Growth and Reproduction in the First Two and Summer Generations of Two Citrus Aphids, *Aphis citricola* VAN DER GOOT and *Toxoptera citricidus* (KIRKALDY) (Homoptera: Aphididae), under Different Thermal Conditions¹

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Growth and reproduction were compared between *Toxoptera citricidus* and *Aphis citricola*. Comparisons were also made among the first generation, which consisted of fundatrices, the second generation, and the subsequent summer generations of each species. In both species, fundatrices developed more slowly than second and subsequent generation individuals. The fastest development took place in the summer generations in *T. citricidus* and the second generation in *A. citricola*. Capacity for increase, net reproductive rate and the maximum fecundity were largest in the second generation in both species. The difference in maximum fecundity between the summer generations and the first two generations in *A. citricola* was less than that of the same category in *T. citricidus*. Net reproductive rate of *T. citricidus* was usually larger than that of *A. citricola*. Reproductive schedule as displayed by the distribution of age specific fecundity changed with temperature and among generations. As for cohort generation time, the second generation was intermediate between the first and summer generations in *T. citricidus*, while in *A. citricola* the first and second generations were nearly the same.

INTRODUCTION

Various morphs that differ in morphology and/or biology are found in aphids. The viviparous female developing from the overwintering egg is called the fundatrix. Fundatrices differ in many morphological respects from the apterous viviparous females of later generations (HILLE RIS LAMBERS, 1966). In addition, there are some reports that fundatrices and their successors, i.e. fundatrigeniae, differed in reproductive potential from parthenogenetic females which appeared in later seasons (TAKAOKA, 1960; TAYLOR, 1975; DIXON and DHARMA, 1980; LEATHER and DIXON, 1981; TAKADA, 1984; LEATHER and WELLINGS, 1981; WIKTELIUS and CHIVERTON, 1985).

In the present study, growth and reproduction of two citrus aphids, *Aphis citricola* and *Toxoptera citricidus*, were investigated at various temperatures and comparisons of these features were made among generations and between species. These species are the major aphids which overwinter on citrus trees (KOMAZAKI et al., 1979; KOMAZAKI, 1983; KOMAZAKI et al., 1985) and the collected data will be beneficial in forecasting the

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Table 1. The number of aphids used at respective temperatures tested

	Generation								
	First				Second				Summer ^a
<i>Toxoptera citricidus</i>									
Temperature (°C)	10.0	15.2	20.1	24.9	10.0	15.0	20.2	24.8	9.9
No. aphids used	47	42	46	40	48	43	47	50	35
<i>Aphis citricola</i>									
Temperature (°C)	10.6	15.0	19.5	25.1	10.0	14.9	20.0	24.9	10.1
No. aphids used	16	38	43	33	57	52	49	51	42

^a Data on other temperatures are described in KOMAZAKI (1982).

spring occurrence of these aphids. In addition, the comparison between species and among generations provides information on the differences in reproductive strategy of these aphids.

MATERIALS AND METHODS

In the summer of 1979, aphids were collected from a citrus orchard at the Okitsu Branch, Fruit Tree Research Station in Shimizu and reared on potted *Citrus unshiu* MARK. in net cages. These pots were put in growth cabinets whose temperatures were maintained at 17°C (night) and 23°C (day) in hot seasons. *A. citricola* aphids used in experiments were of the citrus biotype (KOMAZAKI, 1986). In fall, the sexual forms (apterous ovipara and alate male) appeared and eggs were deposited on the potted trees in the net cages.

The following spring, fundatrices within one day after eclosion were collected with a fine brush and used for the experiments. The generation of fundatrices is hereafter called the first generation.

For the experiments with individuals of the second generation, fundatrices were reared until maturation and then transferred to new shoots of potted plants in growth cabinets and the newly born nymphs within one day of appearance were used for experiments.

These two generations were reared at temperatures between about 10°C to 25°C, while the subsequent summer generations were reared at about 10°C, data for temperatures between 15° and 25°C being cited from KOMAZAKI (1982). Experiments on summer generations were carried out during the summer season (from July to September), without regard to any particular generation.

All experiments were done during 1980 to 1985. The number of aphids used at respective temperatures is listed in Table 1. Aphid maturation and larviposition were observed daily. The pre-reproductive period (from birth to reproduction), longevity, total fecundity per female, age specific survival rates (l_x) and age specific fecundities (m_x) were calculated. For comparison of reproductive capacity among the first, second, and summer generations, the net reproductive rate (R_0), cohort generation time (T_c), and capacity for increase (r_c) (LAUGHLIN, 1965) were estimated instead of the

² Calculations were done by the computer at the Computing Center for Research in the Ministry of Agriculture, Forestry and Fisheries.

innate capacity for increase (r_m) and mean generation time (T), because stable age distribution was not realized in the early generations. The equations are $R_0 = \sum l_x m_x$, $r_c = \ln (R_0 / T_c)$, and $T_c = \sum x l_x m_x / \sum l_x m_x$.

RESULTS

The pre-reproductive periods at different temperatures and the regression lines of

Fig. 1. Pre-reproductive period and developmental rate in *Toxoptera citricidus* at different temperatures. Straight lines show regression of developmental rate with temperature. F: fundatrices, FG: second generation individuals, V: summer generation individuals.

Fig. 2. Pre-reproductive period and developmental rate in *Aphis citricola* at different temperatures. Straight lines show regression of developmental rate with temperature. F: fundatrices, FG: second generation individuals, V: summer generation individuals.

Table 2. Threshold temperatures for development and thermal constants in the respective generations of the two aphid species

	Generation		
	First	Second	Summer
<i>Toxoptera citricidus</i>			
Threshold temperature (°C)	6.9	7.9	7.4
Thermal constant (Day °C)	149.3	106.4	108.7
<i>Aphis citricola</i>			
Threshold temperature (°C)	7.3	7.7	6.7
Thermal constant (Day °C)	108.0	80.6	109.1

Fig. 3. Relationship between temperature and capacity for increase (r_c) in *Toxoptera citricidus*. O, ● and Δ represent the first (fundatrix), second and the summer generations, respectively. Fig. 4. Relationship between temperature and capacity for increase (r_c) in *Aphis citricola*. O, ● and Δ represent the first, second and the summer generations, respectively.

developmental rate with temperature are illustrated in Fig. 1 (*T. citricidus*) and Fig. 2 (*A. citricola*). In *T. citricidus*, the development was fastest in the summer generation and slowest in the first one at all temperatures. Second generation individuals required nearly the same time to mature as summer generation ones, except at 10°C. In *A. citricola*, development of fundatrices was slowest, as was also true in *T. citricidus*. The quickest development took place in the summer generation in *T. citricidus* but in the second generation in *A. citricola*.

The threshold temperatures for development and thermal constants during the pre-reproductive period were estimated from the regression lines and given in Table 2. The thermal constant was somewhat larger in the first generation for *T. citricidus*, and smaller in the second generation for *A. citricola* than the other generations. In the first and second generations, the thermal constants of *A. citricola* were smaller than those of *T. citricidus*.

Figures 3 and 4 give relationships between temperature and r_c for the respective species. In *T. citricidus*, there is no difference between the second and summer generations, while all points in the first generation are lower than in the other two. In *A. citricola*, r_c values for the second generation are distinctly high at 20°C and 25°C as compared with those for the other generations.

Table 3. Net reproductive rate, maximum fecundity per female and survival rate at various temperatures in two aphid species

	Generation											
	First				Second				Summer			
<i>Toxoptera citricidus</i>												
Temperature (°C)	10.0	15.2	20.1	24.9	10.0	15.0	20.2	24.8	9.9	14.9	20.1	24.9
Max. fecundity	29	129	139	118	50	135	142	125	64	85	88	87
Net reproductive rate	5.53	67.7	76.0	58.3	15.4	98.4	74.3	76.5	13.6	53.2	56.2	62.7
Survival rate ^a	.600	.881	.804	.762	.875	.977	.851	.900	.763	.982	.977	.931
<i>Aphis citricola</i>												
Temperature (°C)	10.6	15.0	19.5	25.1	10.0	14.9	20.0	24.9	10.1	14.7	19.5	25.1
Max. fecundity	72	108	110	100	101	118	128	104	53	88	107	85
Net reproductive rate	27.3	39.2	37.7	40.1	34.9	75.3	79.4	52.6	23.6	50.8	61.1	30.7
Survival rate ^a	.647	.949	.935	.868	.807	.904	.959	.980	.955	.951	.944	.818

^a Survival rate at the time of the beginning of larviposition.

Fig. 5. Age specific fecundity in *Toxoptera citricidus* at 10°C (A) and 25°C (B). —, --- and ---- represent the first, second and summer generations, respectively.

Fig. 6. Age specific fecundity in *Aphis citricola* at 10°C (A) and 25°C (B). —, --- and ---- represent the first, second and summer generations, respectively.

Fig. 7. Relationship between temperature and cohort generation time (T_c) in *Toxoptera citricidus*. ○, ● and △ represent the first, second and the summer generations, respectively.

Fig. 8. Relationship between temperature and cohort generation time (T_c) in *Aphis citricola*. ○, ● and △ represent the first, second and the summer generations, respectively.

As seen in Table 3, the maximum fecundity was lowest at 10°C and highest at 20°C in all generations in both species. At all temperatures but 10°C for *T. citricidus*, values are considerably lower in the summer generation than in the other generations.

As seen in Table 3, net reproductive rates (R_0) became maximum between 15° and 20°C except for the first generation of *A. citricola*. Generally speaking, R_0 values in *T. citricidus* were larger than those in *A. citricola*.

The m_x curves at 10°C and 25°C are shown in Figs. 5 and 6. In fundatrices, the peak of m_x curve came on the first day of their reproductive life and their reproductive period was much shorter than individuals in the subsequent generations at lower temperatures, while at the higher temperature, the peak appeared much later and their reproductive period was never shorter.

As shown in Figs. 7 and 8, cohort generation time (T_c) became shorter as temperature rose in both species. Similar trends in relationship between temperature and T_c were observed among the generations.

The survival rates at the beginning of larviposition were relatively low in fundatrices, especially when reared at 10°C (Table 3).

DISCUSSION

As mentioned, results of the experiments suggest that in both species the second generation individuals can increase more rapidly than the fundatrices. Generation specific ovariole number and fecundity were reported in several aphid species (DIXON and DHARMA, 1980; WELLINGS et al., 1980; LEATHER and WELLINGS, 1981). These facts indicate the existence of a generation specific increase rate. The large increasing capacity observed in the second generation is believed to have been brought about by the short maturing time, while the small r_c values observed in the fundatrix generation by the low developmental speed and low survival rate at the immature stage.

The second generation individuals were more fecund than fundatrices in the two citrus aphids dealt with in this paper. A similar result was obtained for *Rhopalosiphum padi* (L.) (LEATHER and DIXON, 1981). However in *Aphis fabae* SCOP. (DIXON and DHARMA, 1980) fundatrices are more fecund than the second generation individuals. It is thus suggested that difference in fecundity between these generations is dependent on the species, though the reason for this is unknown.

The fundatrices of *A. citricola* developed from the middle of March to the middle of April, while those of *T. citricidus* did not develop until late in March (KOMAZAKI et al., 1979). Meteorological data at this Experimental station shows the mean temperature this season usually rises from about 10°C (in the latter half of March) to 15°C (in the middle of April). The study revealed that at this range of temperature, fundatrices of these two citrus aphids needed more time from birth to maturation than the other generations. The same result was reported for *Myzus persicae* (SULZ.) by TAKAOKA (1960). As shown in a model analysis (GADGIL and BOSSERT, 1970), delayed maturation in fundatrices is closely related to severe environmental conditions, i.e. low temperature and low food availability, to which they may be subjected.

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