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Full Length Research Paper

Life history of the Potato Psyllid *Bactericera cockerelli* (Homoptera: Psyllidae) in Controlled Environment agriculture in Arizona

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The life history parameters were studied for a western isolate of *Bactericera cockerelli* (Sulc) from a southern Arizona commercial tomato greenhouse (AZ - 06) during 2006. Life history parameters were determined at 26 - 27°C and 60 - 70% humidity, with a 12:12 day/night cycle. The mean pre-mating period was 4.2 days, with a range of 3.8 – 5 days, and the mean pre-oviposition period was 6.9, with a range of 5.9 – 8.0 days. The mean incubation period for the egg stage was 6.7 days (range 5.7 - 8.2 days), with a nymphal period of 21.9 (19.1 - 23.8 days). The total developmental period was 25 to 33 days, with an average of 28.4 days. The survival of eggs, nymphal stage and total (all stages) survival was 62.7, 47.3 and 40.6%, respectively. The complete life cycle at 26 - 27°C required 34.7 days, ranging from 29.9 to 37 days. Female's fecundity was 231.8 eggs per female, with a range of 184. The longevity for single females and males when reared separately from one another was 48.7 and 22.0 days. In contrast, when males and females were reared together on the same leaf they lived for the same number of days (41.5 days), irrespective of sex. It is not clear if the discrepancies noted here in life history traits are due to genetically inherited differences among different psyllid isolates, as they could as readily be modulated by environment and/or even their histories of host plant association. Also, an additional possibility by which differences in fitness observed herein, compared to psyllid isolates studied previously (for which no voucher specimens are available), might be due to infection by some prokaryotes like *Wolbachia,* which already reported in literature that might influenced host fitness, e.g. fecundity and longevity.

Key words: *Bactericera*, fecundity, longevity, life cycle, tomato pest.

INTRODUCTION

In the U.S.A. the potato psyllid was first studied for a psyllid isolate collected from potato plants in Colorado by T. D. Cockerell. It was described by Sulc in 1909 and subsequently designated *Trioza cockerelli* and assigned to the genus *Paratrioza* by Crawford (Crawford, 1911). Recently the potato psyllid has been reassigned to the genus *Bactericera.* Until recently, this homopteran insect was reported as a pest primarily in potato, however, periodically it also has colonized tomato and pepper in the western U.S.A. (Arizona, California, Idaho, Kansas, Nevada, New Mexico, North Dakota, Oklahoma, South Dakota, Texas, Utah, and Wyoming) (Blood et al., 1933; Carter, 1950; Pletsch, 1947) therefore, it is commonly known as the potato or tomato psyllid. In addition to cultivated species, the potato psyllid's natural host range is rather wide, including species in 20 plant families with strong preference for solanaceous species (Pack 1930; Pletsch, 1947; Wallis, 1955; Liu and Trumble, 2006).

The first psyllid outbreak in California was recorded in 1940, and a second major outbreak was reported in the Midwestern USA in 1970 owing to unusual weather conditions (Hill, 1947; http://www.panhandle.unl.edu /potato/html/potato_psyllid.htm). Until about 2001, the potato psyllid was either unnoticed and/or of little consequence. However, during 2001 present, a series of outbreaks have been noted in tomato and potato recurring each year in the western US states of Arizona, California, Colorado, New Mexico, and Texas (west), in several northwestern US states, western Mexico (Al-Jabar, 1999; Hamm et al., 2003; Leyva-Lopez et al., 2002; Liu and

Trumble, 2004, 2005) and in Canada (Ferguson and Shipp, 2002). In 2006, the potato psyllid was a serious pest in potato in Guatemala and Honduras where it has been associated with discoloration and damage of potato tubers. Finally, during 2003 - 2004 the potato psyllid was shown to over-winter in vegetable fields for the first time in Ventura County, CA during 2004 (Lui et al., 2006).

The potato psyllid is migratory and has not survived winters in the High Plains or in the western U.S. or Sunbelt States without 'artificial' shelter. Temperature is a critical factor in psyllid outbreaks and range because they do not tolerate high temperatures, preferring 26°C (80 F). 2 h at 100 F has been shown to be lethal to eggs and nymphs, and temperatures > 30°C (90 F+) will reduce or cease egg laying, hatching and nymph survival. In Mexico and Central America, it cannot survive the high summer temperatures and so it migrates northerly through the Great Plains and west coast corridors, as temperatures increase and local solanaceous (and other) native winter and spring hosts decline. It is capable of living year round in certain locations in southern Texas and Mexico where temperatures are mild and food is available continuously. The characteristic habit, however has been migration northward during the spring and summer, and its dispersal is greatly facilitated by wind by which it can be carried great distances (Abernathy, 1991; Knowlton and Janes, 1931).

Diseased tomato plants exhibit decreased growth and reduced fruit size, and thus significant yield loss (Abernathy, 1991; Al-Jabar 1999). Up to 85% of mature plants have been reported affected by 'yellows' disease in California (Liu and Trumble, 2004). The economic damage caused by psyllids to potato or tomato is manifest as a 'yellows' symptom known as 'tomato yellows'. The disease is suspected to be caused by a toxin associated with feeding of the nymphal instars (Richards, 1928; Blood et al., 1933; Carter, 1950). However, Carter (1950) found that not all nymphs have the ability to produce this toxic reaction. Daniel (1954) reported a toxic reaction in tomato seedlings associated with adult feeding. Recently, reports from Mexico have attributed disease symptoms in tomato to phytoplasma infection, and it is suspected that the potato psyllids found on tomato plants may vector the phytoplasma although evidence for transmission is lacking.

During 2003 present, potato psyllid outbreaks have become routine occurrences in controlled environment facilities devoted primarily to fresh market tomato production in Arizona, California, and west coast Mexico. Available information in the literature on potato psyllid biology and life history are inconsistent, and there have been no studies published for this psyllid as a pest or vector of plant pathogens in controlled environment agriculture. For example, it has been reported by one group that oviposition is on the edge or on underside of the leaf, while another study indicated that eggs are scattered in the upper plant canopy (Knowlton and Janes, 1931; List, 1939; Pletsch, 1947). Female psyllids are reported to deposit as many as 500 eggs (Wallis 1955), and nymphal hatching has been reported to occur over a range of 3 - 15 d (Pack, 1930) depending on temperature. Other reports indicate a range of developmental times from 12 – 21 d (Knowlton and Janes, 1931; Pack, 1930). Herein, we hypothesize that published differences in life history traits could be do to adaptive differences in host preferences and temperature optima that might lead to biotype formation, and to the effects of *Wolbachia* or other prokaryotic organisms causing reproductive abnormalities that may have a fitness cost.

The objectives of this study were to: determine the life history parameters for an isolate of *B. cockerelli* recently problematic in controlled environment tomato production in the western U.S. (e.g. AZ - 06). Also, provided photographic renditions of psyllid eggs and anatomical differences between males and females under a stereo light microscope.

MATERIALS AND METHODS

Psyllid colony and manipulation

Studies of the life history of *B. cockerelli* AZ-2006 were conducted in the Department of Plant Sciences at The University of Arizona, on tomato *Lycopersicon esculentum* Mill. 'Humava'. Seeds were sown in pots (6.25 x 7.00") in an insect-free growth room (78 Fº, 12:12 day-night cycle) and plants were fertilized (15 – 20 - 15, soluble). Tomato plants at the four-six true leaf stage (~30 days post sowing) were infested with psyllids by introducing adults to caged plants. The colony was initially established by seeding it with 40 - 50 *B. cockerelli* adults that were collected from a tomato greenhouse located in southern Arizona (Cochise County, AZ) during March 2006. This isolate of *B. cockerelli* is hereafter referred to as the western US-Arizona psyllid (AZ-06) isolate.

Life history traits

For life history studies adult psyllids were released onto young tomato plants (4/cage) that had been transferred to and maintained inside a cage, and subsequent generations of adults were serially transferred to young plants, replacing older colonized plants, sequentially, as needed to sustain a continuous supply of psyllids from the colonies. Experimental conditions were 26 -27°C, with 60 - 70% humidity, and 12:12 day/night cycle. A number of small leaf cages (3.0 cm in diameter and 2.0 cm in height) were constructed to confine the adult psyllids to tomato leaves plants for various studies (Figure 1). The leaf cages were made from cylindrical semi-transparent plastic. A hole (0.75 cm diam) was made on side of each leaf cage to facilitate releasing of psyllids inside the cage. This hole later on was plugged with a stopper. On the cut end of the leaf cage, a piece of muslin mesh was glued into place to allow ventilation. A tomato leaf was inserted through the bottom of leaf cage and a sheet of sun-mica (4 cm^2) was used to support the cage on the underside of the leaf, which was covered with a thin piece of sponge (10 mm thick) using a hair clip. The leaf and stem to which the cage was attached were tied to a wooden stake to provide additional support.

Plants colonized by abundant last instars nymphs of *B. cockerelli* were taken from main colony after removing all the adults from them. The adults emerged from those nymphs were collected im-

Figure 1. Leaf cage attached to tomato leaf.

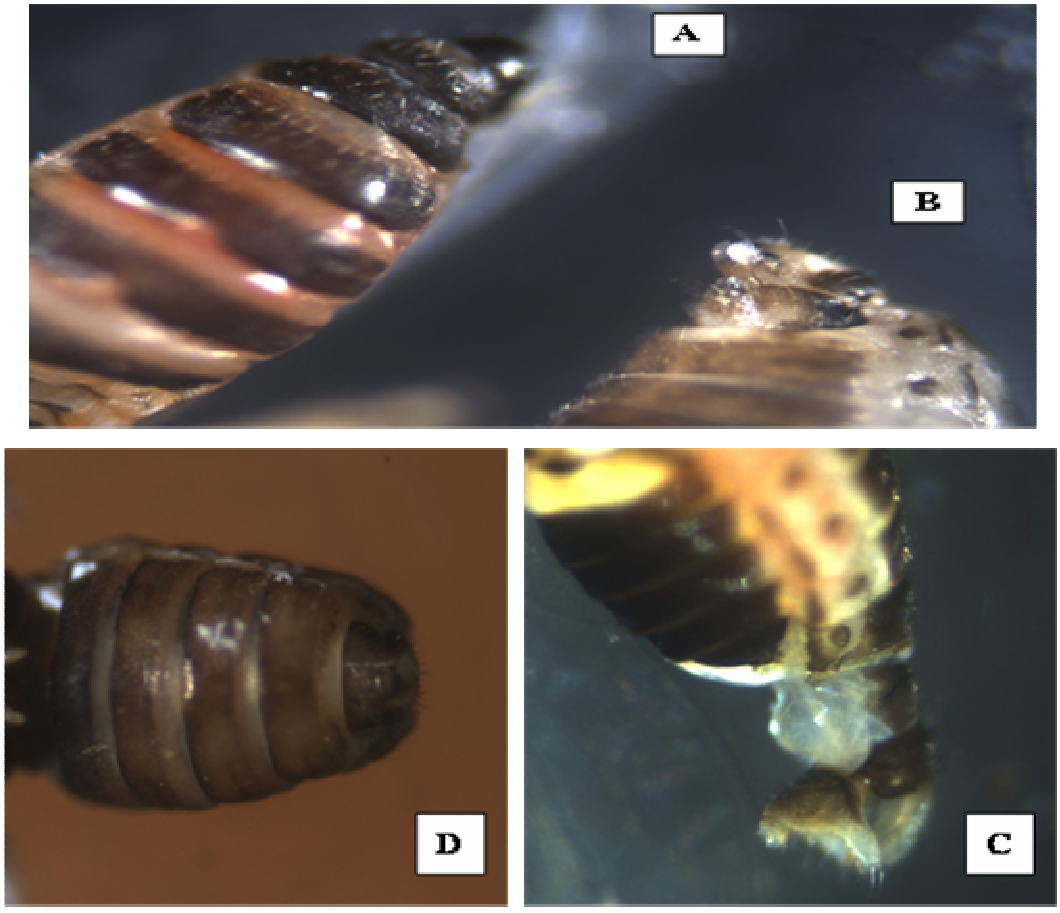

Figure 2. (A) Male of *B. cockerelli* with six abdominal segments plus the genitalia segment and mating organ out (C). Female (B and D) with five abdominal segments, plus the genital one.

diately upon emergence, sexed, and used for the life history study. Males and females were differentiated based on the apex of the abdomen, which is rounded and robust and terminates with a short ovipositor for females, compared to males, which have a more blunt appearance (Figure 2).

Pre-mating and pre-oviposition period

The newly emerged adults were sexed, grouped in pairs, and allowed to interact. Pairs were observed from the time they were collected until they initiated mating, which was considered the 'pre-

Table 1. Development period for *B. cockerelli* at each development stage*.

Total life cycle	Total developmental period	Nymphal instar development	Incubation	Pre-oviposition	Pre-mating
34.7 ± 2.76	28.4 ± 3.05	21.6 ± 2.82	6.74 ± 0.72	6.9 ± 0.67	4.2 ± 0.49

* Mean for 15 replications.

Table 2. Survival for the immature stages of *B. cockerelli**.

Total survival (%)	Nymphs (%)	Eggs (%)
40.6 ± 18.69	47.3 ± 21.77	62.7 ± 15.87

* Mean for 15 replications

Table 3. Longevity and fecundity of *B. cockerelli**.

Fecundity (No. eggs/ female)	Longevity (day)		
	Male	Female	Groups of males and females
231.8 ± 35.2	22.0 ± 3.4	48.7 ± 6.8	41.5 ± 2.4

*Mean for 15 replications.

mating period'. The time from emergence to oviposition of the first egg was considered the 'pre-oviposition period'.

Duration and survival of different immature stages

Leaf cages were attached to the lower leaf surface of fully opened top leaves. Ten pairs of *B. cockerelli* adults from the main colony were confined to each leaf cage for oviposition. After 24 h, adults and leaf cages were removed. The leaf portion located where the leaf cage had been attached was marked and the space under the marked zone was observed using a binocular stereomicroscope (20X) to count the eggs. Only 20 eggs (Figure 3A) were allowed to remain on the leave for the life history study. The surplus eggs were removed carefully with the help of needle and fine brush. The leaf cages were reattached to leaves using the marked area as a guide, in order to prevent any unintended oviposition and movement of crawlers outside the marked area. The eggs and then development of instars (Figure 3B and 3C) in the marked area were observed daily using a binocular stereomicroscope, and observations were recorded at intervals of 24 h.

The time period between oviposition and the first appearance of the crawlers (first nymphal instar) was considered the 'incubation period'. Similarly, the time period between the appearance of crawlers and first adult emergence was defined as the 'immature stage period'. The period from egg laying to the appearance of an adult was considered the 'total developmental period', whereas 'total developmental period' plus 'pre-oviposition period' was used to calculate the duration of the 'total life cycle'.

In addition, the survival of eggs, nymphs and the total survival were recorded. The adults emerging from the last nymphal stage were collected and sexed for recording the sex ratio.

Fecundity and longevity

For fecundity studies, one newly emerged male and one female were collected and released inside a leaf cage attached to lower leaf surface of fully opened top leaves. The number of eggs deposited by each female was counted until all pairs of mated adults had died. The newly hatched nymphs were counted as eggs.

For longevity studies, ten individual and five pairs of newly emerged females and males were released in separate leaf cage each attached to the top of a fully expanded tomato leaf. The mortality of the adults in each cage was counted daily and the weighted mean of longevity, and the standard deviation, were determined for fifteen replications.

RESULTS AND DISCUSSION

Life history

Under these experimental conditions the total developmental period ranged from 25 to 33 d, with an average of 28.4 d (Table 1). The pre-mating period was 4.2 d in duration, with a range of 3.8 – 5 d. The pre-oviposition period was 6.9, and ranged from 5.9 – 8.0 d (Table 1). The incubation period for the eggs was 6.7 d (range 5.7 - 8.2 d), making the nymphal period 21.9 (19.1 - 23.8 d). The survival of different immature stages (Table 2) was 62.7 percent eggs, 47.3 percent for nymphs, whereas, total survival was 40.6 percent. The highest mortality was recorded for nymphal instars. Females exhibited moderate fecund (Table 3) at 231.8 eggs per female, with the range being 184 to 258 eggs, per female. The longevity (Table 3) of female psyllids maintained separate from males was greater than males reared analogously, whereas, males and females both lived for longer periods of time when they were reared together, as demonstrated by longevity of lone females and males at 48.7 and 22.0 d, respectively. The sex ratio for the western US potato psyllid indicated a slight female bias, at 1.1 ± 0.12 (range 1.0 - 1.3), a value that is in agreement with Knowlton

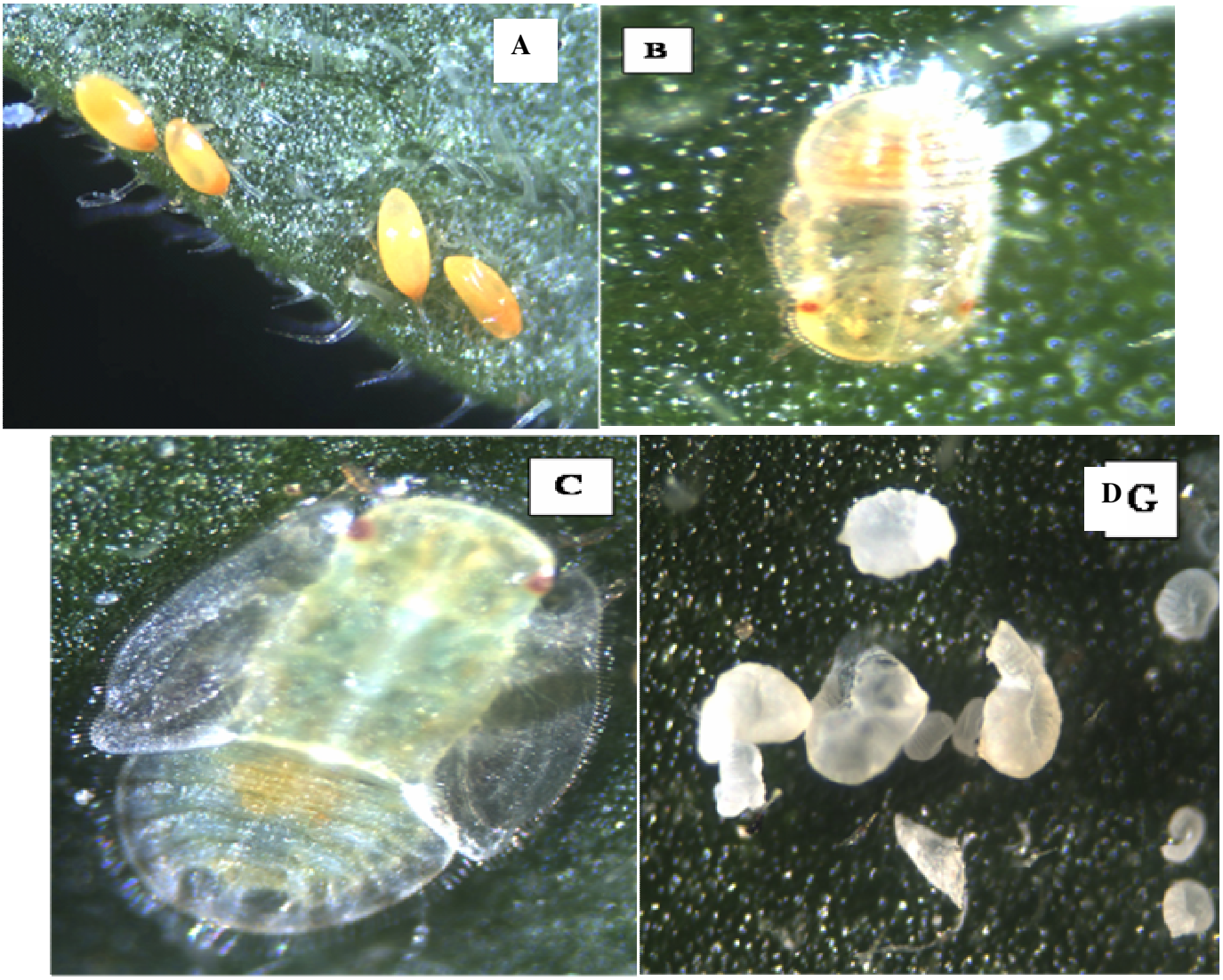

Figure 3. (A) Eggs along the leaf margin with stalks visible, (B) First (crawler) nymph stage, (C) Last nymphal instar of *B. cockerelli*, and (D) crystalline honeydew.

and Janes (1931), or about an equal number of males and females.

The potato psyllid has only recently colonized and reached high densities in greenhouse grown tomatoes in Arizona, California, and west coast, coinciding with a similar timeframe for unprecedented infestations in field-grown, fresh-market tomato crops in northwestern Mexico and California (Liu and Trumble, 2004), where disease symptoms affected 70 - 80% of the plants. These reports coincide with the increased practice of cultivating tomato crops in protected and/or hydroponics/greenhouse culture systems, and so it is probably accurate to state that until several years ago, the potato psyllid was not considered a major pest of tomato until quite recently.

Also, we observed that the immature psyllids produced copious amounts of honeydew on tomato plants, which appears to be excreted in droplets that harden soon after making contact with the air. This crystalline honeydew, which contains sugars and hydrocarbons (P. Evans, J. K. Brown, and N.M.M. Abdullah, unpublished data) is only partially water soluble and can be a problematic contaminant on tomato leaves and fruit (Figure 3D). The presence of this substance has provided an excellent indicator of psyllid infestations given the tiny size of nymphs and the difficulty associated with identifying them particularly when infestations are mixed with whiteflies including the sweet potato whitefly, *Bemisia tabaci* (Genn.), and the greenhouse whitefly, *Trialeurodes vaporariorum* (West.).

Information in the literature on the life history of the potato psyllid was found to be highly inconsistent. Also, no information was available concerning life history parameters under conditions employed in controlled environment facilities for tomato cultivation. For example, females have been reported to oviposit on the edge or the un-

derside of the leaf, and also eggs can be scattered over the upper plant canopy (Knowlton and Janes, 1931; List, 1939; Pletsch, 1947). Female psyllids have been reported to produce as many as 500 eggs (Wallis, 1955), with minimum and maximum numbers at 250 and 1300, respectively (Knowlton and Janes, 1931). We noted that the fecundity for the AZ - 2006 colony, at 231.8 eggs per female, was moderate to low, with respect to the published range. Compared to egg survival at 62.7% for AZ - 06 (Table 2), results of Knowlton and Janes (1931) indicated a much greater survival rate (73%). Hatching of nymphs from eggs was reported to be temperature dependent, though herein we maintained a constant temperature (26 - 27^{0}C) and so did cannot comment on differences that might be attributable to temperature fluctuations. Values for egg hatch published in the literature ranged from 3 - 15 d (Pack, 1930), however, the incubation and nymphal periods for the AZ isolate of *B. cockerelli* at 6.74 and 21.6 d, which were in agreement with the results reported by Pack (1930), in which incubation periods of 3 - 15 days and nymphal periods of 14 to 17 days were observed. The time of development from egg to adulthood ranged from 12 – 21 d for two other studies (Knowlton and Janes, 1931; Pack, 1930). Further, Knowlton and Janes (1931) observed incubation and nymphal periods for *B. cockerelli* of 3 to 9, and 12 to 21d, respectively. This was in contrast to incubation and nymphal periods for the AZ-06. Previous studies indicated that the potato psyllid life cycle was completed in as short an interval as 15 - 17 d, or that it could require as long as 30 - 32 d. In contrast, the life cycle of AZ-06 at 26 - 27°C was 34.7 d (range, 29.9 to 37 d), or about one week longer than previously reported. Longevity values reported for males and females range from 1 to 64 d, and 1 to 189 d, respectively, under the laboratory conditions (Knowlton and Janes, 1931). In comparison, the longevity for AZ-06 males and females reared in isolation from one another was 22.0 and 48.7 d, respectively, making it 1.4 times greater for females than that reported by Knowlton and Janes (1931). Further, when males and females were reared together, their longevity was 41.5 d, irrespective of the sex. This is the first report for longevity for males and females reared on the same plant and likely provide a more realistic estimate of longevity, as well as suggesting that they are capable of synchronizing their activities, possibly including the reproductive period, under the conditions provided. It is not clear if the discrepancies noted here in life history traits are due to genetically inherited differences among different psyllid isolates, as they could as readily be modulated by environment and/or even their histories of host plant association.

We have considered an additional possibility by which differences in fitness observed herein, compared to psyllid isolates studied previously (for which no voucher specimens are available), might be due to infection by some prokaryotes like *Wolbachia* (Prakash, and Puttaraju, 2007) that might influenced host fitness, e.g. fecundity and longevity. However, individual psyllids from field collections were found to be infected with two *Wolbachia* species based on PCR amplification of the *wsp* gene (Liu et al., 2006). In the long run, *Wolbachia* may confer negative fitness to the host, which can be manifest as reduced fecundity (Stouthamer et al., 1999; Werren, 1997). *Wolbachia* also induces reproductive aberrations that can involve a number of distinctive phenotypes, including female offspring mortality, feminization of males, and parthenogenesis (Werren, 2000; Kageyama et al., 2002; Duron et al., 2007; Kassem and Osman, 2007). *Wolbachia*-associated reproductive alterations include the induction of parthenogenesis (Arakaki et al., 2001; Weeks and Breeuwer, 2001), conversion of genetic males into functional females, male killing, and the induction of cytoplasmic incompatibility (CI) (Breeuwer and Werren, 1990; O'Neill and Karr, 1990; Hoffmann and Turelli, 1997 Hurst et al., 1999; Fialho and Stevens, 2000; Hurst et al., 2000). CI is manifest as embryonic lethality in crosses between males and females for which only one of the isolates is infected, or when both are infected but with different *Wolbachia* (Koukou et al., 2006; RongRong et al., 2006; Zeh and Zeh 2006; Sanogo et al., 2005; Tagami et al., 2006).

Liu et al. (2006) examined collections from the western US and Mexico using several molecular markers (mtCOI, ITS2, ISSR) and speculated based on the results that a new biotype of psyllid may have emerged there in tomato and pepper fields. Analysis of the collective markers for a collection of potato psyllids from fields in the USA and eastern Mexico revealed one possibly significant marker, the ISSR (60 - 83% polymorphic loci), a result which suggests a possible geographic range expansion of a distinct genotype. Also, individual psyllids from field collections were found to be infected with two *Wolbachia* species based on PCR amplification of the *wsp* gene (Liu et al., 2006).

The result of Liu et al. (2006) is very interesting nonetheless; because it suggests the possibility that examining this more highly divergent *Wolbachia* gene may facilitate the discovery of co-infecting *Wolbachia*. In contrast, it is also possible that the particular psyllid populations associated with controlled environment tomato production have become ecologically isolated from psyllid field populations in the region owing to their year round association and adaptation to these unique controlled environments, which provide shelter and sustained resources that are not proximally available in field cropping systems, which typically implement voluntary or weather-induced host-free periods. If the former is the case, short and long-distance migration may well occur exclusively between greenhouse facilities within and across the regional corridor, having the effect of selecting for a psyllid population(s) that has adapted to controlled environment facilities. A second possibility for the recent resurgence in potato psyllid in western North America in general is the seasonal increase in temperature, which could support

psyllid survival spatially and temporally where it has been incapable of surviving until now.

Finally, a previously once rare or incidental pest and vector of biotic and/or abiotic disorders, including psyllid yellows disease as yet of unknown etiology, and phytoplasma infection, have become more prevalent in both field and greenhouse grown solanaceous crops. Thus the speculation by Lui et al. (2006) that the potato psyllid now prevalent in and adjacent to the western U.S., may have emerged as a separate biotype, has some validity. If this is found to be so, life history traits, host preference, and pathogen transmission promises to take on an entirely new venue. Certainly, studies carried out decades ago may serve as a guide for understanding and controlling the potato, or tomato, psyllid but it is apparent from the study reported here that certain parameters were inconsistent with those in the published literature, in that the fecundity and longevity are lower than expected, while developmental time is longer. It is possible that these life history traits make this isolate of psyllid most adaptable to greenhouse environmental conditions, which are generally more consistent with respect to the external environment, in which conditions (temperature, humidity) fluctuate to greater extremes than they do inside controlled environment, or protected, facilities. The present wisdom would advocate caution and further study of this pest and potential vector, given the possibility that a new biotype may have arisen and has become pervasive in the western US owing to one or more variables (changing agri-cultural practices, monoculture, altered environment / temperature-humidity, relaxed natural enemy pressures, and/or *Wolbachia* infection), which are still not understood. Nonetheless, it has become clear that a new set of considerations for psyllid management will be required, and likewise, for the control of several associated pathogens/abiotic diseases associated with psyllid infestations, respectively. Based on the collective recent observations, it is clear that the causality of psyllid-associated biotic and/or abiotic diseases now needs to be determined.

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