Effects of Temperature and Photoperiod on Wing Form
Determination and Reproduction of *Thrips nigropilosus*
UZEL (Thysanoptera: Thripidae)

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Females of *Thrips nigropilosus* UZEL were reared at 18°C and 15L–9D from egg to pre-pupa, and then transferred to 4 experimental conditions: 18°C and 15L–9D; 18°C and 10L–14D; 25°C and 15L–9D; and 25°C and 10L–14D. The numbers of eggs subsequently laid by the females were counted, and the sex and wing form of their offspring were determined. Under the 4 conditions, only males were produced by virgin females, while both sexes were produced by once-mated females. Male offspring were all brachypterous. Female offspring were macropterous at both 18°C and 25°C and 15L–9D, brachypterous at 18°C and 10L–14D, and macropterous, brachypterous and intermediate at 25°C and 10L–14D. These results suggested that long-day photoperiods lead to the occurrence of the macropterous female and short-day photoperiods induce the development of the brachypterous female, and that high temperatures partly inhibit the development of the brachypterous female. The total number of eggs laid per female was significantly lower at 18°C and 10L–14D than at any other conditions. This indicated that moderate temperature and short-day photoperiod partly suppress the reproduction of the female thrips.

**Key words:** *Thrips nigropilosus*, photoperiod, temperature, wing polymorphism, arrhenotoky

INTRODUCTION

Wing polymorphism is a widespread phenomenon among insects. In some species, wing form is under simple genetic control or subject to polygenic influence (Roff, 1986). However, in most species wing form is determined by environmental factors, such as temperature, photoperiod, food quality or density (Harrison, 1980). Understanding how wing forms are determined is a first step to explain the adaptive significance of wing polymorphism.

Morison (1957) reported that the females of the chrysanthemum thrips, *Thrips nigropilosus* UZEL, exhibit wing polymorphism from macroptery to scale-like microptery, but no information is available about the factor determining the wing forms. Although wing polymorphism occurs in some of Thripidae, little attention has been devoted to the factors controlling wing forms in the group. The aim of this study is to clarify the effect of temperature and photoperiod on the wing form as well as on longevity and fecundity of female *T. nigropilosus*.
MATERIALS AND METHODS

Culture of insects. Twelve female adults of *T. nigropilosus* were collected from leaves of *Artemisia princeps* PAMP. at Mukaijima in Kyoto, Japan, in March, 1990. A laboratory culture was established from their offspring (generation 1). The culture was maintained at 18°C and 15L–9D by a modification of Murai’s method (1988) (Fig. 1). Pieces of *A. princeps* leaves were provided as hosts in the first 2 generations, and those of *Chrysanthemum morifolium* RAMAT. [variety: Kokkasoun] leaves in the third generation onwards. Female adults were reared individually in rearing cages (Fig. 1A) and transferred every 1–2 days to fresh ones. Leaf pieces containing eggs were separately sandwiched between moist cotton cloths in hatching cages (Fig. 1B), and newly hatched larvae were transferred to a rearing cage with a new leaf piece and reared till adult eclosion. Thrips from the third generation onward were used for experiments.

Rearing trials under different temperature and photoperiod conditions. Thirty-five female pupae were transferred within 24 h after exuviation from the stock culture to fresh cages and reared individually throughout their lives under one of the following 4 conditions: 1) 18°C and 15L–9D, 2) 18°C and 10L–14D, 3) 25°C and 15L–9D, and 4) 25°C and 10L–14D. Two days after adult eclosion, 16 of the 35 females were allowed to mate once with newly emerged males. The other females were not allowed to mate. Four or 7 virgin and 4 once-mated females were reared under each of the 4 conditions.

![Fig. 1. Apparatus for rearing *T. nigropilosus*. A: rearing cage, B: hatching cage, C: container in which cages are kept.](image-url)
These females were transferred to fresh cages every 1–2 days, and the number of eggs laid by them were counted under a binocular microscope.

**Measurements of body and wings of female thrips.** All cages with leaf pieces containing eggs were kept under the same temperature and photoperiod condition as the parents. Within 3 days of hatching, all larvae in a cage (1–18 individuals at 18°C and 1–25 individuals at 25°C) were transferred to a fresh cage and reared till adult eclosion. Soon after eclosion, the sex and the wing form were examined under a binocular microscope. Then some thrips were put in a 8:1:1:5 mixture of ethyl alcohol, glycerol, acetic acid and distilled water, respectively (Kudo, 1988). They were heated in 92% lactic acid and mounted in Neo-shigara® on glass slides to measure body length, head width, mesonotal width and wing length under a microscope.

**RESULTS**

**Wing form**

Under the 4 conditions tested, only males developed from the eggs laid by the 19 virgin females, whereas both sexes developed from the eggs laid by the 16 once-mated females (Table 1). The mean proportion of females among the offspring of the once-mated females was >73%.

Under the 4 conditions, male offspring were all brachypterous; apices of both fore wings never reached the third abdominal segment, and the left and right fore wings did not differ by ≥0.01 mm in length (Fig. 2A). On the other hand, female offspring showed various degrees of wing development and were classified into the following 2 groups: 1) females with normal wings: fore wings were longer than hind wings, left and right fore wings did not differ by ≥0.01 mm in length, and wings were not curled, 2) females with abnormal wings: all the other females.

Figure 3 shows the frequency distributions of the ratio of left fore wing length to head width (RWL) of females with normal wings. RWL was 3.9–4.9 at both 18°C and 25°C and 15L–9D, and 0.7–1.2 at 18°C and 10L–14D. RWL at 25°C and 10L–14D was 0.8–1.9 or 3.2–4.7. I define normally winged females with RWL above 3.0 as macropterous forms (Fig. 2B) and ones with RWL below 2.1 as brachypterous forms (Figs. 2G and H). The mean RWL of the macropterous females reared at 25°C and 10L–14D was significantly lower than that of females reared at 18°C or 25°C and

<table>
<thead>
<tr>
<th>Temperature and photoperiod</th>
<th>Mating experience of parents</th>
<th>No. of parents</th>
<th>No. of eggs laid</th>
<th>% survival during developmental period</th>
<th>% female</th>
</tr>
</thead>
<tbody>
<tr>
<td>18°C, 15L–9D</td>
<td>virgin</td>
<td>7</td>
<td>1,663</td>
<td>73.9</td>
<td>0.0</td>
</tr>
<tr>
<td></td>
<td>once-mated</td>
<td>4</td>
<td>630</td>
<td>84.0</td>
<td>73.9</td>
</tr>
<tr>
<td>18°C, 10L–14D</td>
<td>virgin</td>
<td>4</td>
<td>415</td>
<td>68.9</td>
<td>0.0</td>
</tr>
<tr>
<td></td>
<td>once-mated</td>
<td>4</td>
<td>373</td>
<td>60.3</td>
<td>76.9</td>
</tr>
<tr>
<td>25°C, 15L–9D</td>
<td>virgin</td>
<td>4</td>
<td>702</td>
<td>77.1</td>
<td>0.0</td>
</tr>
<tr>
<td></td>
<td>once-mated</td>
<td>4</td>
<td>641</td>
<td>82.2</td>
<td>83.9</td>
</tr>
<tr>
<td>25°C, 10L–14D</td>
<td>virgin</td>
<td>4</td>
<td>691</td>
<td>74.1</td>
<td>0.0</td>
</tr>
<tr>
<td></td>
<td>once-mated</td>
<td>4</td>
<td>752</td>
<td>77.3</td>
<td>76.2</td>
</tr>
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</table>
15L-9D (Table 2). The mean RWL of the brachypterous form was significantly lower at 18°C and 10L-14D than at 25°C and 10L-14D (Table 2).

Only 1 female reared at 18°C and 15L-9D (n=391) and 215 females at 25°C and 10L-14D (n=443) were with abnormal wings. Their relative wing lengths ranged from 0.6 to 4.9 continuously. These females were designated as “intermediate form”. Intermediate form was categorized into 4 types: 1) CU-type (Fig. 2C): the fore wings were curled, 2) LR·FH-type (Fig. 2D): the left and right fore wings differed by $\geq 0.01$ mm in length, and the left and/or right fore wing was shorter than the hind, 3) LR-type (Fig. 2E): the left and right fore wings differed by $\geq 0.01$ mm in length, and the fore wings were longer than the hind, 4) FH-type (Fig. 2F): the left and right fore wings did not differ by $\geq 0.01$ mm in length, and the left and/or right fore wing was shorter than the hind. An intermediate form at 18°C and 15L-9D was the LR-type with relative wing lengths of 1.4 and 1.6. Among intermediate forms at 25°C and 10L-14D the LR-type was predominant (60.5%), followed by LR·FH-type (34.9%), FH-type (3.7%) and CU-type (1.0%).

**Measurements of macropterous and brachypterous females**

Both the macropterous and brachypterous females reared at 18°C had wider heads and longer bodies than those at 25°C (Table 2). At 18°C the brachypterous females had wider heads and longer bodies than the macropterous ones, while at 25°C the brachypterous females had narrower heads and shorter bodies than the macropterous.
Wing Polymorphism of Chrysanthemum Thrips

Fig. 3. Frequency distribution of relative fore wing length to head width in *T. nigropilatus* females reared under 4 temperature and photoperiod conditions from egg to adult eclosion (females with abnormal wings are excluded).

ones (Table 2). The ratio of mesonotal width to head width tended to be lower in the brachypterous females than in the macropterous ones (Table 2).

*Longevity and fecundity of females*

All 35 female parents used were macropterous. Under each of the 4 conditions no significant difference was found in the longevity, fecundity, oviposition period, pre- and postoviposition periods between the virgin and once-mated females (MANN-WHITNEY *U*-test, *p* > 0.05). Therefore, data of the virgin and once-mated females were combined (Table 3 and Fig. 4). Longevity did not significantly differ between 15L–9D and 10L–14D at either temperature (MANN-WHITNEY *U*-test, *p* > 0.05). At 18°C the total number of eggs laid per female under 10L–14D was significantly lower than that under 15L–9D (MANN-WHITNEY *U*-test, *p* < 0.05). This difference resulted from lower oviposition rate (Fig. 4) and shorter oviposition period under 10L–14D (MANN-WHITNEY *U*-test, *p* < 0.05; a single female under 10L–14D that laid 1 egg 68 days
Table 2. Biometric data on macropterous and brachypterous females of *T. nigropilosus* reared under 4 temperature and photoperiod conditions

<table>
<thead>
<tr>
<th>Temperature and photoperiod</th>
<th>Wing form</th>
<th>n</th>
<th>Absolute measurements (mm)</th>
<th>Ratios to head width</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Head width (mean±S.E.)</td>
<td>Body length (mean±S.E.)</td>
</tr>
<tr>
<td>18°C, 15L−9D</td>
<td>Macropterous</td>
<td>33</td>
<td>0.155±0.001 d</td>
<td>1.316±0.013 c</td>
</tr>
<tr>
<td>18°C, 10L−14D</td>
<td>Brachypterous</td>
<td>33</td>
<td>0.161±0.001 c</td>
<td>1.392±0.010 d</td>
</tr>
<tr>
<td>25°C, 15L−9D</td>
<td>Macropterous</td>
<td>33</td>
<td>0.150±0.001 c</td>
<td>1.275±0.011 b</td>
</tr>
<tr>
<td>25°C, 10L−14D</td>
<td>Macropterous</td>
<td>33</td>
<td>0.148±0.001 b</td>
<td>1.266±0.009 b</td>
</tr>
<tr>
<td>25°C, 10L−14D</td>
<td>Brachypterous</td>
<td>33</td>
<td>0.145±0.001 a</td>
<td>1.186±0.017 a</td>
</tr>
</tbody>
</table>

Values followed by different letters are significantly different at the 5% level by Duncan's multiple range test.
Table 3. Longevity in days and fecundity of macropterous females of *T. nigropilous*,
which were transferred from 18°C and 15L–9D to given temperature and
photoperiod conditions at the pupal stage

<table>
<thead>
<tr>
<th>Temperature and</th>
<th>n</th>
<th>Preoviposition</th>
<th>Oviposition</th>
<th>Postoviposition</th>
<th>Total adult</th>
<th>No. of eggs laid</th>
</tr>
</thead>
<tbody>
<tr>
<td>photoperiod</td>
<td></td>
<td>period</td>
<td>period</td>
<td>period</td>
<td>longevity</td>
<td>per female</td>
</tr>
<tr>
<td>18°C, 15L–9D</td>
<td>11</td>
<td>1.5 (1–2)</td>
<td>41.7 (18–54)</td>
<td>10.1 (1–48)</td>
<td>53.3 (37–67)</td>
<td>208.5 (55–293)</td>
</tr>
<tr>
<td>18°C, 10L–14D</td>
<td>8</td>
<td>2.4 (2–3)</td>
<td>33.8 (26–66)</td>
<td>34.5 (8–53)</td>
<td>70.8 (43–86)</td>
<td>98.5 (79–140)</td>
</tr>
<tr>
<td>25°C, 15L–9D</td>
<td>8</td>
<td>0.6 (0–1)</td>
<td>23.5 (11–32)</td>
<td>6.1 (2–13)</td>
<td>30.0 (23–40)</td>
<td>180.4 (82–265)</td>
</tr>
<tr>
<td>25°C, 10L–14D</td>
<td>8</td>
<td>0.8 (0–1)</td>
<td>29.3 (19–33)</td>
<td>2.9 (0–9)</td>
<td>32.9 (28–38)</td>
<td>180.5 (122–223)</td>
</tr>
</tbody>
</table>

Values are mean (min.–max.).

Fig. 4. Age-specific fecundity and survival rate of macropterous females in *T. nigropilous*,
which were transferred from 18°C and 15L–9D to given temperature and photoperiod condi-
tions at the pupal stage.

after adult eclosion was excluded from this analysis). At 25°C the total number of
eggs laid per female under 15L–9D and that under 10L–14D did not differ (MANN-
WHITNEY *U*-test, *p* > 0.05). Both pre- and postoviposition periods were significantly
longer under 10L–14D than under 15L–9D at 18°C (MANN-WHITNEY *U*-test, *p* < 0.05),
but not so at 25°C (*p* > 0.05).
DISCUSSION

In many cosmopolitan species of thrips the sex ratio differs among different regions (Lewis, 1973). *T. nigropilosus* is widespread throughout northern temperate regions and known to reproduce thelytokously (Morison, 1947); no male is recorded, at least for the British Isles and New Zealand (Morison, 1957; Walker and Michaux, 1989). In the present experiments, however, only males developed from the eggs laid by virgin females, while both sexes developed from the eggs laid by once-mated females (Table 1). This result indicates that *T. nigropilosus* reproduces arrhenotokously in the Kyoto population.

The macropterus form occurred in *T. nigropilosus* females reared under 15L–9D at 18°C and 25°C (except 1 intermediate form at 18°C), whereas the brachypterous form occurred at 18°C and 10L–14D. Various wing forms including macropterus, brachypterous and intermediate forms occurred at 25°C and 10L–14D. These results suggest that long-day photoperiods induce the development of macropterus form, that short-day induces the development of brachypterous form and that high temperatures partly inhibit the effect of short-day photoperiods.

Köppä (1970) and Kamm (1972) demonstrated that the proportion of brachypterous forms increased under short-day photoperiods in *Anaphothrips obscurus* (Müller) females. Kamm (1972) indicated that temperature had no effect on wing form determination in this thrips. Seasonal variation in wing form frequency occurs in some Thripidae. In *A. obscurus, Thrips angusticeps Uzel, T. dilatatus Uzel, T. discolor Haliday, Frankliniella fusca (Hinds), F. iridis (Watson), Platythrips tunicatus (Haliday) and Sericothrips abnormis (Karny)*, the proportion of brachypterous or apterous females to macropterus ones seems to be higher in cooler seasons (Köppä, 1969; Morison, 1970; Lewis, 1973; Mound et al., 1976; Ananthakrishnan, 1984). Short-day photoperiods and/or lower temperatures may induce wing reduction in females of these thrips.

In female *T. nigropilosus* with normal wings, the discontinuous variation of RWL suggests that the alternative of the macropterus and brachypterous forms in the developmental pathway is a threshold response to particular effectors. In intermediate form, RWL was continuously distributed, and most of the intermediate forms occurred under a high temperature and short-day photoperiod condition that produced both macropterous and brachypterous forms. These results intimate that intermediate form represents an intermediate state between the macropterus and brachypterous forms. In several insects, juvenile hormone (JH) acts to induce wing reduction (Hardie, 1980; Iwana and Tojo, 1986; Zera and Tiebel, 1988; 1989). A general hypothesis is that the apterous or brachypterous form is produced if the JH titer exceeds a critical threshold during a particular stage of development. Assuming that the wing form of female *T. nigropilosus* is controlled by a similar endocrine system as has been shown in other insects, an excess of JH may be induced by short-day, and high temperature may partly cancel the effect of short-day photostimulation. Perhaps under 25°C and 10L–14D the JH titer is near the critical threshold level where the switching mechanism provides “on” and “off” irregularly. This must have resulted in a mixed response involving various types of intermediate form. Intermediate forms of female *T. nigropilosus* in fact emerge under natural conditions in Kyoto in late April and late October when brachypterous form production finishes and initiates, respectively (Nakao, unpublished data).
In some insects, wing reductions are related to simplification of thorax and an increase in body weight or body length that results in increased reproductive output (Harrison, 1980; Fujisaki, 1986; Denno et al., 1989). In female T. nigropilosus the wing reduction was not always accompanied by an increase in body size (Table 2). On the other hand, the macropterus female tended to have a larger mesothorax than the brachypterous one (Table 2). This seems to represent the difference in the extent of flight muscle developments between them.

Short-day photoperiod and low or moderate temperature induce reproductive diapause in females of A. obscurus and Frankliniella intonsa (Trybom) (Kamm, 1972; Murai, 1987). In the present study, female adults under short-day at 18°C had a shorter oviposition period and lower fecundity than those under long-day photoperiod. However, such differences did not occur at 25°C. In addition, at 18°C the survival rate is likely to decrease slower under short-day than under long-day, but not so at 25°C (Fig. 4). These results suggest that short-day photoperiod and moderate temperature partly suppress the reproduction of female T. nigropilosus. It is possible that female T. nigropilosus developing under short-day and low or moderate temperature during egg and larval stages enter reproductive diapause as in A. obscurus and F. intonsa.

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* The paper marked with asterisk was cited from ANANTHAKRISHNAN (1990).