Spatio-Temporal Distribution of *Ceratothripoides claratris* (Thysanoptera: Thripidae) on Tomatoes in Thailand

DAMMINI W.T.S. PREMACHANDRA,[1, 2] CHRISTIAN BORGEMEISTER,[1, 3] MAMOUDOU SÉTAMOU,[4] THOMAS ACHILLES,[1] AND HANS-MICHAEL POEHLING[1]

Environ. Entomol. 34(4): 883–890 (2005)

ABSTRACT *Ceratothripoides claratris* Shumsher is one of the most important thrips pest of tomatoes in central Thailand. Hence we conducted studies to determine the intra- and inter-plant distribution of *C. claratris* on tomatoes in two types of greenhouses, i.e., open-plastic and closed net house. The experiments were conducted on the campus of the Asian Institute of Technology in Bangkok, Thailand. Both adults and larvae of *C. claratris* showed foliage-biased distribution. Sex ratios of adult *C. claratris* did not significantly differ on flowers and leaves, whereas on fruits males significantly outnumbered females. On flowers, no diurnal periodicity of occurrence of *C. claratris* was detected. Generally, thrips infestation commenced in the lower parts of the tomato plants and gradually spread to the higher strata of the plants. Depending on the greenhouse type and the stem system thrips infestation differed significantly over time in the lower but not in the uppermost strata of the plants. In the net house, infestations of *C. claratris* commenced one week after planting of the tomato seedlings. Soon after the peak in infestations, thrips numbers dramatically decreased. Estimates of Taylor's power showed that *C. claratris* had an aggregated distribution pattern on the foliage of tomato plants. The importance of these findings for future monitoring programs of *C. claratris* infestations on tomatoes is discussed.

KEY WORDS *Lycopersicon esculentum*, thrips, greenhouses, density, strata, Taylor's power law

Ceratothripoides claratris Shumsher (Thysanoptera: Thripidae) is the most prevalent thrips species attacking field- and greenhouse-grown tomatoes *Lycopersicon esculentum* Mill. (Solanaceae) in Thailand (Murai et al. 2000, Rodmui 2002, Premachandra et al. 2004). Larvae and adults of *C. claratris* damage tomatoes by voraciously feeding on the foliage, stems and fruits; in addition, oviposition by females on fruits leads to scarification and malformation of tomatoes (Premachandra et al. 2004). Moreover, *C. claratris* is vectoring a yet to be identified tospovirus of the serogroup IV, serologically and genetically closely resembling the recently described Capsicum Chlorosis Virus (CaCV) (McMichael et al. 2002), which causes severe losses in tomato production in central and northern Thailand (D. Premachandra, unpublished data). Hence, the development of integrated management strategies against *C. claratris* is vital. Information on the spatio-temporal distribution of a pest on a given host plant provides basic information for developing reliable and cost-effective sampling schemes that are a cornerstone in future integrated management programs (IPMs) against *C. claratris.* In addition, population density estimates are essential for determining the precise timing of control measures in IPM programs, as well as to assess their effectiveness (Reitz 2002). To date, little is known about the spatial and temporal distribution of *C. claratris* and its population dynamics on tomatoes. The objectives of this study were therefore to (1) investigate the intra- and interplant distribution of *C. claratris* on tomatoes and (2) to record thrips population development over time under greenhouse conditions in central Thailand. This research was conducted as part of a project that aims at developing sustainable vegetable production systems under protected cultivation in the humid tropics.

Materials and Methods

Greenhouses and Plants

The trials were conducted in two 200-m^2 big greenhouses, located at the campus of the Asian Institute of Technology (AIT), in Bangkok, Thailand. One was an open side-wall plastic house (polythene plastic, 200 micron UV-stabilized polyfilm; Ludvig Svensson, Kinna, Sweden) with an opening of 50–200 cm above the ground level. The second was a closed net house (Econet M, pore size 0.18 mm; Ludvig Swensson) equipped with two exhaust fans (550 m^3/min, 1.5 HP, 960 rpm; Sriroz Co., Maharushtra, India) at the front side of the net house. The fans were operated by a computerized control system that automatically

[1] Institute of Plant Diseases and Plant Protection, University of Hanover, Herrenhäuser Str. 2, 30419 Hanover, Germany.
[2] University of Ruhuna, Matara, Sri Lanka.
[3] Corresponding author, e-mail: borgemeister@ipp.uni-hannover.de.
[4] ARS-USDA Beneficial Insects Research Unit, 2413 E Highway 83 Bldg. 200, Weslaco, TX 78596.

0046-225X/05/0883–0890$04.00/0

switched on one fan when temperatures inside the net house exceeded 25°C and the second one at temperatures >30°C. The climate in the two greenhouses was monitored using a data logging system (ITG data logger, University of Hanover, Hanover, Germany). During the trials, mean temperatures and relative humidities were 28–30°C and 70–80% and 26–28°C and 60–80% in the closed and open house, respectively. The total planting area of each greenhouse was 160 m^2. Three-week-old tomato seedlings (cultivar King Kong II, an indeterminate variety) were planted in plastic pots (30 by 25 cm) filled with a commercial growing substrate composed of clay, sand, and silt in proportions of 31, 30, and 39%, respectively, and 29% of organic matter. Pots were placed on a black ground plastic cover (Chaisiri Nylon Canvas Factory, Bangkok, Thailand) and arranged in six rows with no interpot distances within a row. The distance between rows was 160 cm. Plants were irrigated and fertilized with a drip irrigation system controlled by solar light integral. Tomato plants were irrigated and fertilized seven to nine times per day (2.5 liters/d). The fertilizers [Hakaphos (N-P-K), 2.5 kg/100 liters; COMPO Austria, and Bai-plus (calcium), 1.8 kg/1001; Bayer, Bangkok, Thailand] were injected to the irrigation system with mechanical injectors (DI 16; Dosatron, Bordeaux, France). Tomato plants were supported by ropes that were fixed to the structure of the greenhouse.

Experiment 1: Intraplant Distribution of *C. claratris*

Distribution on Different Plant Parts. In the first trial, the distribution of *C. claratris* on leaves, buds, fruits, and flowers of tomatoes were determined in the open and net house using destructive sampling techniques. The aim of this experiment was to select the most consistent plant parts for subsequent monitoring and sampling. In this experiment, tomato plants were maintained in a single-stem system at a density of 360 plants per house. In both houses, plants were naturally colonized by *C. claratris.* Previous studies showed that *C. claratris* is the predominant thrips species on tomatoes in the greenhouses on the AIT campus (Premachandra et al. 2004). Data were recorded 8 wk after planting (WAP) of the tomato seedlings into the greenhouses. Fully expanded nonsenescent leaves, fully opened nonsenescent individual flowers, terminal buds (length ≈5 cm), and fruits (both immature and ripen) were sampled in each house from 30 randomly selected tomato plants. Plants in the edge rows were excluded from sampling. To minimize the potential diurnal variations in thrips distribution, all data were gathered between 0700 and 0800 hours. For flowers, two additional samplings were made at noon and between 1600 and 1800 hours to determine any potential diurnal periodicity of thrips occurrence. All samples were separately collected using self-sealing plastic bags by pulling them over leaves, buds, or flowers and breaking the stem and immediately sealing the bag to avoid any losses of thrips. Thereafter, the sealed bags were transported to the laboratory. Tomato leaves, buds, and fruits were washed three times for ≈10 s in a plastic box (15 by 9 cm) containing 250 ml of 70% ethanol. Subsequently, the thrips-containing solution was poured into a conical flask (200 ml), shook thoroughly, and stored for 30 min for settling. Thereafter, the supernatant was gently decanted to 50 ml, the remaining suspension was poured onto a counting plate, and the thrips were counted under a stereomicroscope. For flowers, the petals were carefully dissected and transferred into a petri dish (8.5 by 1.5 cm) containing 70% ethanol to extract the thrips. Thereafter, they were also counted under a stereomicroscope. Thrips that remained in the plastic bags were also included for the counts.

Distribution of *C. claratris* on Leaves with Respect to Strata. A second trial was conducted to determine the vertical distribution of thrips on leaves. Data were recorded only on leaves because *C. claratris* densities in the previous experiment were always higher on leaves than on other plant parts (see the Results section). For this, the plants were divided into three different strata, i.e., lower (0–50 cm), middle (51–100 cm), and upper (>101 cm), above the soil surface. At least 10 plants were randomly selected, and fully expanded nonsenescent leaves were taken from each stratum. Thrips counts were made as previously described.

Experiment 2: Inter- and Intraplant Distribution of *C. claratris* Over Time

Presence-Absence Sampling. This trial was conducted to investigate the vertical distribution pattern of *C. claratris* over time using presence-absence sampling techniques. The trial was carried out from June to September 2002 in an open and closed net house with a plant density of 360 tomatoes (cultivar King Kong II) arranged in six rows. Tomato plants were maintained in single- (only one branch) and double-stem systems (two branches), arranged in an alternating manner (i.e., a single-stem row was followed by a double-stem one) and occupying a total of four rows (60 plants/row). Plants in the two edge rows were cultivated in a single-stem manner. Forty plants were randomly selected in each stem system, i.e., 20 plants per row, for weekly monitoring. Monitoring commenced 1 WAP of tomato seedlings into the greenhouse and continued for 10 consecutive wk. On each monitoring date, the total number of leaves and the number of thrips-damaged leaves, i.e., leaves showing thrips-feeding damage, were recorded with respect to the four different plant strata, i.e., strata 1 (0–50 cm), 2 (51–100 cm), 3 (101–150 cm), and 4 (>151 cm) above the soil surface. In the double-stem system, the second stem emerged after the fourth WAP, and thus data collection commenced here from fourth WAP onward in the 51–100 cm stratum.

Presence-Absence Sampling with Density Estimations. Two trials were conducted. The first trial was conducted from January to March 2003 in a closed-net house that was equally partitioned with screens (Econet T, pore size 0.05 mm; Ludvig Swensson) into two

Table 1. Mean no. ± SE of *C. claratris* (adults and larvae) recorded on different plant parts of tomatoes in an open and closed greenhouse

Plant structure	Mean ± SE no. of thrips					
	Closed house (net)			Open house		
	Adults	Larvae	Total	Adults	Larvae	Total
Buds	0.00 ± 0.00c	0.00 ± 0.00b	0.00 ± 0.00b	0.00 ± 0.00b	0.00 ± 0.00b	0.00 ± 0.00c
Flowers	1.14 ± 0.20c	0.00 ± 0.00b	1.14 ± 0.20b	0.55 ± 0.12b	0.00 ± 0.00b	0.55 ± 0.12c
Fruits	5.40 ± 0.50	2.07 ± 0.61b	7.47 ± 0.74b	1.78 ± 0.24b	0.63 ± 0.19b	2.41 ± 0.36b
Leaves	8.83 ± 1.28a	27.93 ± 5.67a	36.76 ± 6.44a	3.43 ± 0.26a	8.30 ± 1.34a	10.73 ± 1.70a

For each type of greenhouse, means followed by the same letter in columns indicate no significant differences ($P = 0.05$, LSD multiple range test; SAS Institute 1999). In both house types, significant differences were recorded for thrips numbers on flowers (closed house: $t = 5.59$; df = 42; $P < 0.0001$; open house: $t = 4.64$, df = 39; $P < 0.0001$), fruits (closed house: $t = 4.21$; df = 58; $P < 0.0001$; open house: $t = 3.77$; df = 100; $P < 0.0003$), and leaves (closed house: t = −4.14; df = 30.9; $P < 0.0025$; open house: $t = -4.14$; df = 35.6; $P < 0.0002$).

partitions. Both presence-absence sampling and density estimations were performed in this trial over time. Three-week-old tomato seedlings ($n = 360$; cultivar King Kong II) were arranged in three rows (60 plants/row) per partition in a single stem system. Monitoring was initiated 1 WAP of tomato seedlings into the greenhouse and continued until the thrips population declined to low infestation levels, i.e., < 20% attacked leaves per plant. All plants, including the ones in the edge rows, were weekly monitored for thips infestation. Before the onset of the monitoring, the leaves were numbered in an ascending manner, starting from the cotyledons. On each monitoring date, the total number of leaves and the number of thrips-attacked leaves, together with their position on the stem, were recorded for each plant. In addition, density estimates were made on each sampling date using the above mentioned destructive sampling methods. At least 20 leaf samples were selected from each row in the two sections. Total number of *C. claratris* adults and larvae per leaf and the total leaf area of sampled leaves were recorded using a leaf area meter (LI-3100 area meter Licor Biosciences, Lincoln, NE).

The second trial was conducted from June to July 2004 also in a subdivided net house, and in this trial, only density fluctuations were investigated over time. However, only one-half of the house was used for the trial. Three-week-old tomato plants were transplanted into this section in three rows as described previously. Data were recorded for 7 consecutive wk starting from 1 WAP of the seedlings into the greenhouse. At least 10 plants per row were randomly selected, and one fully expanded nonsenescent randomly selected leaf per plant was destructively sampled and brought to the laboratory for counting the number of thrips.

Statistical Analysis

Initially, data were subjected to Shapiro-Wilk's test for normality and Brown and Forsythe's test for homogeneity of variance (SAS Institute 1999); whenever normality and variance homogeneity were violated, data were subjected to arcsine transformation. Thrips counts and sex ratios on different plant parts in the two types of greenhouses were compared using Student's *t*-test. In addition, analysis of variance (ANOVA) was performed for the comparison of thrips counts on different plant parts, diurnal periodicity on flowers, and leaf infestation levels among the different plant strata using the generalized linear models (GLM) procedure in SAS (SAS Institute 1999). Multivariate repeated measures ANOVA was used to determine the relationship between the percentage of thrips infestation and plant strata over time using mixed models (SAS Institute 1999). In case of significant interactions between factors, the effect of time, i.e., linear and quadratic trends, on thrips infestation in each plant strata was analyzed.

The spatial dispersion pattern of *C. claratris* on tomato leaves was determined by means of Taylor's power law (Taylor 1961), using combined larval and adult counts in the two partitions over four sampling occasions. Taylor's power law is defined as:

$$s^2 = am^b,$$

where s^2 and m are the sample variance and mean, respectively. Parameters a and b of the equations were derived by regressing $\log(s^2)$ on $\log(m)$. The intercept (a) is a sampling factor, and the slope (b) is a measure of dispersion of a species with $b > 1$, $b = 1$, and $b < 1$, indicating aggregated, random, and regular distribution, respectively (Taylor 1961). The slopes were compared with one using dummy variables in the regression analyses (SAS institute 1999).

The relationship between the percentage infested leaves and the thrips density was determined using regression analysis.

Results

Experiment 1: Intraplant Distribution

Distribution on Different Plant Structures. In the net house, adult and larval thrips densities were significantly higher on tomato leaves, flowers, and fruits than in the open house (flowers: $t = 2.50$, df = 67, $P < 0.0149$; leaves: $t = 3.97$, df = 32, $P < 0.0005$; fruits: $t = -6.13$, df = 43, $P < 0.0001$). In both houses, significantly higher thrips numbers were recorded on leaves than on other plant parts (Table 1). No thrips were

Table 2. Mean percentage ± SE infestation of *C. claratris* on four different strata of tomato plants, maintained in a single-stem system in a closed house over a period of 10 wk

Week	Mean percentage ± SE infestation			
	0–50 cm	51–100 cm	101–150 cm	>150 cm
1	48.18 ± 5.49	nl	nl	nl
2	65.67 ± 2.12	0.00 ± 0.00	nl	nl
3	80.89 ± 2.42	11.11 ± 1.82	nl	nl
4	84.55 ± 2.91	13.20 ± 2.86	nl	nl
5	91.11 ± 1.43	29.18 ± 4.63	nl	nl
6	97.11 ± 3.08	48.40 ± 5.30	11.67 ± 6.89	nl
7	100.00 ± 0.00	73.78 ± 6.10	38.14 ± 8.73	nl
8	100.00 ± 0.00	83.30 ± 4.57	47.58 ± 6.12	19.05 ± 14.29
9	100.00 ± 0.00	85.35 ± 3.70	58.31 ± 5.74	30.05 ± 6.97
10	100.00 ± 0.00	100.00 ± 0.00	93.31 ± 2.98	46.24 ± 8.06

Results of the multivariate repeated measure ANOVA for factors strata ($F = 238.22$, df = 3,200, $P < 0.0001$), weeks ($F = 99.853$, df = 9,705, $P < 0.0001$), and for strata × weeks ($F = 18.15$, df = 13,705, $P < 0.0001$) (SAS Institute 1999).

nl, no leaves.

Table 3. Mean percentage ± SE infestation of *C. claratris* on four different strata of tomato plants, maintained in a single-stem system in an open house over a period of 10 wk

Week	Mean percentage (± SE) thrips infestation			
	0–50 cm	51–100 cm	101–150 cm	>150 cm
1	43.28 ± 2.02	nl	nl	nl
2	63.45 ± 1.73	0.00 ± 0.00	nl	nl
3	81.09 ± 1.46	0.00 ± 0.00	nl	nl
4	96.71 ± 1.28	14.27 ± 3.14	nl	nl
5	100.00 ± 0.00	33.41 ± 5.14	nl	nl
6	100.00 ± 0.00	69.04 ± 3.02	19.49 ± 5.10	nl
7	100.00 ± 0.00	74.24 ± 2.20	53.98 ± 7.16	nl
8	100.00 ± 0.00	80.50 ± 3.28	65.91 ± 5.65	21.85 ± 7.37
9	100.00 ± 0.00	86.08 ± 2.21	67.13 ± 4.86	39.84 ± 7.79
10	100.00 ± 0.00	97.98 ± 1.39	83.86 ± 4.29	50.76 ± 5.71

Results of the multivariate repeated measure ANOVA for factors strata ($F = 313.17$, df = 3,176, $P < 0.0001$), weeks ($F = 233.54$, df = 9,894, $P < 0.0001$), and for strata × weeks ($F = 38.99$, df = 14,894, $P < 0.0001$) (SAS Institute 1999).

nl, no leaves.

detected on the buds in either type of greenhouse. Larvae predominated on the leaves, whereas adults outnumbered the larvae on fruits in both houses. On flowers, only adult *C. claratris* were found (Table 1). The sex ratio did not differ significantly on flowers and leaves (flowers net house: $t = -1.76$, df = 67, $P > 0.0823$; open house: $t = -0.51$, df = 77, $P > 0.6147$; leaves net house: $t = -0.46$, df = 56, $P > 0.6464$; open house: $t = 0.47$, df = 58, $P > 0.6376$), whereas on fruits, the proportion of male thrips was significantly higher in both houses (net house: $t = -6.07$, df = 58, $P < 0.0001$; open house: $t = -3.69$, df = 100, $P < 0.0004$). On flowers, no significant diurnal periodicity in adult thrips occurrence was found (net house: $F = 2.42$; df = 2,54, $P > 0.0989$; open house: $F = 1.99$; df = 2, 54, $P > 0.1450$).

Distribution of *C. claratris* on Leaves with Respect to Strata. Combined adult and larval thrips densities varied significantly among the different vertical strata of the tomato foliage, irrespective of the house (net house: $F = 70.94$, df = 2,26, $P < 0.0001$; open house: $F = 86.81$, df = 2, 27, $P < 0.0001$). The thrips density significantly decreased toward the apical point of the plants, and significantly greater numbers of adults and thrips larvae were recorded on the lower compared with the top stratum in both houses (net house: $F = 70.84$, df = 2,26, $P < 0.0001$; open house: $F = 86.81$, df = 2, 27, $P < 0.0001$). In general, both adult and larval counts declined toward the top of the tomato plants.

Experiment 2: Inter- and Intraplant Distribution of *C. claratris* Over Time

Presence-Absence Sampling. In both houses and in the single and double stem systems, *C. claratris* infestations varied significantly with respect to strata and time (Tables 2–5). In addition, significant interactions were found between the strata and time (Tables 2–5). Hence, the effects of time on the development of thrips infestation were determined for each stratum. In the single stem system in the net house, percentage thrips infestation significantly varied with time only in strata 1 ($t = 10.88$, df = 200, $P < 0.0001$) and 2 ($t = -2.99$, df = 200, $P < 0.0032$). In stratum 1, both linear ($t = 10.66$, df = 719, $P < 0.0001$) and quadratic trends ($t = -6.85$, df = 719, $P < 0.0001$) were detected, indicating that thrips infestation first increased and subsequently decreased. In contrast, in stratum 2, thrips infestation showed only a linear trend ($t = 4.06$, df = 719, $P < 0.0001$), indicating infestation increased with time. In the single stem system in the open house, except for stratum 4, thrips infestation significantly varied with time ($t = 9.68$, df = 176, $P < 0.0001$ for stratum 1; $t = -9.17$, df = 176, $P < 0.0001$ for stratum 2; and $t = -4.33$, df = 176, $P < 0.0001$ for stratum 3). In all these three strata, both linear ($t = 18$, df = 909, $P < 0.0001$; $t = 11.07$, df = 909, $P < 0.0001$; 3 $t = 4.42$, df = 909, $P < 0.0001$, respectively, for strata 1, 2, and 3) and quadratic trends ($t = -13.02$, df = 909, $P < 0.0001$ for stratum 1; $t = -4.28$, df = 909, $P < 0.0001$ for stratum 2, and $t = -3.36$, df = 909, $P < 0.0038$ for stratum 3) were found, indicating an initial increase of thrips infestation with time, followed by a decrease in infestation levels. In the double stem system in the net house on the first stem in strata 2, 3, and 4, thrips infestation significantly varied with time (stratum 2: $t = -2.52$, df = 122, $P < 0.0131$; stratum 3: $t = -2.28$, df = 122, $P < 0.0246$; stratum 4: $t = 2.15$, df = 122, $P < 0.0336$), and significant linear relationships of thrips infestation with time were detected ($t = 3.72$, df = 294, $P < 0.0002$ for stratum 2; $t = 2.19$, df = 294, $P < 0.0290$ for stratum 3; $t = -2.16$, df = 294, $P < 0.0318$ for stratum 4) in development. However, in the net house on the second stem and in the open house on both first and second stems, thrips infestation significantly varied with time only in stratum 2 (net house second stem: $t = -5.53$, df = 88, $P < 0.0001$; open house first stem: $t = -7.61$, df = 103, $P < 0.0001$; open house second stem: $t = -10.29$, df = 137, $P < 0.0001$) and always in a significantly linear manner (net house second stem: $t = 5.20$, df = 306, $P < 0.0001$; open house

Table 4. Mean percentage ± SE infestation of *C. claratris* on three different strata of tomato plants, maintained in a double-stem system in a closed house over a period of 10 wk

Week	Mean percentage ± SE infestation					
	First stem			Second stem		
	51–100 cm	101–150 cm	>150 cm	51–100 cm	101–150 cm	>150 cm
1	nl	nl	nl	nl	nl	nl
2	nl	nl	nl	nl	nl	nl
3	nl	nl	nl	nl	nl	nl
4	27.67 ± 3.54	nl	nl	1.40 ± 0.65	nl	nl
5	34.06 ± 3.30	nl	nl	8.76 ± 3.26	nl	nl
6	58.60 ± 4.60	13.26 ± 5.40	nl	34.63 ± 5.52	12.14 ± 6.39	nl
7	74.19 ± 4.32	48.36 ± 9.04	nl	67.90 ± 5.30	19.65 ± 6.20	nl
8	84.46 ± 3.04	61.72 ± 6.74	30.00 ± 9.74	69.06 ± 4.88	35.37 ± 4.36	nl
9	93.82 ± 1.97	69.29 ± 5.53	13.07 ± 4.65	80.77 ± 4.24	39.58 ± 4.42	28.13 ± 11.02
10	100.00 ± 0.00	85.81 ± 5.00	41.10 ± 7.97	100.00 ± 0.00	80.54 ± 5.50	23.24 ± 1.39

Results of the multivariate repeated measure ANOVA for factors strata (first stem: $F = 66.09$, df = 2,122, $P < 0.0001$; second stem: $F = 68.32$, df = 2,88, $P < 0.0001$), weeks (first stem: $F = 56.23$, df = 6,289, $P < 0.0001$; second stem: $F = 102.23$, df = 6,300, $P < 0.0001$), and for strata × weeks (first stem: $F = 3.15$, df = 5,289, $P < 0.0087$; second stem: $F = 5.22$, df = 5, 300, $P < 0.0001$) (SAS Institute 1999).

nl, no leaves.

first stem: $t = 10.64$, df = 423, $P < 0.0001$; open house second stem: $t = 12.08$, df = 374, $P < 0.0001$).

Presence-Absence Sampling with Density Estimations. In the first trial, in both partitions of the net house, infestation by *C. claratris* started 1 WAP of tomato seedlings (Fig. 1A–D). At 4 WAP, 100% of the plants in all rows of both partitions were thrips infested (Fig. 1B and D). At 5 WAP, percentage thrips-infested leaves peaked and sharply declined thereafter (Fig. 1A and C). Cumulative percentage thrips infestation on individual leaves of tomato plants showed that thrips infestations on the uppermost leaves were zero/negligible compared with the middle and lower leaves; this implies that infestations commenced on the lower leaves and gradually spread toward the apical point of the plants (Fig. 2A and B). Density estimates showed that *C. claratris* larvae largely outnumbered thrips adults in two rows, i.e., except the middle row, on tomato leaves (Fig. 3A and B). Larval density peaked at 5 WAP and sharply decreased thereafter, whereas no such population trend was observed in adults (Fig. 3A and B). Significant linear relationships were detected between the percentage infested leaves (X) and thrips density per leaf (Y) of tomatoes in two partitions (partition 1: $Y = 3.89 \pm 0.46X - 1.15 \pm 10.73$, $R^2 = 0.9345$, $F = 71.39$, df = 1,5, $P < 0.0004$; partition 2: $Y = 2.92 \pm 0.39X + 19.69 \pm 9.21$, $R^2 = 0.9173$, $F = 55.49$, df = 1,5, $P < 0.0007$). No significant correlation between leaf area and thrips density was detected ($P > 0.2499$). The estimates of Taylor's power law showed that the relationships between log variance and log mean for thrips numbers were linear for all 4 wk (Table 6). Because the slopes of the four regression lines did not differ significantly, data of 4 wk were pooled, and a common regression line was fitted ($Y = 2.26780 \pm 0.13X - 1.08823 \pm 0.25$, $R^2 = 0.76$, $F = 304.20$, df = 1,98, $P < 0.0001$). The value of the slope (b) was significantly >1 ($P < 0.0001$), indicating a clumped distribution of *C. claratris* on tomato leaves.

As in the first trial, in the second trial, larval densities were considerably higher than adult thrips numbers (Fig. 4). However, in contrast to the previous

Table 5. Mean percentage ± SE infestation of *C. claratris* on three different strata of tomato plants, maintained in a double-stem system in an open house over a period of 10 wk

Week	Mean percentage ± SE infestation					
	First stem			Second stem		
	51–100 cm	101–150 cm	151–200 + > 200 cm	51–100 cm	101–150 cm	> 150 cm
1	nl	nl	nl	nl	nl	nl
2	nl	nl	nl	nl	nl	nl
3	nl	nl	nl	nl	nl	nl
4	36.63 ± 4.19	nl	nl	18.73 ± 3.99	nl	nl
5	54.47 ± 2.98	nl	nl	37.96 ± 4.14	nl	nl
6	86.81 ± 3.47	19.03 ± 3.98	nl	78.62 ± 4.03	12.55 ± 3.43	nl
7	96.52 ± 1.41	24.02 ± 4.01	nl	91.93 ± 2.41	25.16 ± 4.08	nl
8	100.00 ± 0.00	43.37 ± 5.50	4.04 ± 3.19	100.00 ± 0.00	40.12 ± 5.71	5.48 ± 2.80
9	100.00 ± 0.00	65.49 ± 4.58	16.05 ± 4.84	100.00 ± 0.00	63.74 ± 4.89	14.44 ± 4.93
10	100.00 ± 0.00	71.06 ± 4.11	30.79 ± 4.28	100.00 ± 0.00	70.40 ± 5.03	32.08 ± 3.91

Results of the multivariate repeated measure ANOVA for factors strata (first stem: $F = 503.12$, df = 2,103, $P < 0.0001$; second stem: $F = 443.49$, df = 2,137, $P < 0.0001$), weeks (first stem: $F = 99.08$, df = 6,417, $P < 0.0001$; second stem: $F = 130.85$, df = 6,368, $P < 0.0001$), and for strata × weeks (first stem: $F = 12.53$, df = 6,417, $P < 0.0001$; second stem: $F = 9.46$, df = 6,368, $P < 0.0001$) (SAS Institute 1999).

nl, no leaves.

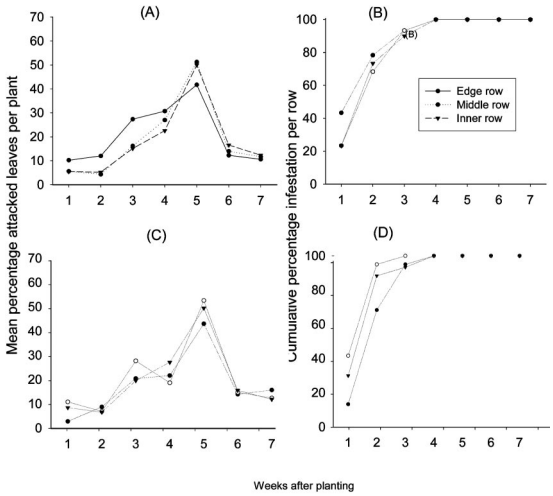

Fig. 1. Infestation of tomatoes by *C. claratris* in a closed house split in two partitions (partition 1, A and B; partition 2, C and D) over a period of 7 wk. A and C show mean percentage of infested leaves per tomato plant and B and D show cumulative percentage of infested plants.

trial, larval densities strongly varied among the three rows, whereas adult densities remained more or less constant (Fig. 4). Peak larval densities were recorded at 4, 5, and 6 WAP in the first, second, and third rows, respectively, always followed by a sharp decline (Fig. 4).

Discussion

Among others, the objectives of this study were to investigate the intraplant distribution of *C. claratris* on tomatoes. Thrips densities differed greatly between the closed net house and the open side wall house, enabling us to study the effects of different *C. claratris* densities on intraplant distribution. Evidently, the pore size (0.18 mm) of the nets in the closed house did not completely prevent a thrips invasion from outside. One possible reason for the higher thrips

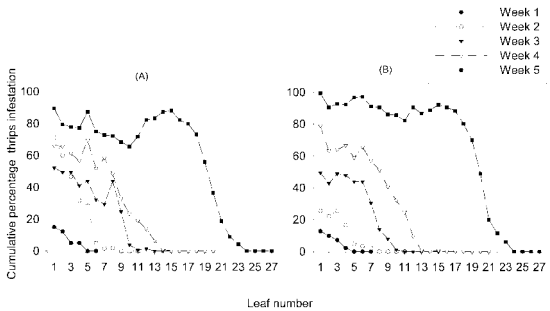

Fig. 2. Vertical distribution of *C. claratris* on tomato plants in two partitions (A and B) of a closed house over a period of 5 wk. Lines show cumulative percentage of infestation of leaves numbered in an ascending manner from bottom to top.

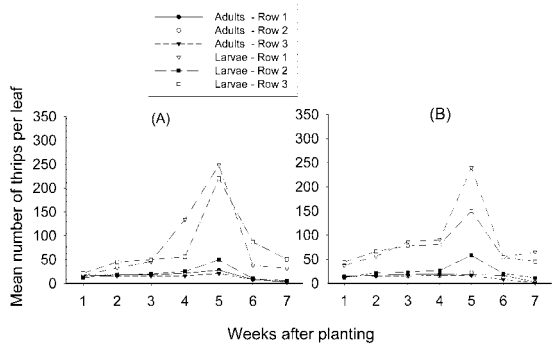

Fig. 3. Mean ± SE density of adults and larvae of *C. claratris* on tomato leaves in a closed house split in two partitions (partition 1, A; partition 2, B) over a period of 7 wk. Plants were arranged in three rows per partition.

densities in the closed net house compared with the open house might have been more favorable microclimatic conditions, particularly in terms of higher temperature and relative humidity. Irrespective of the density, *C. claratris* adults and larvae showed a preference for foliage, resulting in a distinct foliage-biased distribution on tomatoes. Preferential distribution on different plant structures differs among thrips species. Adults of *Frankliniella occidentalis* (Pergande), *F. tritici* (Fitch), *Thrips fuscipennis* Haliday, and *T. major* (Uzel) prefer to inhabit flowers compared with the other plant parts (Kirk 1985a, Atakan et al. 1996, Cho et al. 2000a). In contrast, *T. tabaci* Lindeman (Atakan et al. 1996) and *F. fusca* (Hinds) (Palmer et al. 1989) are mainly foliage feeders. Preference for specific plant parts can also vary among the different life stages of a given thrips species. For instance in *F. occidentalis*, although a flower feeder, >85% of the larvae were found on the foliage of bell peppers and cucumbers (Higgins 1992), indicating niche separation between adults and larvae of *F. occidentalis*. In contrast, for *C. claratris*, both larvae and adults preferred leaves of tomatoes. However, *C. claratris* also occupied flowers and fruits of tomatoes, but the lack of noticeable flower damage and the absence of thrips larvae in the flowers suggest that adult *C. claratris* occasionally inhabit flowers but neither feed nor reproduce there. Pollen and nectar can be important food sources for thrips (Trichilo and Leigh 1988, Higgins 1992). Pollen is rich in protein (Todd and Bretherick 1942), and in several thrips species, positively affects fecundity (Bournier et al. 1979), oviposition rate (Kirk 1985b), development

Table 6. Regression statistics for Taylor's power law for combined numbers of adults and larvae of *C. claratris* on the foliage of tomatoes over a period of 4 wk

Week	Regression equation	R^2	F value	$P > F$
1	$Y = -1.15776 + 2.31753X$	0.67	48.63	0.0001
2	$Y = -0.22187 + 1.91317X$	0.72	61.08	0.0001
3	$Y = -1.29735 + 2.37372X$	0.77	75.19	0.0001
4	$Y = -0.17025 + 1.66580X$	0.30	8.64	0.0074

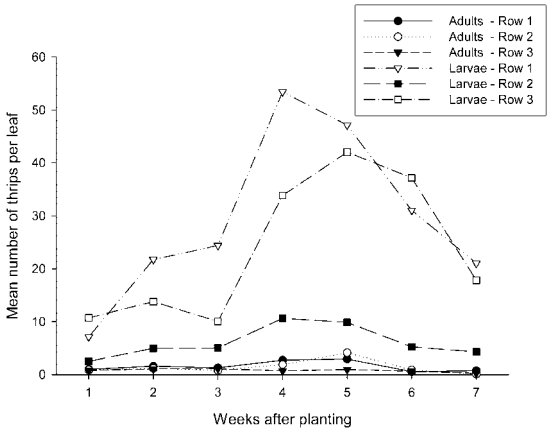

Fig. 4. Mean ± SE density of adults and larvae of *C. claratris* on tomato leaves in a closed house over a period of 7 wk. The plants were arranged in three rows.

rate (Trichilo and Leigh 1988), and larval growth (Murai and Ishii 1982). Thus, in our study, female *C. claratris* most likely aggregated on flowers to feed on pollen and nectar, whereas male thrips may visit flowers to copulate with females in addition to feeding on additional food sources. We did not record any diurnal periodicity in occurrence of *C. claratris* on flowers, corroborating earlier findings of Cho et al. (2000a) with *F. tritici* and *F. fusca* on tomatoes. However, in *F. occidentalis*, the same authors observed significantly higher thrips numbers on tomato flowers in the morning than in the afternoon, indicating species-specific diurnal periodicity in thrips. In our study, we detected significant differences in the sex ratio of *C. claratris* only on fruits of tomatoes, with more males than females present. In *F. occidentalis*, Higgins (1992) recorded more females than males on flowers of bell peppers, whereas in *T. major* males outnumbered females on *Calystegia sepium* L. (Convolvulaceae) flowers (Kirk 1985b). The male-biased sex ratio on fruits indicates that tomato fruits are preferred mating and feeding sites for *C. claratris.* Reitz (2002) speculated that male thrips have a tendency to aggregate in certain locations for mating, whereas females tend to leave these sites after mating, supporting our findings on *C. claratris.* The feeding and oviposition of *C. claratris* on tomato fruits cause malformation and scarification, leading to a downgrading of the fruits. Fruit attack in tomatoes by *C. claratris* commences at a later stage of the infestation cycle, i.e., when the leaves of tomatoes are already hardened and deteriorated as a result of serious feeding by thrips (Premachandra et al. 2004).

The proportion of thrips-infested leaves in the uppermost stratum of the plants was not affected by time, whereas in the two lowest strata, depending on the greenhouse type and the stem-system used, infestation by *C. claratris* significantly fluctuated over time. For the latter, in several cases, we recorded significant quadratic trends, indicating initially an increase of thrips infestation with time, subsequently followed by decreasing or constant infestation levels. Moreover, we observed a gradual upward development of *C. claratris* infestations over time irrespective of the stem system and the greenhouse type used. In addition, we always recorded low abundance of *C. claratris* on the top leaves and no thrips on the apical buds. In contrast, Cho et al. (2000b) and Salguero Navas et al. (1991) recorded higher densities of *T. palmi* Karny and *F. occidentalis* on the upper canopy of potatoes and tomatoes, respectively. However, *F. fusca* density did not significantly differ among the upper and lower strata in tomatoes (Cho et al. 2000a). Among others, vertical distribution pattern in insects is influenced by the species-specific behavior and flying capacity (Ramachandran et al. 2001). The clear preference of *C. claratris* for lower plant strata in tomatoes might be explained by its sluggish movements and/or weak flying capacity.

One week after planting in one partition of the net house, comparatively higher *C. claratris* numbers were recorded in the edge row. Body width in *C. claratris* ranges from 0.18 to 0.23 mm (Rodmui 2002). Hence, most likely the pore size (0.18 mm) of the nets did not completely exclude thrips invasion from the outside. Presently little is known on the sources of *C. claratris* infestations in greenhouses. Possibly a *C. claratris* invasion from yet to be identified sources outside the greenhouses, coupled with its high reproductive potential at high temperatures, frequently prevailing in greenhouses in the humid tropics (Premachandra et al. 2004), as well as the arrangement of the pots within the rows with no interpot distance, were responsible factors for the rapid distribution of *C. claratris* in the net houses. Other factors for the relatively higher *C. claratris* infestation in the edge row of the first and the middle row of the second partition might have been the prevailing wind direction and the wind stream caused by the exhaust fan of the opposite greenhouse, respectively.

In the first interplant distribution trial, 4 wk after planting the tomato seedlings into the net house, 100% of the plants were infested by *C. claratris.* One week later, the highest thrips density was recorded, probably a result of a previous oviposition and subsequent emergence of the larvae. The following sharp drop in infestation was most likely caused by poor quality of the remaining foliage because of deterioration of tomato plant as a result of severe thrips damage.

One important possible reason for the differences in *C. claratris* densities between the two interplant distribution experiments might have been seasonal effects. Thrips densities were relatively low during the rainy season (April to September) compared with the dry season (from October to March). Similar findings have been observed in a greenhouse study in central Thailand from November 2000 to January 2002 using a different tomato variety (Rodmui 2002).

Estimates of Taylor's power law clearly indicated a highly aggregated distribution of *C. claratris* on tomatoes. This information will facilitate the future development of sampling plans for *C. claratris.* An aggregated distribution has been observed in several

other thrips species, e.g., *T. tabaci*, *T. angusticeps* Uzel, *F. occidentalis*, *F. intonsa* (Trybom), and *Aeolothrips intermedius* Bagnall (Steiner 1990, Deligeorgidis et al. 2002).

In conclusion, our results provide basic information for the future development of monitoring programs for *C. claratris*. For *C. claratris* in tomatoes, the most consistent sampling unit is the leaf. Because larvae are the predominant developmental stage on tomato leaves, counts of larvae will suffice to accurately assess *C. claratris* population densities in future monitoring programs. The linear relationship between thrips-infested leaves and density of thrips indicates that the proportion of infested leaves can be used for density estimations. Monitoring should start during an early phase of the crop cycle, and first observations should be made in the lower parts of the tomato plants and continue upward over time. At extremely high thrips densities, as observed in this study, density estimates are very time-consuming and thus less practical. Hence, presence-absence sampling with large number of observations could be an alternative.

Acknowledgments

This study was funded by the German Research Council (DFG) within the framework of the DFG-FOR 431 project.

References Cited

Atakan, E., M. Coll, and D. Rosen. 1996. Within plant distribution of thrips and their predators: effects of cotton variety and developmental stage. Bull. Entomol. Res. 86: 641–646.

Bournier, A., A. Lacasa, and Y. Pivot. 1979. Régime alimentaire d'un prédateur *Aeolothrips intermedius* (Thysanoptera: Thripidae). Entomophaga. 24: 353–361.

Cho, K., J. F. Walgenbach, and G. G. Kennedy. 2000a. Daily and temporal occurrence of *Frankliniella* spp. (Thysanoptera: Thripidae) on tomato. J. Appl. Entomol. Zool. 35: 207–214.

Cho, K., S. Kang, and G. Lee. 2000b. Spatial distribution plans for *Thrips palmi* (Thysanoptera: Thripidae) infesting fall potato in Korea. J. Econ. Entomol. 93: 503–510.

Deligeorgidis, P. N., C. G. Athanassiou, and N. G. Kavallieratos. 2002. Seasonal abundance, spatial distribution and sampling indices of thrip populations on cotton, a 4-year survey from central Greece. J. Appl. Entomol. Zool. 126: 343–348.

Higgins, C. J. 1992. Western flower thrips (Thysanoptera: Thripidae) in greenhouses: population dynamics, distribution on plants and associations with predators. J. Econ. Entomol. 85: 1891–1903.

Kirk, W.D.J. 1985a. Aggregation and mating of thrips in flowers of *Calystegia sepium*. Ecol. Entomol. 10: 433–440.

Kirk, W.D.J. 1985b. Pollen-feeding and the host specificity and fecundity of flower thrips (Thysanoptera) Ecol. Entomol. 10: 281–289.

McMichael, L. A., D. M. Persley, and J. E. Thomas. 2002. A new tospovirus serogroup IV species infecting capsicum and tomato in Queensland, Australia. Aust. Plant Pathol. 31: 231–239.

Murai, T., and T. Ishii. 1982. Simple rearing method for flower thrips (Thysanoptera: Thripidae) on pollen. Jap. J. Appl. Entomol. Zool. 26: 149–154.

Murai, T., S. Kawai, W. Chongratanameteekul, and F. Nakasuji. 2000. Damage to tomato by *Ceratothripoides claratris* (Shumsher) (Thysanoptera: Thripidae) in central Thailand and a note on its parasitoid, *Goethena shakespearei* Girault (Hymenoptera: Eulophidae). J. Appl. Entomol. Zool. 35: 505–507.

Palmer, J. M., L. A. Mound, and G. J. du Heaume. 1989. CIE guides to insects of importance to man. 2. Thysanoptera, C.A.B. International Institute of Entomology, Oxon, UK.

Premachandra, W.T.S.D., c. Borgemeister, A. Chabi-Olaye, and H.-M. Poehling. 2004. Influence of temperature on the development, reproduction and longevity of *Ceratothripoides claratris* (Thysanoptera: Thripidae) on tomatoes. Bull. Entomol. Res. 94: 377–384.

Ramachandran, S., J. Funderburk, J. Stavisky, and S. Olson. 2001. Population dynamics and movement of *Frankliniella* species and *Orius insidiosus* in field pepper. Agric. Forest. Entomol. 3: 1–10.

Reitz, S. 2002. Seasonal and within plant distribution of *Frankliniella* thrips (Thysanoptera: Thripidae) in north Florida tomatoes. Fla. Entomol. 85: 431–439.

Rodmui, P. 2002. Population dynamics and biological control of thrips, *Ceratothripoides claratris* (Shumsher) (Thysanoptera: Thripidae), on tomato under protected cultivation in Thailand. MSc thesis, Kasetsart University, Bangkok, Thailand.

Salguero Navas, V. E., J. E. Funderburk, R. J. Beshear, S. M. Olson, and T. P. Mack. 1991. Seasonal patterns of *Frankliniella* spp. (Thysanoptera: Thripidae) in tomato flowers. J. Econ. Entomol. 84: 1818–1822.

SAS Institute. 1999. SAS/STAT user's guide. SAS Institute, Cary, NC.

Steiner, M. Y. 1990. Determining population characteristics and sampling procedures for the western flower thrips (Thysanoptera: Thripidae) and the predatory mite *Amblyseius cucumeris* (Acari: Phytoseiidae) on greenhouse cucumber. Environ. Entomol. 19: 1605–1613.

Taylor, L. R. 1961. Aggregation, variance and the mean. Nature (Lond.). 189: 732–735.

Todd, F. E., and O. Bretherick. 1942. The composition of pollens. J. Econ. Entomol. 35: 312–317.

Trichilo, P. J., and T. F. Leigh. 1988. Influence of resource quality on the reproductive fitness of flower thrips (Thysanoptera: Thripidae). Ann. Entomol. Soc. Am. 81: 64–70.

Received for publication 21 September 2004; accepted 11 May 2005.