Movement Behavior of the Pine Needle Gall Midge (Diptera: Cecidomyiidae)

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Abstract

The movement behavior of the pine needle gall midge (Thecodiplosis japonensis Uchida Et Inouye (Diptera: Cecidomyiidae)), an invasive species in China, was determined by using a tethered flight technique and digital videography in the laboratory. The flight distance, duration, and speed of females were compared at different ages (2–10 h) and ambient temperatures (17, 21, 26, and 30°C). Female flight distance and duration at 26°C were significantly greater than those at 17°C and 21°C. The age of T. japonensis did not significantly affect the three flight characteristics. For females at 2–10 h of age at 26°C and 70% RH, the maximum flight distance was 667.59 m; the longest flight time was 6,222.34 s; and the fastest flight speed was 0.44 m·s⁻¹. For larvae wetted with water, the highest jump was 5.7 cm; the longest jump was 9.6 cm; and the greatest distance moved in 5 min was 27.13 cm, which showed that the active dispersal potential of larvae was very low.

Keywords: pine needle gall midge, flight capacity, tethered flight, temperature, age

Dispersal is a fundamental behavior in the life history and ecology of insects; it is important in avoiding natural enemies, searching for food, securing mates, and finding suitable habitat. Dispersal is also of central importance to population biology, behavioral ecology, and conservation (Rudd and McEvoy 1996). Therefore, insect dispersal has a key role in predicting population spread, improving eradication surveys, and successfully managing of destructive pest populations (Mazzi and Dorn 2012, Rafter et al. 2018). In addition, an understanding of the dispersal behavior of natural enemies can assist in developing effective augmentative release strategies and in assessing the spread and potential nontarget effects of an introduced natural enemy (Smith 1996, Orr et al. 2000). Dispersal (i.e., the spatial redistribution of populations) and movement (i.e., the spatial behavior of individuals) are closely related, because the random movement of individuals, in part, underlies the redistribution of a population in space (Turchin 1998, Nathan et al. 2008, Schellhorn et al. 2014). Insects move by walking or flying, and their movements are usually influenced by many intrinsic (physiological) and extrinsic (environmental) factors, such as temperature, wind, and photoperiod (Taylor 1963, Walters and Dixon 1984, McManus 1988, Roderick and Caldwell 1992, Nathan et al. 2008, Baguette et al. 2014).

In this study, the focus was on the movement behavior of the pine needle gall midge (Thecodiplosis japonensis). The pine needle gall midge is native to Japan and has been one of the most important pest of Pinus densiflora Siebold & Zucc. and P. thunbergii Parl. in Korea since the 1920s (Luo 1993, Park and Chung 2006). In 2016, the pine needle gall midge was first recorded in Huangdao, China, and found to attack three species of pine in the field: P. thunbergii, P. densiflora, and Pinus tabuliformis Carrière. In Korea, the pine needle gall midge has one generation per year. The larvae overwinter and then pulate in the soil in early May, with adults beginning to emerge at the end of May. Adults have a short life span of approximately 1 d, and therefore mate soon after emergence. After mating, females lay eggs between a pair of developing needles of the current-year shoots, with eggs hatching approximately 1 wk later. The newly hatched larvae creep to the leaf sheath and feed at the base of needles where they begin to form galls (Nam and Choi 2014). The growth of attacked needle pairs slow down substantially beginning in early July, in contrast to needle pairs that are not attacked. In winter, the attacked needles gradually wither and drop prematurely. Losses are appreciable after 2 and 3 yr of infestation, and seriously infested trees (more than 50% of needles on the current-year shoots are attacked) will wither and die (Soné 1986).

According to available data, the dispersion of the pine needle gall midge is very rapid, and the damage caused is very heavy. The pine needle gall midge was introduced into Korea from Japan in the 1920s and its spread has been described since 1929 (Choi et al. 2011). By 1960, the pine needle gall midge was found throughout Korea. In 1990, the distribution expanded into Cheju Island off the southern coast of South Korea (CABI 2019). Since 1972, approximately 300,000–400,000 ha of P. thunbergii

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forest have been damaged each year by *T. japonensis* in Korea (Park et al. 1985, Lee and Lee 1994). However, the flight capabilities of the pine needle gall midge have not been quantified. To tag adults and determine their flight range and dispersal, a technique was developed in South Korea in which the adults and larvae were labeled with radioactive phosphorus and calcium; however, the experiment failed (Kwon et al. 1978). Air speed is one factor that clearly affects the dispersal of pine needle gall midge adults. Ko and Lee (1975) found that few of the midges initiate flight when wind speeds are greater than that of a light breeze (2.8 m·s⁻¹). Those insects already in flight are blown in the direction of the wind, whereas there is little or no flight in a moderate breeze (6.1 m·s⁻¹).

*Pinus thunbergii*, *P. densiflora*, and *P. tabuliformis*, the three main hosts of the pine needle gall midge in the field, are widely cultivated for timber production and landscape use in China (Li et al. 2015, Ren et al. 2018). Although the pine needle gall midge is currently recorded only in the Huangdao area, it undoubtedly poses a serious threat to pine forest in China. Thus, determining the active dispersion ability of the pine needle gall midge is essential to develop control strategies and to identify new areas of potential invasion. Flying and crawling are the primary modes of movement in the life history of insects. Therefore, the current study was designed to answer the following general questions: 1) How long can *T. japonensis* fly? 2) What is the capacity of *T. japonensis* larvae for movement? 3) What are the effects of age and ambient temperature on flight behavior?

Materials and Methods

Insects

Newly emerged adults were collected by using five emergence traps. The emergence traps were composed of an opaque plastic cage (40 × 40 × 40 cm) and a white transparent packing box (volume, 60 ml; height, 100 cm; width, 4.2 cm). In a seriously damaged pure stand of *P. thunbergii* in Huangdao District, Qingdao City, Shandong province, China (35°58′14″N, 120°11′28″E), in late-V-19, soil (30 cm × 30 cm, to a depth of 10 cm) in which the pine needle gall midge pupated was collected in a plastic bag. The soil was spread evenly on the bottom of a cage in an insect rearing room at 25 ± 1.3°C and 45 ± 10% RH under 16:8 (L:D) h photoperiod. An opaque plastic cover that had a hole (diameter, 2 cm) in the center sealed the top of the cage. A white transparent packing box (volume, 120 ml; height, 10 cm; width, 4.2 cm) was used to cover the hole and collect the newly emerged adults. When an adult flew into the box, the box was replaced, and thus, each box contained one adult.

Longevity of Adults

The newly emerged adults were kept individually in the white transparent packing boxes, and their survival was observed every 8 h in the field where they emerged from the soil. A midge was considered dead when none of its appendages moved after each was touched with a brush. The dead adults were sexed under a microscope (the females have a medium-length ovipositor of approximately 0.5 mm). The ambient temperature was 23–27°C, and the RH was 50–82%. No food or water was supplied during the tests. Within 5 d, 167 males and 100 females emerged. Thirty males and 30 females were randomly selected, and their time of death was recorded on the basis of hourly observation.

Determination of Flight Characteristics

Pretreatment of adults

With a pair of tweezers, a cotton ball impregnated with anhydrous ether was inserted into a white transparent packing box with an adult. The cotton ball was removed when the adult was anesthetized (no appendage movement, approximately 15–20 s). An anesthetized adult was quickly placed on a piece of white filter paper, and the legs, wings, and abdomen were adjusted with pointed tweezers to expose its pronotum. Females were selected under a stereoscopic for use in the flight mill assay.

Flight mill assay

A flight mill system was used to measure the flight capacity of *T. japonensis* females of different ages at different ambient temperatures, following the methods of Lu et al. (2019). The system consisted of a sensor and data acquisition board, a mill, and computer software. In total, 26 individual flight mills were linked to a recorder, which was connected to a computer. Each flight mill was composed of a 10-cm copper thread placed between two small magnets (Fig. 1). One anesthetized adult was attached to the lower surface of the copper thread with a droplet of 502 cyanacrylate adhesive glue (produced by Jinhun Adhesive Co., Ltd, Xiushui County, Jiujiang City, Jiangxi province, China) applied quickly to the pronotum. After the adult was attached, the direction of the copper thread was adjusted in order to keep the flying direction of the insect perpendicular to the copper thread. For each gall midge, the times of flight initiation and cessation and the number of mill revolutions in consecutive 5-s intervals were recorded. Flights interrupted by a >1-min interval were considered separate flights. The number of mill revolutions over a given period was used to compute flight distance, speed, and duration for each gall midge. All trials were performed in a climate-controlled chamber in VI-19.

In the first trial, the effect of age in hours on the flight performance of *T. japonensis* adults was characterized. Flight was recorded at 2, 6, and 10 h after adult emergence, with the ages of tested individuals being 0–2, 2–6, and 6–10 h old, respectively. For each hour age group, 25 adults were tested. The tests were conducted for 3 h at 26°C, 70% RH, and with a 16:8 (L:D) h photoperiod.

In the second trial, the effect of temperature on *T. japonensis* flight capacity was examined by using 2- to 6-old adults at 17, 21, 2, and 30°C. For each treatment, 25 adults were tested. The tests were conducted for 24 h (based on the results of adults longevity) under the same conditions as in the first trial.

Free-Flight Assay

The free-flight performance of newly emerging *T. japonensis* adults was surveyed by using three emergence traps. A trap was composed of a round, dark plastic basin (21.5 cm in diameter) topped by a clear plastic cylinder (diameter, 3 cm; length, 100 cm) whose top was covered with fine-mesh gauze (Fig. 2). The distance of each
The test conditions were the same as those given above. Timings of 30 individuals were analyzed manually on a computer.

Another test was conducted in order to determine the height that larvae could jump. Before observations, a piece of graph paper was attached to the back of a cuboid transparent glass insect tank (5 x 3 x 10 cm). In front of the tank, a digital video camera was concentrated horizontally on the tank. Fifty larvae were placed on the bottom of the tank, in which water was sufficiently deep to soak up onto the bodies of the larvae. The activity tracks of each larva were recorded using the video camera. Observations continued until no larvae jumped in 1 h. The horizontal distance between the camera lens and the graph paper was 0.45 m, and the observation area was 125 cm² (9 cm in length, 14 cm in width). Uninterrupted power was supplied during the experiment. Data in the memory card were analyzed manually on the computer, including distance moved, time, and duration for each larva. In total, 30 individuals were tested and the tests were conducted at 26°C, 70% RH, and under completely enclosed conditions.

Effect of Different Temperatures on the Flying Ability

In the following analysis of the effect of temperature on the flying ability of the pine needle gall midge, reliable data were used from 11 tests at 17°C, 10 at 21°C, 10 at 26°C, and 10 at 30°C.

The average flight distance of 6-h-old females was 34.89 m at 17°C, 48.98 m at 21°C, 185.86 m at 26°C, and 102.86 m at 30°C (Fig. 4). However, there was no significant difference in flight distance among the four temperatures (F = 2.598; df = 3, 37; P = 0.067).

The flight duration of the pine needle gall midge was significantly different at the four temperatures (F = 4.964; df = 3, 37; P = 0.005). At 26°C, the average flight duration was 4,806.26 s; the duration was significantly lower at 17°C (824.74 s; P = 0.001), 21°C (1,840.38 s; P = 0.014), and 30°C (1,230.03 s; P = 0.004) (Fig. 5).

The flight speed was not significantly different at the different temperatures (F = 1.592; df = 3, 37; P = 0.208). The mean flight speed was 0.11 m s⁻¹ in 3 h of tethered flight (Fig. 6).

Effect of Age on Flight Capacity

For each age group of females (0–2, 2–6, and 6–10 h), reliable data from 10 tests were used in the following analysis.

Among the different ages of the pine needle gall midge, there were no significant differences in flight distance (F = 0.18; df = 2, 27; P = 0.835), duration (F = 0.27; df = 2, 27; P = 0.767), or speed (F = 0.80; df = 2, 27; P = 0.462) (Table 1). The mean flight distance was 192.71 m in 24 h of tethered flight; the mean flight duration was 2,035.48 s; and the mean flight speed was 0.16 m s⁻¹. The maximum flight distance was 667.59 m; the longest flight time was 6,222.34 s; and the fastest flight speed was 0.44 m s⁻¹.

Free-Flight Performance

Sixteen free flights of newly emerged adults were observed. The longest free-flight distance, from the point of takeoff to the point of landing, was 60.90 cm. In a distance of 1 m, T. japonensis adults took off an average of 4.88 times.

Movement Ability of Larvae

In this test, without moisture on them, larvae moved only a very short distance by rolling over. However, when their body surface was wet, larvae would crawl or jump, and the maximum crawling distance within 5 min was 4.3 cm. The average height of a jump was 1.45 ± 0.18 cm (mean ± SD), and the average distance jumped was

Results

Longevity of Adults

The longevity of females was 32.13 ± 2.92 h (mean ± SD) and that of males was 22.80 ± 1.70 h (mean ± SD), with females living significantly longer than males (F = 7.660; df = 1, 58; P = 0.008). Of the females that emerged on the same day, 16.75% survived for <1 d, whereas 39.75% survived for 1–2 d (Fig. 3). The longevity of approximately half the males was <1 d, whereas 34% survived for 1–2 d (Fig. 3). Of all adults (females + males), 23.75% lived longer than 2 d (Fig. 3).

Movement Ability of Larvae

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4.17 ± 0.39 cm. The highest jump was 5.7 cm, the farthest jump was 9.6 cm, and the farthest distance moved was 27.13 cm.

**Discussion**

In this study, more than 80% of females and more than 50% of males of *T. japonensis* lived longer than 1 d, which is in contrast to the conclusion of Soné (1987) who reported that the life span of males and females was typically only 1 d in Kyoto, Japan. This difference in longevity might be due to different test conditions. In this study, the results were obtained through field observations, and unfortunately, the experimental conditions of Soné (1987) were not considered. However, in preliminary laboratory observations in the laboratory (25°C, 60% RH), the life span of *T. japonensis* adults was less than 24 h (unpublished).

In the flight mill experiments, the fastest flying speed for *T. japonensis* was 0.44 m·s⁻¹ (26.4 m·min⁻¹), which is relatively slow compared with other dipterans. For example, the flight speed is 67.2 m·min⁻¹ for *Aedes gambiae* Giles and 68.4 m·min⁻¹ for *Culex thalassius* Theobald (Culicidae) (Yukawa et al. 2019). Based on the fastest flight speed and the longest flight time (6,222.34 s), the theoretical flight distance of the pine needle gall midge could reach 2.74 km within 24 h. Because *T. japonensis* is univoltine, this distance could also be regarded as the maximum that adults could achieve by actively flight in a year. In the current study, the maximum flight distance of 2- to 10-h-old adults was...
The flight behavior of \textit{Sitodiplosis mosellana} is similar to the normal field conditions when adults emerge (Doane et al. 2019). The best temperature for flight of \textit{Corythucha ciliata} are significantly different at temperatures below 8°C, and if flight is achieved it is 12–22°C (Cheng et al. 2002). It is difficult for this aphid to take off at temperatures below 8°C, and if flight is achieved then flight time is shortened considerably (Cheng et al. 2002). The flight distances of \textit{Corythucha ciliata} are significantly different at different temperatures, with the strongest flight capacity at 25°C (Lu et al. 2019). The best temperature for flight of \textit{Sitodiplosis mosellana} is similar to the normal field conditions when adults emerge (Doane and Olfert 2008). The flight behavior of \textit{T. japonensis} adults was also affected by temperature, and they were most active at 26°C, with the average flight distance and duration both longer than those at 17, 21, and 30°C. This optimum temperature for flight is slightly higher than the optimum temperatures of overwintered larvae (22.3°C) and pupae (24.0°C) (Choi and Park 2012).

Movement also varies depending on insect age (Rudd and McEvoy 1996). One-day-old diamond back moths (\textit{Plutella xylostella}) are the weakest fliers, whereas 3-d-old moths are strongest, with 10,546 m the longest flight distance (Wei et al. 2013). The flight activity of 1- and 2-d-old beet webworms (\textit{Loxostege sticticalis}) is significantly less than that of 4- and 5-d-old moths (Tang et al. 2016). However, age within 12 h did not significantly affect the flight performance of \textit{T. japonensis} in this study. This absence of an age effect may be an adaptation to the short life span of \textit{T. japonensis} (more than 75% of adults survived <2 d; Fig. 3).

Mature \textit{T. japonensis} larvae leave the galls and drop to the ground from November to March of the following year (CABI 2019). These larvae crawl into the litter layer or the surface soil, where most spin cocoons (Ko 1982). According to Hyun (1982), soil moisture is the most important factor influencing the mortality of larvae hibernating in the soil. In the current study, moisture was also the key factor that determined larval movement. However, the distance that larvae moved was determined on a smooth surface in this study, and therefore, the influence of the soil environment on the movement of larvae needs to be studied further.

### Conclusions

The longevity of pine needle gall midge adults was relatively short, and only 23.75% of adults lived longer than 2 d, with the longest life spans less than 4 d. Because \textit{T. japonensis} is a univoltine insect, the short life span limits the active dispersal distance. In addition, the environmental temperature was also an important factor limiting adult flight behavior. Female flight distance and duration at 26°C were significantly longer than those at 17°C and 21°C. The age of \textit{T. japonensis} had no significant effect on flight distance, duration, or speed. The active dispersal of larvae that relied on crawling and jumping was greater than that of larvae that only rolled over. A primary measure to control the pine needle gall midge could be the timely springtime treatment of soil that is near attacked host trees.

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| Ages (hours) | Flight distance (m) | Flight velocity (m/s) | Flight duration (s) |
|-------------|---------------------|----------------------|---------------------|
| 2           | 219.31 ± 71.87a     | 0.16 ± 0.02a         | 2,337.69 ± 581.35a  |
| 6           | 190.66 ± 57.38a     | 0.19 ± 0.03a         | 1,761.81 ± 501.73a  |
| 10          | 168.14 ± 49.47a     | 0.14 ± 0.02a         | 2,006.93 ± 586.52a  |

\( n = 10 \) for each age. The same lowercase letters for each flight characteristic indicate no significant differences among ages (\( P > 0.05 \)).
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