Phenology, Life Tables, and Reproductive Biology of *Tetraleurodes perseae* (Hemiptera: Aleyrodidae) on California Avocados

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ABSTRACT *Tetraleurodes perseae* Nakahara (Hemiptera: Aleyrodidae) is an exotic whitefly in California that is a minor pest of avocados, *Persea americana* Miller (Lauraceae). Field monitoring over a 4.5-yr period (1997–2002) in a commercial avocado orchard in southern California indicated that *T. perseae* is probably univoltine, and adult densities show single distinct peaks each year around August. The only hymenopteran parasitoid found attacking *T. perseae* in California was an aphelinid, *Cales noacki* Howard, and parasitism over February–April each year ranged from 30 to 100%. Partial life tables constructed from cohorts of *T. perseae* in the field indicated that survivorship from settled first and second instars to emerged adult whiteflies ranged from 34 to 37%. There were no significant differences in marginal mortality rates by life stage for whitefly cohorts enclosed in sealed mesh bags, open mesh bags, or on unenclosed avocado leaves. Survivorship curves constructed from field phenology data indicated that average egg-to-adult survivorship was around 3.5%, which is substantially lower than that suggested from the life table analyses. Laboratory studies conducted at 25°C on excised avocado leaves indicated that ≈43–46 d is needed by *T. perseae* to complete development from egg to adult. Demographic analyses of laboratory data indicate that *T. perseae* has a high reproductive potential with net reproductive rate and intrinsic rate of increase estimates being 21.15 ± 1.39 and 0.07 ± 0.001, respectively.

KEY WORDS demography, *Cales noacki*, fortuitous biological control, jackknife, *Persea americana*

The genus *Tetraleurodes* is one of the larger known whitefly genera with >50 described species (Nakahara 1995). Most members of the genus seem to be of little economic importance and may be occasional pests [e.g., *Tetraleurodes acaciae* (Quaintance)] on the fabaceous hosts *Calliandra hematocephala* Hassk. (Dowell 1982) or *Gliricidia sepium* Jacq. (Villacarlos et al. 2003) that are generally very well controlled by hymenopterous parasitoids (e.g., aphelinids or signiphorids), generalist predators (e.g., coccinellids and chrysopids), or entomopathogenic fungi (e.g., *Aschersonia aleyrodis* Webber or *Entomophthora* sp.) (Dowell 1982, Villacarlos et al. 2003, Rose and Zolnerowich 2004).

Tetraleurodes perseae Nakahara (Hemiptera: Aleyrodidae) (Nakahara 1995) was first discovered on avocados, *Persea americana* Miller (Lauraceae) in San Diego, California, in 1982 (Rose and Wolley 1984a,b). At the time of discovery, this insect was a new species, and it was formally described in 1995. *T. perseae* currently infests ≈95% of avocado acreage in California where it is considered a pest of minor economic significance (M.S.H., unpublished data).

T. perseae has conspicuous rusty, reddish brown lines on the wings of adults (Nakahara 1995, Hoddle 2005). Female whiteflies lay beige-colored eggs horizontally on the undersides of immature avocado leaves. The first two instars are light yellow-brown; third, fourth, and pupal instars are melanic with a white wax fringe. In the pupal stage, the wax fringe is highly developed and curls upwards to partially cover the dorsal margin. Occasionally, cast exuviae may collect on the dorsal surface of larvae; this tends to be more common for the first three instars (for colored photographs of all life stages, see Hoddle 2005). This whitefly is native to Mexico and Central America, having been recorded from commercial avocado-growing areas in Mexico, and from plants in El Salvador (Nakahara 1995). Host plants in addition to avocado are all Lauraceae and include *Laurus nobilis* L., *Litsea* sp., *Persea* spp., and *Umbellularia californica* (Hook and Arn.) Nutt. (Nakahara 1995).

In Mexico, *T. perseae* can be a sporadic pest in avocado orchards after pesticide applications that disrupt biological control by *Eretmocerus* sp. and *Encarsia* spp. (Hymenoptera: Aphelinidae) (Rose and Woolley 1984a,b; Rose and Zolnerowich 2004). In California, this whitefly is reportedly under very good control by *Cales noacki* Howard (Hymenoptera: Aphelinidae), which was originally released for biological control of woolly whitefly, *Aleurothrixus floccus* (Maskell) (Hemiptera: Aleyrodidae) on citrus (Rose and Wool-

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ley 1984a,b). *C. noacki* can parasitize up to 92% of *T. perseae* larvae in some coastal areas of California (Rose and Woolley 1984a,b). However, this level of control is not consistent in all avocado-growing regions of California, and *T. perseae* seems to less effectively controlled by *C. noacki* in more arid interior areas where summer temperatures are hotter.

Although considered a minor pest in California, *T. perseae* can increase to high densities for short periods in mid- to late summer on succulent young avocado leaves (i.e., summer flush growth), which are ideal for adult feeding and oviposition. Honeydew production by feeding larvae can promote the growth of black sooty mold on leaves, and feeding by adult whiteflies can deform immature leaves, which in some circumstances can lead to premature leaf drop. Damage of this nature is not uncommon for whiteflies. High density populations of the congeneric *T. acaciae* on *C. hematocephala* in Florida have similar adverse impacts on this host plant (Dowell 1982). *T. perseae* successfully invaded Israel in 2001, most likely on illegally imported avocado foliage from California; and in 2002, it was reported from Lebanon (EPPO 2005). Consequently, it is likely that *T. perseae* will successfully infiltrate other commercial avocado-growing areas around the Mediterranean, in particular, southern Spain.

At the time this work was done, little was known about the phenology, field ecology, or developmental or reproductive biology of *T. perseae.* Subsequently, field and laboratory studies were undertaken to address some of these shortcomings. Specifically, the phenology of *T. perseae* and natural enemy activity in an avocado orchard in southern California was monitored for 4.5 yr, and cohorts of *T. perseae* larvae were observed at this study site and survivorship rates were used to develop partial life tables. In the laboratory, the developmental and reproductive biology of *T. perseae* was studied at 25°C to determine the duration of life stages and the reproductive output of females.

Materials and Methods

Field Studies in Southern California. A 20-yr-old commercial 'Hass' avocado orchard in Temecula (33° 28.512′ N, 117° 10.613′ W; elevation 435 m), Riverside County, California, was selected for field studies on *T. perseae.* No pesticides were applied during the course of this study (20 June 1997–26 February 2002).

Population Monitoring. Every 7–14 d, 50 mature avocado leaves were randomly picked at shoulder height from a 0.5-ha block within the 2-ha orchard. These leaves were returned to the laboratory and examined under a dissecting microscope. The number of eggs, first and second (combined), third, and fourth instars, pupae, and pupal cases that yielded adult whiteflies was recorded per leaf. *T. perseae* larvae exhibiting circular exit holes were recorded as being parasitized by sampling date. Additionally, at each sampling event, 50 randomly selected young leaves (bronze colored, approximately three-quarter expanded leaves) were examined in the field, and the number of adult *T. perseae* on selected leaves was recorded. The average number for each life stage monitored for each sampling event was calculated and plotted over time. During the course of this study, 568 third and late fourth instars and pupae were excised from leaves on host plant material and maintained in sealed one-fourth dram vials and monitored for emergence of either adult whiteflies or parasitoids. Emerged parasitoids were identified to species.

Life Table Construction. In addition to population monitoring, cohorts of *T. perseae* larvae were followed over time and survivorship rates by life stage were recorded. Cohorts of *T. perseae* were followed in one of three treatments: 1) fine mesh bags that enclosed avocado branches, sealed tightly at the proximal end of the branch and closed at the distal end (natural enemy exclusion treatment; $n = 10$ enclosed branches on 10 different trees); 2) mesh bags that were not closed distally (control for bag effect but not excluding natural enemies; $n = 10$ bagged branches on 10 different trees), and 3) unenclosed branches ($n = 20$ branches on 15 different trees) that had naturally occurring cohorts on leaves. This set up resulted in a total of 40 branches on 35 different trees that were used in these experiments. In the two bag treatments (open and closed), branches that were enclosed with bags were ≈60 cm in length and had a mixture of immature, almost mature, and fully mature leaves. Bags were made from white organdy (95-μm space between threads) and were 80 cm in length and 40 cm in diameter. Two circular wire supports were stitched into bags 15 cm from each end. Both ends of the bags were closed by drawstrings that could then be wrapped around pinched excess fabric at the end of an experimental bag further tightening the seal against the branch being enclosed.

To establish *T. perseae* cohorts in mesh bags, 10–20 adult whiteflies were aspirated from young avocado foliage and released into the 20 experimental bags that were then closed tightly. After 10 d, all bags were opened, and leaves were examined for *T. perseae* eggs. Leaves with whitefly eggs were tagged with flagging tape and examined weekly for egg hatch. Ten bagged branches were randomly assigned to the "closed bag" treatment and were only opened on days that cohorts were examined. The remaining 10 bags comprised the "open bag" treatments, which were not closed at the distal end, thereby allowing natural enemies access to the contents of each bag. Cohorts of first and second instars that settled on individually tagged and numbered leaves within all 20 bags were sequentially numbered with a nontoxic indelible marker. Numbered larvae (five to 27 larvae per leaf) on individual leaves (five to eight tagged leaves per bag), for each treatment are referred to here as subcohorts. Each subcohort of numbered whitefly larvae on a tagged leaf was examined weekly, and the developmental stage of numbered larvae was recorded per leaf by bag number (i.e., 1–10) and treatment (bag open or closed). The fate of naturally occurring *T. perseae* subcohorts (i.e., whitefly larvae from eggs oviposited by free ranging

and unmanipulated adult *T. perseae* that occurred naturally on leaves of exposed branches not enclosed by experimental bags) was determined by following numbered larvae on 37 tagged leaves on 20 branches across 15 trees. All whitefly subcohorts across all three treatments were set up in July 1998 and established within a 2-d period. Subcohorts were monitored weekly until February 1999. Weekly observations continued until numbered larvae in subcohorts in all treatments had died from unknown causes, disappeared, been parasitized, or emerged as adult whiteflies. For life table construction, all subcohorts on individual leaves within each treatment were collated to form three summary cohorts. Collation produced one summary cohort each for the open bag and closed bag treatments, and one summary cohort for the naturally occurring whitefly larvae on unenclosed branches.

Calculating Marginal Probabilities of Mortality. Marginal rates of mortality were calculated to separate mortality from each observed cause (unknown death, disappearance, and parasitism). The marginal probability of mortality is the number of hosts that would die from a factor in the absence of all other contemporaneous mortality agents. It is the net probability of dying (as opposed to the crude probability of dying which is the apparent mortality calculated from numbers observed to die from a cause) (Royama 1981, Elkinton et al. 1992). The marginal probability of mortality was calculated for each factor as $m_i = 1 - (1 - d)^{d_i/d}$, where m_i is marginal probability of mortality from the ith cause, d_i is death rate from the ith cause, and d is death rate from all causes combined (Elkinton et al. 1992). The marginal probabilities for each mortality factor were calculated for each subcohort. Mean marginal probabilities for each mortality factor by life stage for each subcohort within a treatment were calculated. Individual marginal probability of mortality estimates for each factor were square-root arcsine-transformed and compared by life stage across treatments with analysis of variance. Significant differences between means were identified with Tukey's studentized range test at 0.05 level of significance in SAS (SAS Institute 1990).

Laboratory Studies on Development and Reproduction. Laboratory studies on the developmental and reproductive biology of *T. perseae* were conducted in temperature-controlled cabinets set at 25°C and 60% RH under long days (a photoperiod of 14:10 [L:D] h).

Preimaginal Development and Life Table Construction. Adult whiteflies collected from the Temecula field site were placed (approximately three to five females and two males) in 15 circular glass cells, 25 mm in width and 15 mm in height, with one opening covered with organdy. The open ends of glass cells were attached to the adaxial surface of excised avocado leaves with Duco stick-tak (Devcon Consumer Products, Des Plaines, IL). Aspirated adult *T. perseae* were introduced into cells through a 5-mm-diameter hole on the side of the cell by gently tapping the glass aspirating tube. The hole was then sealed with a silicone bung. Avocado leaves with cells and adult *T. perseae* were placed abaxial side down on water-saturated foam pads and placed in temperature-controlled cabinets and left to oviposit for 24 h. After this time, adult whiteflies were anesthetized with CO_2 and moved daily to fresh Hass avocado leaves until death. Avocado leaves (three-quarter expanded) were collected daily from the University of California, Riverside, biological control grove and inspected under a dissecting microscope for *T. perseae* eggs. Whitefly-infested leaves were discarded. Each experimental leaf exposed to female whiteflies was numbered, and the number of eggs laid during each exposure period was recorded.

Eggs were monitored daily to determine time to egg hatch. Settled first instars that eclosed from eggs were numbered with a nontoxic indelible marker, and subsequent developmental stages were recorded daily and used to calculate the mean duration of each developmental stage at 25°C. Once the pupal stage was reached, glass cells were placed on leaves over individual pupae to trap emerging adult whiteflies. Emerged adults were sexed, and placed as male–female pairs within glass cells. Adult *T. perseae* paired in this manner were used for daily fecundity and longevity studies and were anesthetized with CO_2 and moved daily to fresh Hass avocado leaves until adults died.

Demographic Growth Parameters. Egg to adult survivorship data, daily fecundity, and sex ratio of reared progeny were used to construct l_xm_x life tables from which demographic growth parameters were calculated.

Daily development and survivorship data, and daily progeny production for mated *T. perseae* females were used to produce a birth cohort of females reared and maintained at 25°C. The proportion of larvae produced by females reared and maintained at 25°C that were female (i.e., no. females/[males + females]) was used to adjust daily progeny production in the m_x column to estimate the number of daughters produced daily by surviving females. The following demographic parameters were calculated from l_xm_x life tables:

1. Net reproductive rates ($R_o = \Sigma l_xm_x$ [where l_xm_x is the net female maternity, where l_x is the fraction of females alive at age x, and m_x is the number of daughters born to surviving females at age x]) express the per generation growth rate of the population as the number of daughters produced by females ($R_o > 1.0$, the population increases in size; $R_o = 1.0$, no increase in population size; and $R_o < 1.0$, population growth is declining) (Carey 1993).
2. Mean generation time ($T_c = \Sigma xl_xm_x/R_o$) is the average interval separating births of one generation from the next (Carey 1993).
3. The intrinsic rate of natural increase, r_m (found as the solution to $1 = \Sigma l_xm_x\exp(-r_mx)$ [this equation was iterated for r_m until a value of one was obtained]), is the maximum exponential rate of increase by a population growing within defined physical conditions (Birch 1948).

4. Doubling time ($T_d = \ln(2)/r_m$) is the time required by a population growing exponentially without limit to double in size when increasing at a given r_m (Carey 1993).

Mean demographic parameter estimates with SE values were generated by jackknife analysis of $l_x m_x$ life table data. The jackknife method removes one observation at a time from the original data set and recalculates the statistic of interest from the truncated data set. These new estimates, or pseudo-values, form a set of numbers from which mean values and variances can be calculated and compared statistically (Miller 1974, Efron 1981, Meyer et al. 1986, Shao and Tu 1995). The jackknife method of resampling is well suited for estimating variance for population growth statistics (Meyer et al. 1986).

Survivorship Curves. Survivorship curves were calculated by dividing the number of whiteflies entering a stage by the size of the initial number of eggs used to generate that cohort (Southwood 1978). Phenology data indicated that *T. perseae* is univoltine in California (see below), and this permitted survivorship curves to be generated from leaf count data for field populations surveyed for a full 12-mo period in 1998, 1999, 2000, and 2001. The total number of *T. perseae* eggs counted over each 12-mo period was used to divide the total number of each successive life stage observed over the course of the year. The mean proportion ± SE entering the stage as a function of counted eggs was calculated across 1998–2001. A survivorship curve was constructed in the same manner for the laboratory cohort of *T. perseae* that was used for the demographic study.

Results and Discussion

Population Phenology and Parasitism. *T. perseae* populations were followed for ≈4.5 yr at the study site in Temecula. For each completed year of the survey (1998, 1999, 2000, and 2001), densities of eggs tended to increase from June of each year and typically peaked around October and declined to low levels by March–April of the following year. An exception to this trend was observed in April 2000, when *T. perseae* egg counts increased before declining in late May–early June 2000. The presence of first and second instars tended to peak ≈2 mo after peak egg production, and peak densities were substantially lower than that observed for eggs (≈50–66% lower in some years) (Fig. 1A). Third and fourth instar densities were substantially lower than densities of first and second instars, and both life stages had similar, overlapping, and noisy population trends (Fig. 1B). The mean densities of pupae, and pupae from which adult *T. perseae* emerged, were comparably lower than densities observed for third and fourth instars. Both life stages showed similar densities and overlapping trends (Fig. 1C). Adult whiteflies counted on young avocado leaves typically increased from late June each year and generally peaked around mid-August before declining to low densities in September–October (Fig. 1D). The distinct peaks in egg and adult numbers suggest that this whitefly may be univoltine in California. In comparison, *T. acaciae*, a native of California and Mexico, reportedly has eight generations per year on *C. hematocephala* in Florida (Dowell 1982).

Parasitoid emergence in the field was observed February through April each year. During this period, field parasitism ranged from 30 to 100% (data on emerged parasitoid counts are not shown). The only parasitoid reared from excised larvae and pupae was *C. noacki.* In the laboratory, 19% (n = 108) of collected material yielded parasitoids. Adult *T. perseae* emerged from 17% (n = 94) of excised material, and 64% of larvae and pupae (n = 366) died after being placed in sealed one-fourth dram vials. This method of measuring parasitism in the laboratory may have underestimated the impact of *C. noacki* at the study site as premature death of hosts and subsequently parasitoids most probably occurred as leaf material desiccated in vials. Dissections of dead whitefly larvae and pupae were not conducted to determine whether they had been parasitized in the field. Voucher material of *C. noacki* has been deposited in the Entomology Museum at the University of California, Riverside.

Field Life Tables. Survivorship for first and second instars of *T. perseae* larvae to adulthood in closed and open bags, and on exposed leaves, was 36, 37, and 34%, respectively (Table 1). Only two marginal rates of mortality comparisons across treatments were significant, unknown death for third instars (F = 3.62; df = 2, 32; P = 0.038) and disappearance of pupae (F = 19.47; df = 2, 32; $P < 0.005$). The biological significance of these statistically significant differences is uncertain. Interestingly, enclosure of cohorts of whitefly larvae within protective mesh bags that were open or closed did not significantly affect survivorship rates in comparison to unprotected cohorts developing on avocado leaves that were exposed to natural enemies. Possible explanations for this discrepancy are as follows. 1) The closed bags failed to exclude small natural enemies such as phytoseiid mites. *Neoseiulus californicus* (McGregor) was observed attacking immature *T. perseae* in the field, and *Euseius hibisci* (Chant), an omnipresent phytoseiid in avocado orchards, was observed periodically in closed bag treatments. Predatory mites may have accidentally been enclosed in closed bag treatments at time of set up or were able to enter bags because points of closure were not tight enough to exclude access. 2) Weather acted impartially on all treatments causing similar levels of mortality, indicating that bags had no adverse or beneficial effect on survivorship rates. 3) Marking larvae and regular handling and inspection of leaves had some undetermined, equalizing, and perhaps beneficial impact on *T. perseae* survivorship rates across all treatments. Furthermore, no parasitism was observed in any of the three treatments, although larvae that had been parasitized successfully and identified from parasitoid exit holes were observed during concurrent leaf counts for the phenology study at the field site. This observation may in part support suggestion 3 regard-

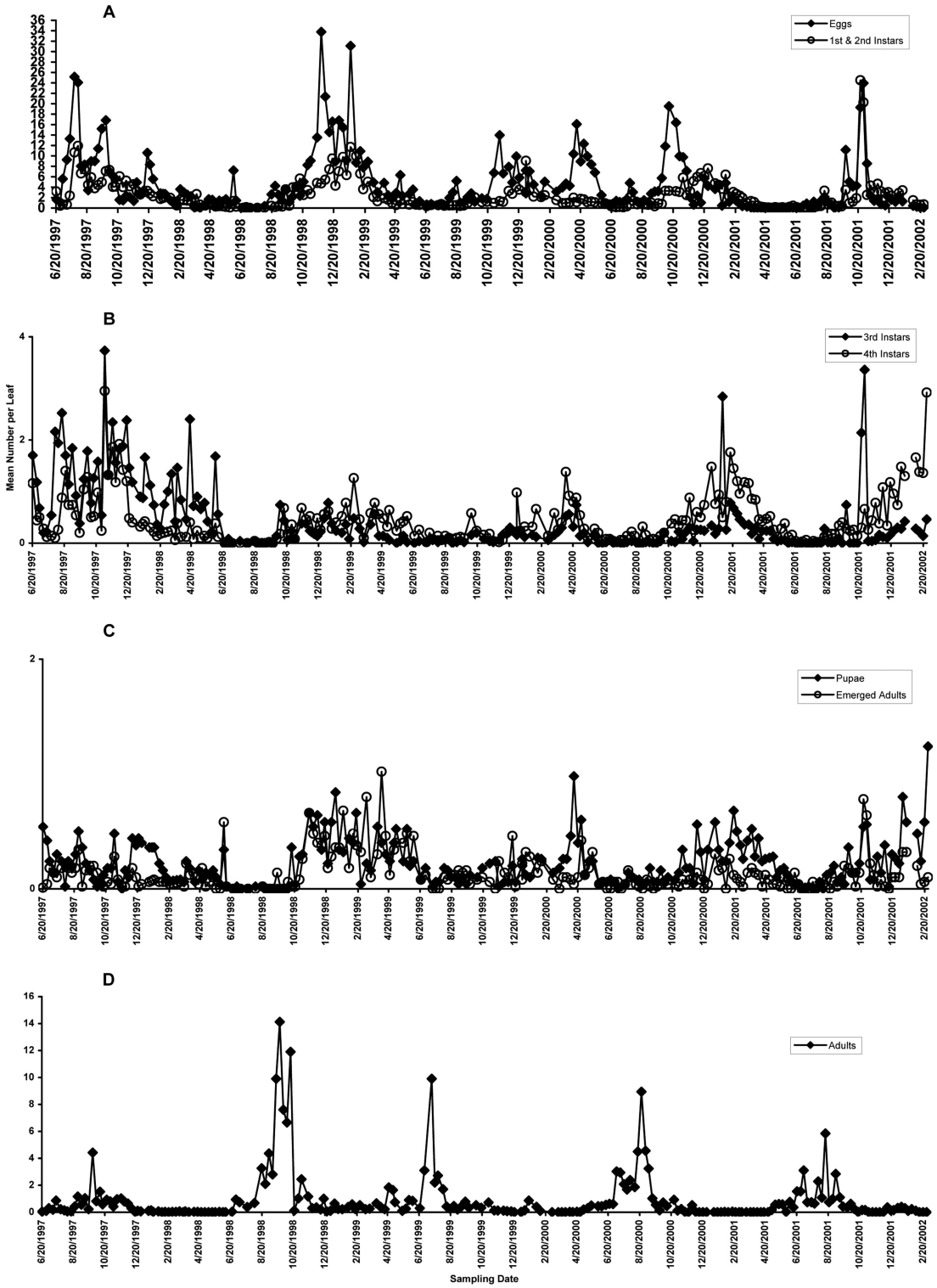

Fig. 1. Phenology graphs for *T. perseae* on avocados in a commercial Hass avocado orchard in California. Mean numbers of eggs and first and second instars (both larval stages combined) (A), third and fourth instars (B), pupae and pupal cases from which adult whiteflies emerged (C), and adults on immature foliage (D).

Table 1. Partial life table for *T. perseae* on avocado leaves in a commercial Hass avocado orchard in California

Stage	l_x			f_{dx}	d_x			Marginal probability of mortality ± SE		
	T_1	T_2	T_3		T_1	T_2	T_3	T_1	T_2	T_3
First/second instars	244	241	287	Unknown death	47	25	52	0.31 ± 0.05a	0.22 ± 0.03a	0.32 ± 0.04a
				Disappeared	85	79	105	0.24 ± 0.07a	0.37 ± 0.06a	0.36 ± 0.03a
Third instars	112	137	130	Unknown death	1	4	2	0.004 ± 0.002a	0.02 ± 0.007b	0.009 ± 0.006a
				Disappeared	6	12	7	0.05 ± 0.008a	0.05 ± 0.02a	0.08 ± 0.03a
Fourth Instars	105	121	121	Unknown death	0	0	1	0.00 ± 0.00	0.00 ± 0.00	0.009 ± 0.009
				Disappeared	2	5	3	0.04 ± 0.01a	0.02 ± 0.004a	0.02 ± 0.01a
				Parasitized	0	0	0	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Pupae	103	116	117	Unknown death	2	1	0	0.02 ± 0.005a	0.005 ± 0.002a	0.009 ± 0.009a
				Disappeared	13	25	18	0.14 ± 0.02a	0.16 ± 0.03a	0.02 ± 0.01b
Adults	88	90	99							

T_1, closed mesh bags; T_2, open mesh bags; T_3, unenclosed whitefly cohorts. l_x, numbers entering stage; f_{dx}, mortality factor; d_x, numbers dying in stage from each identifiable mortality factor.

ing leaf handling and overall low mortality rates of *T. perseae.*

Laboratory Demography. In the laboratory, *T. perseae* exhibited high mortality (86%) at the egg–crawler stage, and egg-to-adult survivorship on excised Hass avocado leaves was 3% (Table 2). At 25°C, eggs and first instars had the longest developmental times of ≈10–11 d on average (Table 2). Total duration of all life stages combined was ≈43 d (cf. generation time estimate of ≈ 46 d from l_xm_x life table; Table 3) of which an average of 3 d was spent in the adult stage (Table 2). The sex ratio of adult *T. perseae* was female biased at 66% of emerged progeny. Emerged females laid approximately two to three eggs per day and approximately nine eggs over the course of an average life span of close to 3 d. The mean longevity estimate of ≈3 d for adults is almost certainly an underestimate. Anesthetizing adults with CO_2 to move them to new leaves each day for fecundity estimates and conducting these studies on immature excised avocado leaves that may have been older (leaves needed to be of certain minimum size and consequently age for adhering glass cells) than those preferred by adults in the field may have acted together to reduce estimates of adult survivorship times and female fecundity. Consequently, estimates of daily and life time fecundity in this study are likely to have been adversely affected and should be viewed with some caution. Even at these low survivorship and fecundity rates, a cohort of six *T. perseae* females still demonstrated a moderately high capacity for population increase (r_m = 0.07) and a potential to double their population size every 9 to 10 d under laboratory conditions (Table 3).

Survivorship Curves. In the field and laboratory, immature whiteflies did not die in consistent proportions across successive life stages. The transition from eggs and crawlers to settled first and second, and third instars exhibited high levels of mortality, with >80% of eggs failing to reach the third instar (Fig. 2). Survivorship rates past the third instar and final emergence as adults (i.e., observed pupal cases from which adults emerged) were relatively constant for field and laboratory populations. Overall, ≈3 to 4% of eggs produced adult whiteflies in the field and laboratory (Fig. 2).

In conclusion, this work provides some of the only available field and laboratory data on a member of the genus *Tetraleurodes,* species of which are often considered biological or scientific curiosities because of their limited economic importance. This situation is unlikely to change unless a *Tetraleurodes* sp. becomes a successful invader on a host of economic importance in an area that lacks generalist natural enemies that can provide fortuitous biological control, as was observed in California with *C. noacki.* The movement of *T. perseae* on avocados throughout the Mediterranean may provide an opportunity to learn more about this whitefly.

Table 2. Laboratory-derived life table and developmental times for *T. perseae* on excised Hass avocado leaves at 25°C

Life stage	No. entering stage (l_x)	No. dying in stage (d_x)	Proportion dying in stage (q_x)	Mean ± SE duration of stage (d)
Eggs/crawlers	336	290	0.86	11.17 ± 1.68
Settled first instars	46	13	0.28	9.89 ± 2.67
Second instars	33	9	0.27	4.48 ± 1.23
Third instars	24	2	0.08	5.08 ± 0.83
Fourth instars	22	12	0.55	3.45 ± 1.53
Pupae	10	0	0	6.30 ± 1.83
Adults	10			2.70 ± 2.75

Egg-to-adult survivorship, 3%; female sex ratio, 66%; daily fecundity, 2.48 ± 0.58 eggs; and lifetime fecundity, 8.89 ± 3.62 eggs.

Table 3. Mean ± SE jackknifed demographic statistics derived from l_xm_x life tables for *T. perseae* reared on excised Hass avocado leaves at 25°C

Net reproductive rate (R_o)	Generation time (T_c)	Intrinsic rate of increase (r_m)	Doubling time (T_d)
21.25 ± 1.39	45.81 ± 0.28	0.07 ± 0.003	9.90 ± 0.02

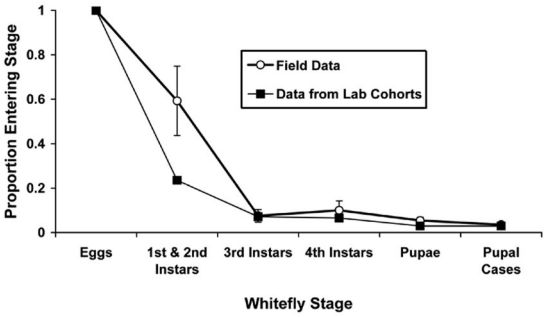

Fig. 2. Survivorship curves for *T. perseae* life stages. The survivorship curve for the field surveys was averaged from 4 yr of population counts. The laboratory survivorship curve was generated from cohorts used in the reproductive and developmental biology studies. The total number of *T. perseae* eggs counted was used as the denominator for calculating the proportion entering each life stage.

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