 and 248 cocoons were observed on *T. sebifera* in 2005, 2006 and 2007, respectively. These figures were 11.4, 4.2 and 5.9 times greater than those on *Q. myrsinaefolia* (5, 193, and 42, respectively in 2005, 2006 and 2007).

Life tables of the second generation in deciduous *T. sebifera* and evergreen *Q. myrsinaefolia*

Table 2 describes the life tables in the second generation both on *T. sebifera* and *Q. myrsinaefolia* over three years, 2005-2007. At the start of the second generation the total egg density was 3079 on *T. sebifera*, which was 4.0 times higher than that on *Q. myrsinaefolia* (779 eggs). This tendency was the same both in 2006 and 2007, with 5.3 and 1.7 times greater production of eggs on *T. sebifera* (**Table 2**).

Egg mortality due to the parasitoid fluctuated from

Table 2a. Life tables of the second generation of *P. lepida* on *T. sebifera* and *Q. myrsinaefolia* in 2005.

| Host plant | <i>T. sebifera</i> | | | | <i>Q. Myrsinaefolia</i> | | | |
|------------|--------------------|--|----------------------|-----------------------------|---------------------------------|--|----------------------|-----------------------------|
| | Age class X | No. of alive at beginning of X Nx (lx) | Factors of Mx MxF | No. of dying during X Mx | Mortality rate (%) Mx/Nx*100 | No. of alive at beginning of X Nx (lx) | Factors of Mx MxF | No. of dying during X Mx |
| Egg | 3079 (1000) | parasitoid unknown and miscellaneous | 467 | 15.2 | 779 (1000) | parasitoid unknown and miscellaneous | 19 | 2.4 |
| | | | 82 | 2.7 | | | 29 | 3.7 |
| Larva | 2530 (821.7) | unknown and miscellaneous | 2355 | 93.1 | 731 (938) | unknown and miscellaneous | 579 | 79.2 |
| Cocoon | 175 (56.8) | | | | 152 (195.1) | | | |

Table 2b. Life tables of the second generation of *P. lepida* on *T. sebifera* and *Q. myrsinaefolia* in 2006.

| Host plant | <i>T. sebifera</i> | | | | <i>Q. Myrsinaefolia</i> | | | |
|------------|--------------------|--|----------------------|-----------------------------|---------------------------------|--|----------------------|-----------------------------|
| | Age class X | No. of alive at beginning of X Nx (lx) | Factors of Mx MxF | No. of dying during X Mx | Mortality rate (%) Mx/Nx*100 | No. of alive at beginning of X Nx (lx) | Factors of Mx MxF | No. of dying during X Mx |
| Egg | 21138 (1000) | parasitoid unknown and miscellaneous | 2581 | 12.2 | 3955 (1000) | parasitoid unknown and miscellaneous | 659 | 16.7 |
| | | | 3747 | 17.7 | | | 295 | 7.5 |
| Larva | 14810 (700.6) | unknown and miscellaneous | 14774 | 99.8 | 3001 (758.8) | unknown and miscellaneous | 2864 | 95.4 |
| Cocoon | 36 (1.7) | | | | 137 (34.6) | | | |

Table 2c. Life tables of the second generation of *P. lepida* on *T. sebifera* and *Q. myrsinaefolia* in 2007.

| Host plant | <i>T. sebifera</i> | | | | <i>Q. Myrsinaefolia</i> | | | |
|------------|--------------------|--|----------------------|-----------------------------|---------------------------------|--|----------------------|-----------------------------|
| | Age class X | No. of alive at beginning of X Nx (lx) | Factors of Mx MxF | No. of dying during X Mx | Mortality rate (%) Mx/Nx*100 | No. of alive at beginning of X Nx (lx) | Factors of Mx MxF | No. of dying during X Mx |
| Egg | 11851 (1000) | parasitoid unknown and miscellaneous | 3054 | 25.8 | 6917 (1000) | parasitoid unknown and miscellaneous | 1002 | 14.5 |
| | | | 3616 | 30.5 | | | 1736 | 25.1 |
| Larva | 5181 (437.2) | unknown and miscellaneous | 5060 | 97.7 | 4179 (604.2) | unknown and miscellaneous | 3864 | 92.5 |
| Cocoon | 121 (10.2) | | | | 315 (45.5) | | | |

2.4% on *Q. myrsinaefolia* in 2005 maximally up to 25.8% on *T. sebifera* in 2007, though the tendency was not consistent between the two host plants. In contrast, the total egg mortality was slightly higher on *T. sebifera* (17.8%, 29.9%, and 56.3% in 2005, 2006, and 2007, respectively) than on *Q. myrsinaefolia* (6.2%, 24.1%, and 39.6% in 2005, 2006 and 2007, respectively) ($P < 0.0001$ in all three years, Fisher's exact test).

The total mortality during the larval stage was significantly higher in the second generation than in the first generation on both hosts ($P < 0.001$, $P < 0.0001$, and $P < 0.0001$ in 2005, 2006, and 2007, respectively, on *T. sebifera*; $P < 0.0001$ and $P < 0.02$ in 2006 and 2007, respectively, on *Q. myrsinaefolia*, Fisher's exact test). The opposite trend was seen on *Q. myrsinaefolia* in 2005 ($P < 0.0001$). The enhanced larval mortality in the second generation was particularly evident on *T. sebifera*, contrasting to the opposite trend in the first generation. A large number of larvae were found dead in a typical wilted state with their prolegs clinging to leaf petioles. These larvae were identified as being killed by nuclear polyhedrosis virus (NPV) because of the presence of a large number of polyhedrosis in the blood. NPV is known also from another Limacodidae moth *Scopelodes contractus*, which has similar ecological and life history properties (Aratake and Watanabe, 1973).

Factors responsible for the host-related difference in cocoon density

Fig. 2 compares the cocoon density (C), the egg density (E), the egg survival (S(E)), and larval survival (S(L)) between *T. sebifera* and *Q. myrsinaefolia* on the logarithmic scale.

In the first generation, the cocoon density was consistently higher on *T. sebifera* than on *Q. myrsinaefolia*, the tendency of which agreed with the results of the field observation based on data obtained from 404 trees of 51 species (**Fig. 1**). The higher density on *T. sebifera* than on *Q. myrsinaefolia* may be ascribed to the higher egg density and the higher larval survival, as typically observed in 2005. In contrast, the higher egg survival on *Q. myrsinaefolia*, being consistently observed over the 3 years, affected host-related differences in the cocoon density very little (**Fig. 2**). The higher egg density on *T. sebifera* may be due to the oviposition preference of *P. lepidus* females on the grounds that both plant species are quite similar in the tree height, shape and foliage area.

On the other hand the enhanced larval survival on *T. sebifera* may be ascribed at least partly to better nutritional quality of *T. sebifera* as the food resource. Sawada *et al.* (2008) examined developmental performances of *P. lepidus* larvae by providing them with either leaves of *T. sebifera* or *Q. myrsinaefolia*, and concluded that developmental performance was better on the former than on the latter in terms of both mass gain and developmental period. Further study is necessary to confirm that the above tendencies are prevalent between other deciduous species and evergreen species.

In contrast to the first generation, life table data revealed that the cocoon density was higher on *Q. myrsinaefolia* than on *T. sebifera* in the second generation in 2006 and 2007, or was virtually equivalent between the two hosts in 2005. The field census detected no significant differences in cocoon density in the second generation between the deciduous and evergreen species based on data from 404 trees of 51 plant species (**Fig. 1**). This was exclusively because of substantially lower survival of larvae on *T. sebifera* than on *Q. myrsinaefolia* considering the fact that the egg density was rather higher on the former host (similar to the position in the first generation) (**Fig. 2**). Moreover, it is noteworthy that the larval mortality was particularly enhanced when the density of eggs (E) and larvae (L) were higher, as was observed on *T. sebifera* in 2006. This density-dependent larval mortality led to density over-compensation, finally resulting in a lower cocoon density in the second generation in years of higher density of the first generation than in ordinary years (**Table 2**). A large number of larval deaths due to NPV were observed, particularly in years when the larval density was high, though we could not identify various mortality factors accurately. In general, infection of NPV spreads very rapidly as the host density increases, and thus NPV is regarded as one of the critical factors to end outbreaks of moth larvae (Stairs, 1971). Studies on outbreaks of the gypsy moth *Lymantria fumida* Butler, a major pest of fir forests, revealed that most of the outbreaks ended due to the prevalent infection of NPV (Koyama and Katagiri, 1959). In this context, further study is necessary to examine the transmission and infection mechanisms of NPV to understand better the population dynamics of *P. lepidus*.

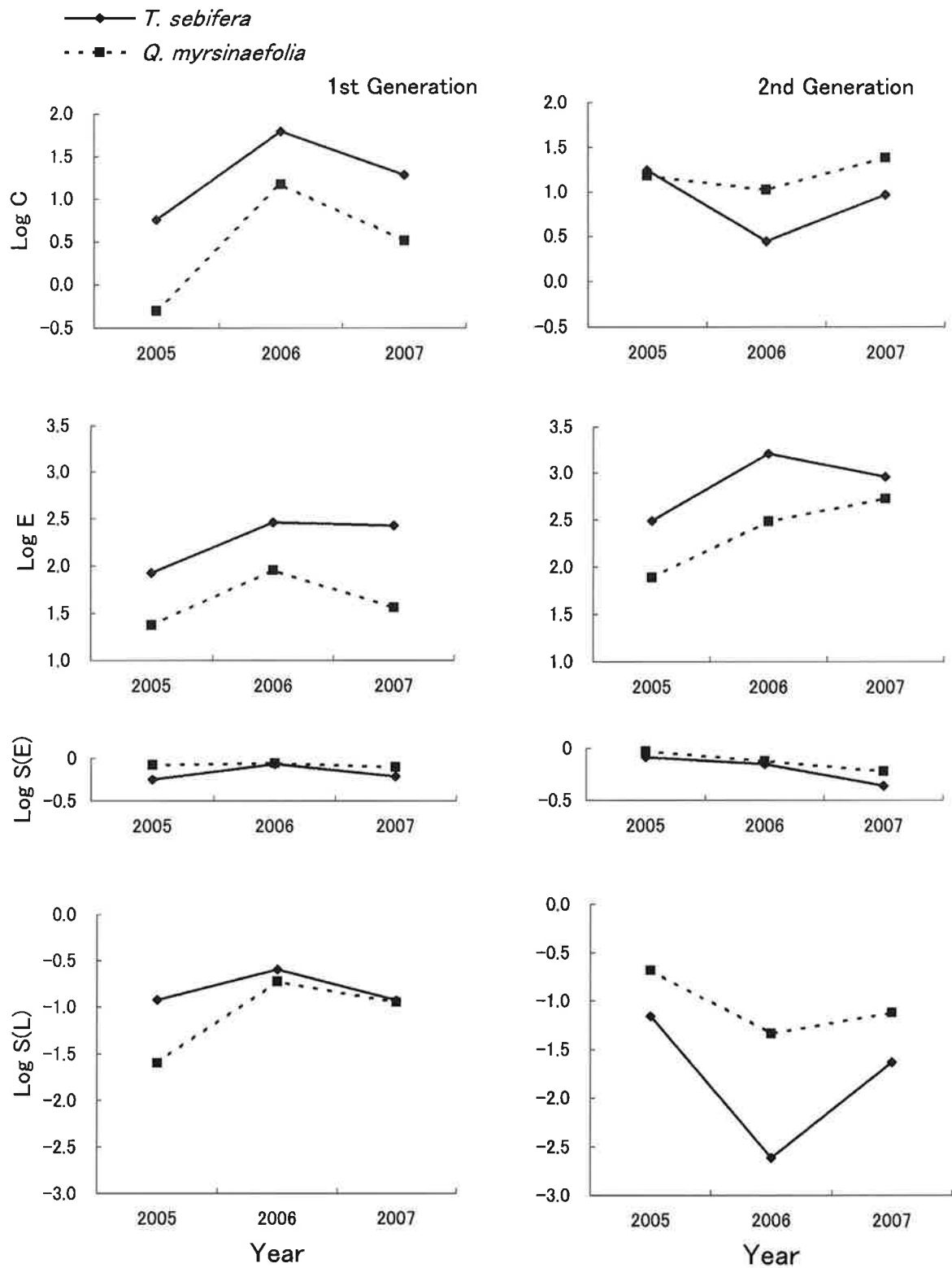


Fig. 2 Comparisons of the cocoon density (C), egg density (E), survival rate during egg stage (S(E)), and survival rate during larval stage (S(L)) of the *Parasa lepida* between deciduous (*Triadica sebifera*; straight lines with diamond symbols) and evergreen tree (*Quercus myrsinaefolia*; broken lines with square symbols) in the first (left-hand) and second (right-hand) generation from 2005 to 2007.

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落葉樹と常緑樹でのヒロヘリアオイラガ *Parasa lepida* (Cramer) の繭密度と個体群増殖過程の比較

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2004～2007年の4年間、滋賀県彦根市にある滋賀県立大学構内において、36種282株の落葉樹と、15種122株の常緑樹でヒロヘリアオイラガの繭密度を調査するとともに、落葉樹のナンキンハゼと常緑樹のシラカシで、生命表の作製を含む詳細な個体群調査を行った。第1世代では、落葉樹の繭密度は常緑樹より有意に高いことが示され、また第2世代では、落葉樹と常緑樹で繭密度に有意な差は認められなかった。ナンキンハゼとシラカシでの生命表調査の結果、第1世代の繭密度は落葉樹であるナンキンハゼで高く、他方、第2世代の繭密度は常緑樹であるシラカシで高い傾向が認められた。第1世代にナンキンハゼでの繭密度が高い理由として、卵密度が高いことと、幼虫期生存率が比較的高いことが重要だと考えられた。他方、第2世代では、ナンキンハゼでの卵密度は、第1世代と同様、シラカシより高いにもかかわらず、幼虫期の死亡率が著しく高く、その結果、ナンキンハゼでの繭密度はシラカシより低い傾向を示した。ナンキンハゼでの幼虫期の死亡要因として、核多角体病ウイルス (NPV) の感染による死亡が重要だと考えられた。

Causes of larval mortality in relation to host plant quality in the invasive grub moth, *Parasa lepida* (Cramer)

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Abstract

We examined the development and mortality of first and second generation larvae of the invasive grub moth *Parasa lepida* (Cramer) on Chinese tallow tree *Triadica sebifera* (L.) Small and an oak *Quercus myrsinaefolia* Blume in Hikone, Shiga Prefecture, in 2006 and 2007. These food plants represent typical deciduous and evergreen host plants, respectively. Larval body size and growth speed were examined, and the water, carbon (C) and nitrogen (N) contents and C/N ratios of the host plant leaves were determined, as indicators of plant quality of the larval food resource. In 2007, larvae fed on *T. sebifera* grew faster and attained longer body lengths than those fed on *Q. myrsinaefolia*, though the difference was not significant in 2006. This suggests better leaf quality of *T. sebifera*. First generation larvae survived better on *T. sebifera* than on *Q. myrsinaefolia*, presumably due to both better leaf quality of *T. sebifera* and to the occurrence of fungal disease in *Q. myrsinaefolia*. Larval mortality was far higher in the second than in the first generation, and was higher on *T. sebifera* than on *Q. myrsinaefolia*, due to the frequent occurrence of nuclear polyhedrosis virus (NPV), particularly in larvae feeding on *T. sebifera*. We discuss the consequences of these diseases for populations of *P. lepida* in relation to leaf quality of host plants and host-related differences in larval density.

Key words : *Parasa lepida* (Cramer), Life table, Mortality factor, Fungal disease, Nuclear polyhedrosis virus (NPV)

Introduction

Larvae of the invasive grub moth *Parasa lepida* (Cramer) often occur in large numbers and can cause serious defoliation of ornamental trees in urban areas in western Japan, where they are regarded as notorious pests. The larvae of early instars are highly aggregative, forming compact feeding groups. Contact with the spines of *P. lepida* larvae can also cause dermatitis in humans (Oda and Hattori, 1981; Miyata, 1981). Recently, Wakamura *et al.* (2007) identified the sex pheromone of *P. lepida* and evaluated its attractiveness with regard to field monitoring and control.

P. lepida feeds on a wide range of plants. Yamazaki *et al.* (1994a, b) examined 62 plant species of 31

families and found cocoons on all but four species of the broad-leaved trees. Yamazaki *et al.* (1994a, b) noted that the cocoon density was highest on Formosa sweetgum *Liquidambar formosana*, Yoshino cherry *Prunus X yedoensis*, and *T. sebifera*, but found no significant correlations between plant phylogeny and utilization by *P. lepida*. Sawada *et al.* (2008) compared the cocoon density among 282 individual trees of 36 deciduous species and 122 individual trees of 15 evergreen species, and concluded that the density of the first generation was greater on deciduous trees, but no such tendency was observed in the second generation. By conducting detailed population censuses of the larval stage both on deciduous *T. sebifera* and evergreen *Q. myrsinaefolia*, Sawada *et al.* (2008) showed that 1) the egg density was higher on *T.*

sebifera in both the first and second generations, 2) larval survival was better on *T. sebifera* in the first generation, resulting in increased first generation cocoon density, but 3) larval survival was significantly lower on *T. sebifera* in the second generation, compared with *Q. myrsinaefolia*, resulting in a lower cocoon density in the second generation. Seasonal differences in cocoon density were therefore attributable to host-related seasonal differences in larval mortality.

In this study we assessed the quality of the host plants from two different aspects: host plant quality as a larval food resource, and host-related differences in larval mortality, including the effect of natural enemies. We evaluated host plant quality in terms of larval development and larval size, as well as the water, carbon (C) and nitrogen (N) contents, and C/N ratios in the leaves of the two host plants. We measured host-related differences in larval mortality, in particular in relation to fungal disease and nuclear polyhedrosis virus (NPV), by tracking the survival of groups of larvae until cocoon formation. We also discuss the population consequences of the larval mortality factors in relation to host-related differences in leaf quality, and larval density.

Materials and Methods

Parasa lepida (Cramer)

P. lepida is an invasive moth, originally distributed over a wide area of the tropics to sub-tropics, including southern China-southeast Asia, India, and central-southern Africa (Hirashima, 1989; Zhang, 1994). *P. lepida* was first recorded in Kagoshima in 1921, and then gradually expanded its range north-eastwards in western Japan. During the 1980s it established its pest status by seriously defoliating persimmon, cherry and other street trees (Oda and Hattori, 1981). Its distribution has recently expanded to reach Kanto district, eastern Japan (Nakano, 2003). *P. lepida* is also notorious because contact with its larval spines can cause dermatitis in humans (Oda and Hattori, 1981; Miyata, 1981).

In its original distribution range, *P. lepida* feeds on a wide range of plants. Robinson *et al.* (2001) documented 78 species of 35 families as host plants, including legumes (Fabaceae), palms (Arecaceae), and Euphobias (Euphobiaceae) in India and southeast Asia. *P. lepida* is known as a fruit tree pest, damaging coconuts, coffee, mango and cacao in Indonesia

(Kalshoven, 1981) and is regarded as a serious pest of mango in India (Kapoor *et al.*, 1985; Jeyabalan and Murugan, 1996).

Mortality factors during the larval stages

We examined the factors affecting mortality of *P. lepida* during the egg to pupa stages. First and second generation larvae were studied on two typical host plants, *T. sebifera* and *Q. myrsinaefolia* (two individual trees for each), at the campus of the University of Shiga Prefecture in the suburbs of Hikone (35° 17'N, 136° 15'E) in 2006 and 2007. *T. sebifera* and *Q. myrsinaefolia* were chosen as representatives of deciduous and evergreen hosts, respectively. The census period covered the whole developmental period from the start of oviposition to the end of cocoon formation; from late May to early September and from mid-August to early November, for the first and the second generations, respectively (Nishida *et al.* 2006). Larval aggregations derived from the same egg batch were checked every day for larval survival and possible causes of mortality, since the hatched larvae feed on host plant leaves as a compact group until middle instar stage. To identify mortality due to storms with strong winds and heavy rain, we placed a net below each larval aggregation to collect larvae that dropped or died. By analyzing survival data for each larval group on each of the two plant species, we constructed life tables and survivorship curves. It was difficult to identify larval instars in the field, so larval developmental stages were classified by 10-day intervals.

Two types of disease were found, each prevalent exclusively in the first and second generations, respectively. In the first generation, most larvae that died as a result of disease exhibited characteristic symptoms including the development of dark brown spots on the body surface, which then darkened up to the time of death. Dead larvae stored in a plastic cup with wetted tissue paper for 3-5 days became covered with whitish fungi. Under a microscope, globular or bean pod-like spores could be seen within the dead larvae, indicating a fungal disease, as described by Fukuhara (1979). In contrast, almost all infected second generation larvae, in particular in 2006, showed different symptoms: They became swollen and yellowish in color, then exuded a whitish body fluid. They remained perched on a twig or leaf in a V-shaped posture until they died and decomposed. These

symptoms are characteristic of NPV infection (Koyama and Katagiri, 1959; Stairs, 1971).

Measurement of larval body length

We measured body lengths of 20 larvae from each larval aggregation every day. If the size of the larval aggregation was less than 20, all the larvae were measured. To determine body length, we photographed the larvae on 1 x 1 mm grid paper using a digital camera. The photographs were enlarged on a computer to measure the body size. Egg hatching occurred during mid-June and early July for the first generation, and during late August and early September for the second generation, on both host plants. We therefore regarded the temperature conditions under which the larvae developed to be similar on both host plants.

Analysis of leaf quality as larval food

In addition to censusing the larvae, five leaves close to where the larvae were feeding were collected from each census tree, to examine the water, carbon (C) and nitrogen (N) contents, and the C/N ratios. The leaves were collected in the morning (10:00-12:00), measured for wet weight, and then dried at 70°C (Yamato DN910) for 1 week, before measuring the dry weight. The water content of leaves was calculated from the percent weight difference between the wet and dry weights. The C and N contents (%) of the leaves were measured using a CHN Corder (Yanaco MT-5), after grinding them into powder.

Results

Life tables for the first generation larvae

Tables 1a and **1b** show the survival of first generation *P. lepidus* larvae on *T. sebifera* and *Q. myrsinaefolia*, respectively, in 2006 and 2007. Five to eight groups of larvae were found in each host plant cohort in both years, except on *Q. myrsinaefolia* in 2007, which had only one egg batch. In the *T. sebifera* 2006 cohort, 876 larvae hatched from six egg batches, and 47.6 % of them successfully developed to cocoons (**Table 1a**), with a larval period (from hatching to cocoon formation) of 29-41 days (**Table 3**). The major causes of larval mortality were predation by spiders, ladybird larvae and mantises (4 larvae, 0.45 %), fungal disease (16 larvae, 1.8 %) and storms (66 larvae, 7.5 %) (**Table 1a**). In contrast, larval mortality was

higher and the larval period was longer on *Q. myrsinaefolia* in 2006, than on *T. sebifera* (larval mortality; logistic regression, Wald's $\chi^2=110.6$, d.f.=1, $P<0.0001$; **Table 1**, larval period; Wilcoxon rank sum test, $z=21.28$, $P<0.0001$; **Table 3**). Only 38 individuals (11.5%) reached the cocoon stage from 332 larvae that hatched from five egg batches, and the larval period ranged from 42-50 days (**Table 1a**, **Table 3**). Larval mortality was due to predation (5 larvae, 1.5%), fungal disease (39 larvae, 11.7%) and storms (30 larvae, 9.0%), of which mortality due to fungal disease was significantly higher than on *T. sebifera* (logistic regression, Wald's $\chi^2=41.76$, d.f.=1, $P<0.0001$; **Table 1a**).

In the *T. sebifera* 2007 cohort, among 481 larvae that hatched from eight egg batches, 15.8 % of them (76 individuals) reached the cocoon stage with a larval period of 34-43 days (**Table 1b**, **Table 3**). During the larval period 1.2% (6 larvae) and 1.0% (5 larvae) were killed by fungal disease and storms. In the *Q. myrsinaefolia* 2007 cohort, only one batch of eggs was laid, from which 68 larvae hatched and 29.4% of them (20 individuals) survived to the cocoon stage. Larval mortality was significantly lower in the *Q. myrsinaefolia* cohort than in the *T. sebifera* cohort in 2007 (logistic regression, Wald's $\chi^2=7.92$, d.f.=1, $P=0.005$; **Table 1b**). The larval period was 41-55 days, which was significantly longer than that in *T. sebifera* (34-43 days), as in 2006 (Wilcoxon rank sum test, $z=8.02$, $P<0.0001$; **Table 3**).

Life tables for the second generation larvae

Life tables for second generation *P. lepidus* larvae were documented for *T. sebifera* and *Q. myrsinaefolia*, in 2006 and 2007. Larval mortalities were higher in the second than in the first generation on both plants and in both years, with survival rates of 11.5-47.6% and 0.0-2.7% in the first and second generations, respectively (for *T. sebifera* logistic regression, Wald's $\chi^2=65.25$, 82.54, d.f.=1, $P<0.0001$, in 2006 and 2007, **Tables 1** and **2**; for *Q. myrsinaefolia*, Wald's $\chi^2=12.40$, 65.46, d.f.=1, $P<0.0004$ and $P<0.0001$, in 2006 and 2007, **Tables 1** and **2**).

In the 2006 *T. sebifera* cohort, only one out of 3571 larvae from 41 batches of eggs (0.03%) developed to the cocoon stage, 35 days after emergence (**Table 4** and **Table 2a**). NPV was a major cause of mortality, being responsible for 24.3% of deaths (867 larvae), which was significantly higher than in the first generation (logistic regression, Wald's $\chi^2=122.66$, d.f.=1, $P<0.0001$, **Tables 1** and **2**). Dislodgement due to

Table 1a Life tables during larval stage of *P. lepid*a on *T. sebifera* and *Q. myrsinifolia* in the first generation of 2006

| Host plant developmental period after hatch X (day) | <i>T. sebifera</i> | | | | <i>Q. myrsinifolia</i> | | | |
|--|--|---|--------------------------------|------------------------------------|--|---|--------------------------------|------------------------------------|
| | No. of alive at beginning of X Nx (lx) | Factors of Mx MxF | No. of dying during X Mx | Mortality rate (%) Mx/Nx*100 | No. of alive at beginning of X Nx (lx) | Factors of Mx MxF | No. of dying during X Mx | Mortality rate (%) Mx/Nx*100 |
| 0 | 876 (1000) (6 groups) | disease failure in molt unknown | 5 1 76 | 0.6 0.1 8.7 | 332 (1000) (5 groups) | predator storm unknown | 1 5 68 | 0.3 1.5 20.5 |
| 10 | 794 (906.4) | predator disease storm unknown | 4 3 47 127 | 0.5 0.4 2.1 16.0 | 258 (777.1) | storm unknown | 11 46 | 4.3 17.8 |
| 20 | 643 (734.0) | disease storm unknown | 4 32 162 | 0.6 5.0 25.2 | 201 (605.4) | disease storm unknown | 14 7 75 | 7.0 3.5 37.3 |
| 30 | 445 (508.0) No. of cocoon:3 | disease storm unknown | 4 17 7 | 0.9 3.8 1.6 | 105 (316.3) | predator disease storm unknown | 1 19 7 29 | 1.0 18.1 6.7 27.6 |
| 40 | 417 (476.0) No. of cocoon:417 | | | | 49 (147.6) | predator disease unknown | 3 6 2 | 6.1 12.2 4.1 |
| 50 | | | | | 38 (114.5) No. of cocoon:38 | | | |

Table 1b Life tables during larval stage of *P. lepid*a on *T. sebifera* and *Q. myrsinifolia* in the first generation of 2007

| Host plant developmental period after hatch X (day) | <i>T. sebifera</i> | | | | <i>Q. myrsinifolia</i> | | | |
|--|--|-----------------------------|--------------------------------|------------------------------------|--|-------------------------|--------------------------------|------------------------------------|
| | No. of alive at beginning of X Nx (lx) | Factors of Mx MxF | No. of dying during X Mx | Mortality rate (%) Mx/Nx*100 | No. of alive at beginning of X Nx (lx) | Factors of Mx MxF | No. of dying during X Mx | Mortality rate (%) Mx/Nx*100 |
| 0 | 481 (1000) (8 groups) | unknown | 127 | 26.4 | 68 (1000) (1 groups) | unknown | 12 | 17.6 |
| 10 | 354 (736.0) | unknown | 163 | 46.0 | 56 (823.5) | unknown | 26 | 46.4 |
| 20 | 191 (397.1) | disease storm unknown | 1 2 48 | 0.5 1.0 25.1 | 30 (441.2) | disease unknown | 2 3 | 6.7 10.0 |
| 30 | 140 (291.1) | disease storm unknown | 5 3 56 | 3.6 2.1 40.0 | 25 (367.6) | disease storm | 3 1 | 12.0 4.0 |
| 40 | 76 (158.0) No. of cocoon:74 | | | | 21 (308.8) | unknown | 1 | 4.8 |
| 50 | | | | | 20 (294.1) No. of cocoon:20 | | | |