Title

The Influence of Maturity and Variety of Potato Plants on Oviposition and Probing of Bactericera cockerelli (Hemiptera: Triozidae)

Permalink
https://escholarship.org/uc/item/8hj7t763

Journal
Environmental Entomology, 43(2)

ISSN
0046-225X

Authors
Prager, Sean M
Lewis, O Milo
Michels, Jerry
et al.

Publication Date
2014-04-01

DOI
10.1603/en13278

PLANT-INSECT INTERACTIONS

The Influence of Maturity and Variety of Potato Plants on Oviposition and Probing of *Bactericera cockerelli* (Hemiptera: Triozidae)

SEAN M. PRAGER,[1,2] O. MILO LEWIS,[1,3] JERRY MICHELS,[3] AND CHRISTIAN NANSEN[1,4]

Environ. Entomol. 43(2): 402–409 (2014); DOI: http://dx.doi.org/10.1603/EN13278

ABSTRACT The ecological theory on host plant choice by herbivores suggests that mothers should choose plants that will maximize their offspring's success. In annual host plants, physiology (and therefore host suitability) is sometimes influenced by maturity and growth stage, which may influence female choice. Potato plants were grown under greenhouse conditions and used in choice and no-choice bioassays to determine the effect of plant maturity and variety on oviposition and number of stylet sheaths (which approximate stylet insertions) by tomato/potato psyllids. No-choice bioassays suggested that maturity (time since planting) did not influence oviposition behavior, but oviposition varied significantly among potato plant varieties. There was a significant effect of both maturity and variety on the number of stylet sheaths, which peak toward the middle of the growing season. We also examined tomato/potato psyllid responses to plants grown in a commercial field and again found no effect on oviposition but differences in stylet sheaths. The results suggest that differential susceptibility to zebra chip disease may be associated with unequal feeding rates. Future studies should examine whether the maturity of plants influences larval fitness. Finally, potato variety has an influence on both oviposition and "probing," and has implications for management strategies and the development of resistant potato varieties.

KEY WORDS potato psyllid, zebra chip, host choice, *Candidatus Liberibacter solanacearum*

Many studies of host plant choice in arthropods are based on the concept that females should choose plants for oviposition that will result in maximum performance of their progeny. This idea, referred to alternatively as optimal oviposition theory (Thompson 1988, Scheirs et al. 2000), the "mother knows best" principle (Valladares and Lawton 1991, Johnson et al. 2006), and the preference–performance hypothesis (P-P) (Jaenike 1978), has been the foundation of countless studies of insect host choice behavior (Wiklund 1975, Futuyma and Moreno 1988, Bar-Yam and Morse 2011). A core element of P-P is the fact that immature stages of herbivores often have limited mobility and subsequently will be forced to feed from those plants on which they emerge, and thus a female should choose plants on which larvae will best survive and develop. However, because fecundity is often associated with the nutritional quality of host plants (Heisswolf et al. 2005), studies of P-P have also been known to incorporate adult feeding behavior (Coyle et al. 2011, Hoffman and Rao 2011).

The maturity or growth state of a plant has an influence on numerous physiological traits including the amount, variety, and location of sugars and carbohydrates; the rate of photosynthesis; the distribution of resources; and elements of plant defense (Jamieson and Bowers 2011, Quintero and Bowers 2012). Studies comparing plant physiology and host plant quality have examined factors including bud burst (Hunter 1992), leaf flush (Murali and Sukumar 1993), leaf aging (Feeny 1970, Raupp and Denno 1983), availability of young tissue (Steinbauer et al. 1998, Tsai and Liu 2000, Nava et al. 2007), and nitrogen concentration (Selman 1994), all of which are associated with plant maturity. In the case of perennial plants, such as trees, these factors are more likely to be associated with old and new growth. However, in annual crop plants or those plants that are completely harvested such as root vegetables, an additional factor is that the plant must not senesce before larvae successfully develop (Fordyce and Nice 2002, Doak et al. 2006). The effect of age on the suitability of leaves has been reviewed on numerous occasions (see Raupp and Denno 1983, and references within). However, studies on this topic in psyllids have been mostly restricted to the Asian citrus psyllid (*Diaphorina citri* Kuwayama) (Moran and Buchan 1975) and are unavailable in potato psyllids (*Bactericera cockerelli* (Šulc) (Hemiptera: Triozidae).

The tomato/potato psyllid (TPP) is a pest of solanaceous crops and is reported to survive and develop

---

[1] Department of Entomology, Texas A&M AgriLife Research and Extension Center, 1102 E FM 1294, Lubbock, TX 79403.

[2] Corresponding author: Department of Entomology, University of California, Riverside, CA 92521 (e-mail: sean.prager@ucr.edu).

[3] Texas A&M AgriLife Research and Extension Center, 6500 Amarillo Blvd., West Amarillo, TX 79106.

[4] The University of Western Australia, School of Animal Biology, The UWA Institute of Agriculture, 35 Stirling Highway, Crawley, Perth, Western Australia 6009.

on ≈40 species in 20 plant families (Pletsch 1947, Wallis 1951, 1955; Butler and Trumble 2012a). Nymph development is known to vary with host plant species (Abdullah 2008, Yang et al. 2010), and host choice has been shown to vary among plant species (Yang et al. 2010, Butler and Trumble 2012a). TPP is the sole known vector of the fastidious pathogenic bacteria *Candidatus Liberibacter psyllaurous* (syn. "*Ca.* L. *solanacearum*") (CLP), the causal agent of "zebra chip" disease (ZC) in potatoes, which has resulted in millions of dollars in losses to potato growers (Butler and Trumble 2012a).

Before the discovery of CLP, Hodkinson and Hughes (1982) found that biochemical and/or mechanical changes resulting from TPP infestation could alter host plant quality. Since then, at least three studies have examined the effect of infection on plant and tuber physiology. Rashed et al. (2013) demonstrated that the time of infection with CLP influences disease symptoms and is associated with changes in levels of phenolics, peroxidases, polyphenol oxidase, and reducing sugars. Similarly, Gao et al. (2009) demonstrated that levels of sugars, including glucose, differ in potato plants with age and time of ZC infestation. Specifically, plants infested earlier (4 wk) exhibited more severe symptoms than those infested at 6 or 10 wk while also exhibiting lower sugar and higher starch levels. Gao et al. (2009) further noted that the size of developing leaves is important in photosynthesis and that the stunted, chlorotic leaves often observed in ZC-infected plants result in an overall reduction in photosynthesis. Although the authors do not present a mechanism for these age (maturity)-related patterns, they suggest that mature leaf material is less palatable to psyllids and thus is not fed on as frequently. Finally, Wallis et al. (2013) examined different potato varieties and multiple times after CLP infection and found that the severity of symptoms at a given time varied among varieties. They also demonstrated that the levels of amino acids, carbohydrates, and phenolic compounds vary among varieties, although no distinct patterns were detected.

We predicted that TPP would preferentially oviposit on plants that are young enough to guarantee successful nymphal development and in which more resources are directed to vegetative growth, but which are old enough to provide suitable leaf material and nutrients. We further expected that oviposition would vary among potato varieties that have different growing season durations. Further, we similarly predict that probing/feeding behavior will be influenced by plant maturity that is also associated with nutrient distribution. To test these predictions, we used controlled laboratory bioassays conducted on greenhouse-grown and field-collected potato plant leaflets.

Materials and Methods

Potato Development. Because this study is based on the concept that time since planting and therefore plant maturity (age) will influence TPP behavior, it is important to understand potato phenology and development. Here we present a brief description of potato development. Potato development is typically divided into five "growth stages" (Stark and Love 2003). During Stage 1, the eyes of a seed tuber develop into sprouts and grow toward the surface. The second stage is essentially vegetative growth, but typically is also when roots and stolons develop and when photosynthesis begins. The third and fourth stages are primarily centered on the tuber. Stage 3 is tuber development from the stolon and Stage 4 is "tuber bulking"; during this stage, tubers become the dominant site for receiving nutrients. In many, but not all, varieties, Stage 3 corresponds to flowering. During the final stage, vines begin to yellow and eventually die, while tuber dry matter is maximized. Critically, these stages are approximate and often defined based on events in the tuber that are not visible without digging out plants (Haga et al. 2012). Moreover, there are few distinct morphological events in potato development (Jefferies and Lawson 1991) and phenology varies among varieties (Tekalign and Hammes 2005). For example, Werner et al. (1998) demonstrated that tuber specific gravity, an indicator of dry matter and starch, generally starts low and reaches a maximum approximately 7–11 wk after tuber set. Unfortunately, even this pattern is of little predictive value (Marwaha and Kumar 1987) because specific gravity can vary among years, fields, and tubers (Lana et al. 1970, Werner et al. 1998). Similarly, flowering, which is visible, is not well correlated with potato maturity or chlorophyll content (Haga et al. 2012).

Insects and Plants. TPPs used in this study were maintained in culture at the Texas A&M AgriLife Research and Extension Center (Lubbock, TX). Cultures were reared on tomato plants, and occasionally supplemented with potatoes. Cultures were maintained at 25°C and 30–60% relative humidity (RH) using artificial light (Ecolux, F40PL/AQ-ECO; GE Lighting Lamps, Fairfield, CT) and at a 14:10 (L:D) photoperiod. Insect cultures were established with individuals from cultures at the Texas A&M Agrilife Research, Weslaco and Bushland, TX.

This study examined four varieties of greenhouse-raised potatoes (*Solanaum tuberosum* L.): Red LaSoda, FL 1867, Atlantic, and Russet Norkotah. Russett Norkotah is an early maturing potato variety, FL1867 is early medium maturing variety, and both Red LaSoda and Atlantic are medium maturing varieties. For context, very early maturation is ≈90 d, whereas very late is beyond 120 d. All plants were planted in 7.6-liter plastic pots with Metromix 900 Professional Growing Mix (Sun Gro Horticulture Canada Ltd., Agawam, MA), fertilized weekly with Peter's Professional 20–20-20 growing media, and watered ad libitum. Plants were maintained in mesh tents (60 cm in height, with a 60 by 60-cm base) (BugDorm, MegaView Science Co., Taichung, Taiwan). In the following, all bioassays were conducted with excised terminal leaflets from potato plants.

Excised Leaflets vs. Intact Plant Bioassays. Excising a leaflet is likely to change physiological aspects of a leaf. It has been suggested that such changes may alter host plant choice and should be considered when conducting host choice bioassays (Clark et al. 2012). To determine how excising leaflets from a plant affects psyllid probing, we compared stylet sheaths between leaflets from whole intact plants and excised leaflets. Kennebec (late maturing) variety potato plants were grown under identical conditions in 15.25-cm pots in a 3:1 soil (Sunshine Mix #1 by Sun Gro Horticulture Canada Ltd.) to sand (Quikrete Play Sand #1113, Atlanta, GA) mixture. Four weeks after planting, plants were then randomly assigned to one of two treatments. In one treatment, a custom-built 1-cm (in diameter) by 2-cm (in height) clip cage was clipped onto a terminal leaflet in the middle of the plant. In the second treatment, terminal leaflets in the middle of the plant were excised and placed into a water-filled plastic vial. A clip cage identical to those used for intact treatments was then placed onto the excised leaflet. In each treatment, two unsexed teneral adult TPPs were added to the cages. After 48 h, TPPs and clip cages were removed and all terminal leaflets were subjected to McBryde's staining process (Backus et al. 1988) and the number of stylet sheaths along the mid-rib was counted. Data were only included if at least one live TPP was recovered and there was either one egg deposited or one probing event.

No-Choice Bioassays with Greenhouse-Reared Potato Plants. No-choice bioassays were conducted in arenas consisting of a 1-l Mason jar covered with a 12-cm square piece of white chiffon fabric. A 40-ml plastic vial was attached to the metallic lid of the Mason jar, filled with tap water, and placed inside the jar to hold leaflets. In each assay, TPPs were presented with a complete (five leaflets) excised leaf cut from the top third of potato plants and trimmed to only the terminal leaflet. Assays were conducted with five post-teneral unsexed TPPs. Following a 72-h exposure, live and dead adults were recovered, the number of eggs on leaves was counted, and leaves subjected to McBryde's staining process and the number of stylet sheaths along the mid-rib was recorded. To determine the effect of "maturity" (days since planting) on oviposition and probing, leaflets were collected at multiple time points and used in bioassays.

No-Choice Bioassays with Potato Plants From Field Plots. Because growing conditions may influence host plant suitability, we also conducted no-choice bioassays with leaflets from plants collected in field plots. All leaflets came from potatoes (variety Russet) collected at Springlake Potato, Springlake Texas (34.1° N, −102.3° W). All potato plants were grown according to local cultural practices, except no insecticides were applied. The first samples' leaflets were collected 6 wk after planting (approximately Stage 2), and leaves were collected for approximately 6 wk. In conducting assays, leaflets were collected from the top third of the plant, processed, and immediately placed into vials of water as in greenhouse bioassays. Vials were subsequently stored in ice chests, returned to the laboratory, and TPPs were added. Assays were otherwise conducted as mentioned earlier.

Greenhouse Three-Choice Bioassays. To determine if TPPs have a preference for leaflets of a given age or either probing or oviposition, and because behavior may differ when an insect is not restricted to one plant, we conducted three-choice bioassays. Bioassays were conducted using leaflets from greenhouse-raised plants (variety Frito Lay 1867). Plants of three maturity levels were used: "young" (30 d after planting), "middle" (45 d after planting), and "old" (60 d after planting). In these bioassays, plastic vials in arenas were replaced with three 6-ml glass vials to hold leaflets. Each arena contained one leaflet of each maturity level, randomly assigned to a position and selected from the same top third of plants. While multiple leaflets were taken from a potato plant, new plants were sampled for each time point. Bioassays were otherwise conducted as mentioned earlier.

Statistical Analyses. The number of stylet sheaths on excised leaflets versus the number from intact plants was compared with a Mann–Whitney *U* test. Because there are few morphological correlates of maturity (Jefferies and Lawson 1991), we chose to create bins of days since planting. Although this has its own complications, for example, potato plants planted at the same time can reach different maturity levels at different times, it solves other issues such as the inability to examine morphological changes below the soil. The number of bins was determined based on Freedman and Diaconis' rule (1981). This process resulted in categories that approximate 5-d periods and were used in all subsequent analyses. This will subsequently be referred to as "bin." For the FL 1867 variety, this process resulted in only three bins, whereas all other varieties were placed into six bins. This difference seemingly results from the relative growing times of the different varieties. Counts of eggs or probing were analyzed using linear mixed models (R 2.15.0) with a negative binomial probability distribution implemented using the MASS package (Venables and Ripley 2002) and a model that included fixed factors for time since planting (leaflet age as bin) and variety. Counts of eggs and probing events in bioassays on field-collected materials were examined with linear mixed models with negative binomial distributions as mentioned earlier. Because all leaves were from a single variety (Russet), no variety term was included in the model.

Three-choice bioassays were examined using a generalized linear model with a negative binomial probability distribution and the fixed factors of age (young, middle, and old) and replicate. The same model was used to examine numbers of stylet sheaths and counts of eggs.

Results

Excised vs. Intact Plant Bioassays. There was no significant difference in the number of stylet sheaths on leaflets that were excised (8.2 ± 6.2) and from intact plants (8.6 ± 7.5) ($W = -175.5$, $P = 0.51$, $n = 20$).

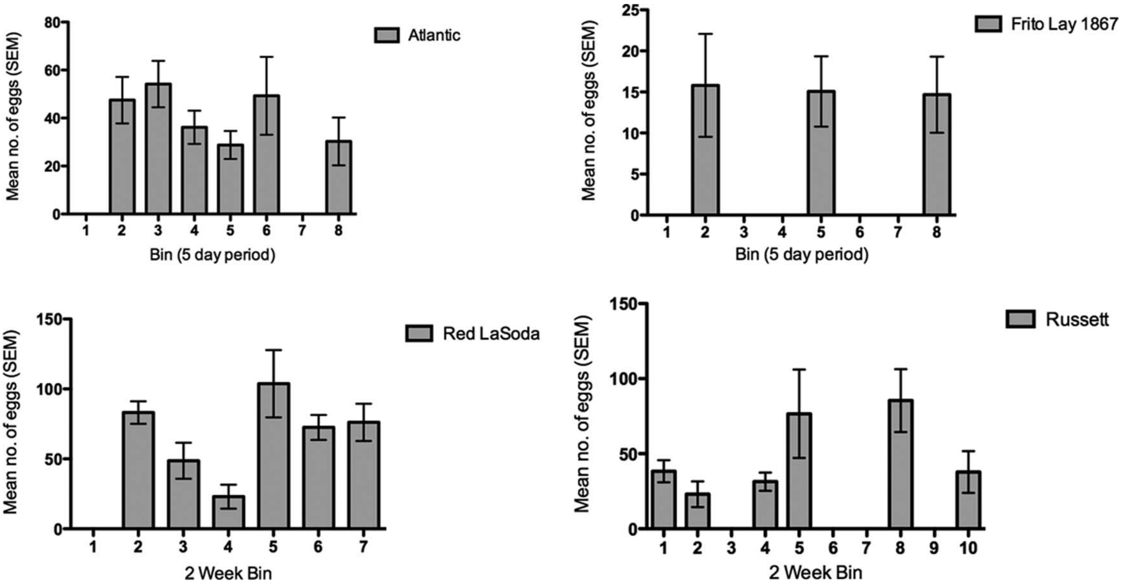

Fig. 1. Mean eggs in no-choice bioassays over time for greenhouse-grown plants. Bins with no bars indicate no data were collected for the period contained within that bin.

No-Choice Bioassays. The linear model of oviposition on leaflets from greenhouse-reared plants revealed a significant effect of variety ($\chi^2 = 33.9$, df = 3, $P < 0.001$) (Fig. 1). However, there was no significant effect of bin ($\chi^2 = 7.7$, df = 9, $P = 0.56$) or the interaction of bin and variety ($\chi^2 = 11.5$, df = 8, $P = 0.17$). In contrast to oviposition, the number of stylet sheaths differed significantly among varieties (Fig. 2) ($\chi^2 = 51.0$, df = 3, $P < 0.001$) and bin ($\chi^2 = 28.0$, df = 9, $P < 0.001$), but interaction of bin and variety was not significant ($\chi^2 = 11.1$, df = 10, $P = 0.35$). In each variety, there is a distinct spike in the number of stylet sheaths about halfway through the season, with few stylet sheaths in the early and late bins. Regarding data obtained from potato plants grown in field plots, oviposition did not differ significantly with bin ($\chi^2 = 3.32$,

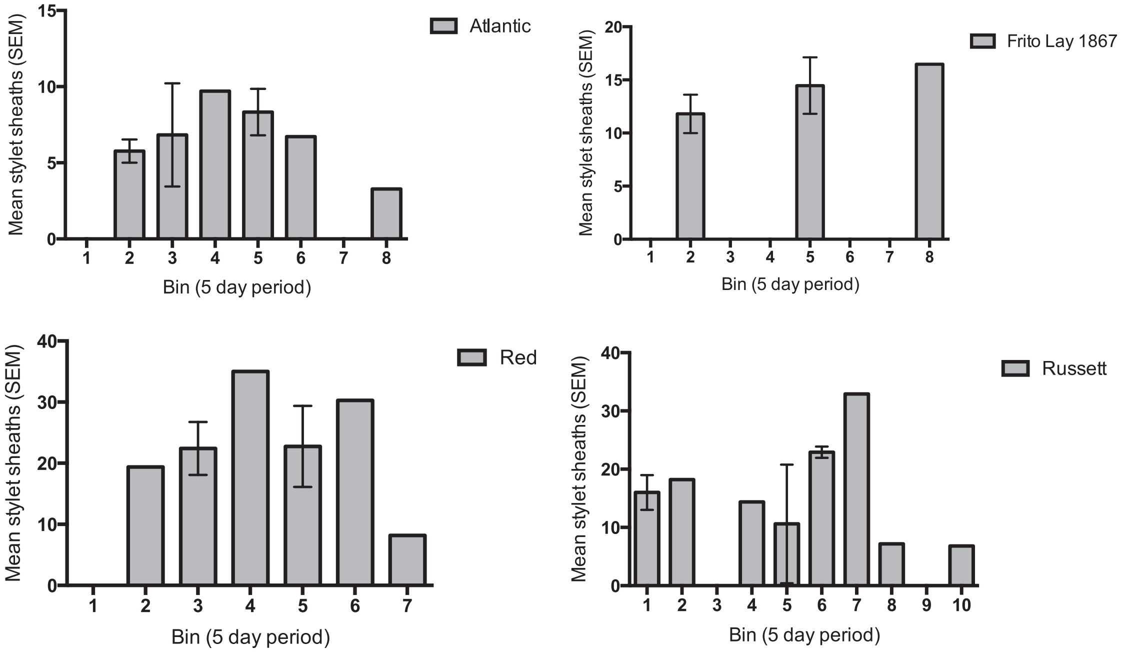

Fig. 2. Mean number of stylet sheaths in no-choice bioassays over time for greenhouse-grown plants. Bins with no bars indicate no data were collected for the -period contained within that bin.

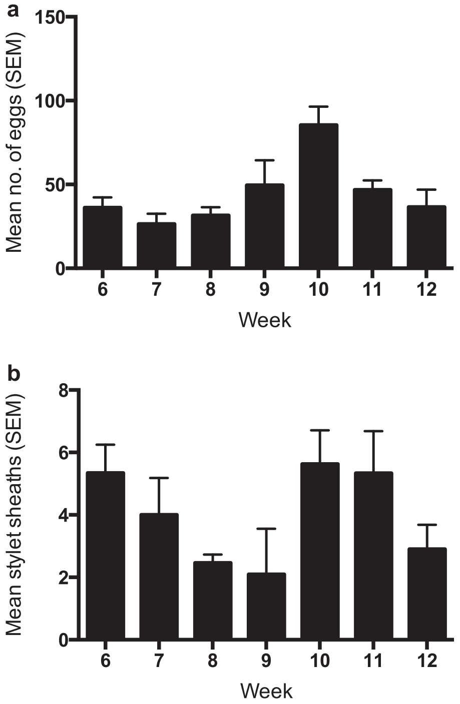

Fig. 3. The mean number of eggs (a) and probing events (b) in no-choice bioassays of field-collected leaves. Week 0 being day of planting, subsequent weeks indicate 7-d spans from that point.

df = 1, $P = 0.07$), but probing did ($\chi^2 = 35.45$, df = 7, $P < 0.001$) (Fig. 3a). Interestingly (Fig. 3b), the pattern with respect to stylet sheaths from field-collected leaflets was nearly bimodal and did not exhibit the pattern observed from the greenhouse plants (Fig. 2).

Three-Choice Bioassays. There was no significant effect of bin ($\chi^2 = 0.5$, df = 2, $P = 0.7$) or replicate ($\chi^2 = 0.9$, df = 1, $P = 0.32$) on oviposition, nor was there a bin by replication interaction ($\chi^2 = 0.96$, df = 2, $P = 0.6$). Likewise, there was no effect of bin ($\chi^2 = 4.2$, df = 2, $P = 0.1$) or replicate ($\chi^2 = 2.2$, df = 1, $P = 0.13$) on the number of stylet sheaths. There was also no replicate by bin interaction ($\chi^2 = 2.6$, df = 2, $P = 0.27$).

Discussion

We conducted no-choice bioassays to examine the maturity and variety of potato plants and what influence they played on oviposition and probing by the TPP *B. cockerelli.* Consistent with our expectation, there were significant effects of variety on both behaviors, and this result was present both in greenhouse and field-grown plants. However, contrary to our expectation, there was no significant effect of maturity on oviposition in any context, including both three-choice and no-choice bioassays. The finding that oviposition varied among varieties is similar to what has been observed with TPP on different tomato varieties, a pattern that is likely due to differences in attractiveness of leaf tissue (Liu and Trumble 2004). Various studies of *B. cockerelli* have demonstrated variation in oviposition rates, and these patterns have been linked to numerous factors including the geographic origin of the psyllid population, nymphal survival rates, and nymphal development period(s), in addition to the attractiveness of the plant material.

The finding that the maturity of a leaflet does not influence oviposition is somewhat intriguing. One explanation is that maturity does not influence nymphal performance, and thus selection has not occurred for a preference. We did not examine the rate of hatching or development of nymphs and this is a possibility we cannot currently address, but which deserves future study. It is also possible that our extreme maturity level (oldest plants) was not old enough to detect a difference, although it is unclear how old is "too old." We did not examine plants that were starting to senesce and it may be that only these are actively avoided, as all others will live long enough for TPP nymphs to develop. A final explanation is that because TPP is synovigenic (S.M.P., unpublished data), there is no substantial cost to mistakenly ovipositing on an old plant aside from the cost and time to develop new eggs. Further, when younger plants or alternative host plants are unavailable, this may still be a more optimal choice.

In contrast to oviposition, TPPs were choosy with regard to the maturity of plants with respect to probing. If feeding and oviposition were associated, one might expect correlated choices in both eggs and stylet sheaths. Possibly, the lack of association is because females choose plants for their own fitness rather than that of their offspring, a variation of "optimal bad motherhood" (Mayhew 2001). This might be possible if plant age influences adult traits such as life span, egg development, or energetics, but not larval performance. This too deserves further study using adult females on plants of different maturities. One final explanation for an age effect on probing/feeding but not on oviposition is sensory. TPPs respond to multiple types of cues, including visual (Demirel and Cranshaw 2006, Wenninger et al. 2009), olfactory (Wenninger et al. 2009, Diaz-Montano and Trumble 2013), and sensory organs on the mouth parts (Butler et al. 2012); these cues also interact (Patt et al. 2011). Therefore, TPPs may choose feeding based on different cues than are used for oviposition and age may not influence these cues. Finally, Davis et al. (2012) noted a decrease in TPP density on plants after flowering. While we did not explicitly examine density, stylet sheaths are correlated with TPP density (O.M.L., unpublished data), and are thus in partial agreement with the findings of Davis et al. (2012).

In potato plants, the top portion of plants consists of newer growth, and multiple studies have demonstrated that TPPs are more prevalent in the top portion of potato plants (Butler and Trumble 2012b, Martini et al. 2012). Similarly, the Asian citrus psyllid prefers new shoots to older leaves (Hall et al. 2012, Grafton-Cardwell et al. 2013), which is not reflected in stratification but does influence where TPPs are located within plants. All the leaf material in our bioassays was collected from the upper third of plants, and bioassays were therefore conducted using relatively new leaf tissue. If TPP prefers not to oviposit on old tissue, it is possible that by selecting young tissue, we inadvertently removed this effect. However, the fact that we did not detect an age effect on oviposition in our assays suggests that spatial distribution in TPP may be influenced by other factors such as microclimate or avoidance of natural enemies.

Unlike oviposition, the number of stylet sheaths (probing) varied with both age and with variety. Interestingly, the maximum numbers of stylet sheaths were not observed in the three highly ZC-susceptible potato varieties, but rather in Red LaSoda. In fact, "Atlantic," which is particularly susceptible, had the fewest stylet sheaths of any variety. In considering probing data, it is important to consider that bioassays were conducted on excised leaves. Excision of leaves might alter the pressure in the phloem and potentially the nutrients available to TPPs. That said, we found no effect of excision on number of stylet sheaths. It is unclear how excision will influence behavior, but one might expect probing to be affected more than oviposition, which is less associated with the phloem. Further, it is not clear how the number of stylet sheaths relates to actual feeding. Butler and Trumble (2012) demonstrated differences in stylet penetration resulting from imidacloprid application, but also found that plant age did not influence the sequence of feeding behaviors. Rashed et al. (2013) found an increase in ZC incidence with increasing TPP numbers and suggested this is associated with more TPPs feeding. However, to our knowledge, no tests of the relationship between stylet sheaths and TPP feeding have been conducted. In electrical penetration graph studies, TPP takes 4 h to access the phloem (Butler et al. 2012). In a 72-h period, this would translate to a maximum of 18 instances of accessing the phloem. As the number of stylet sheaths in some varieties greatly exceeded this number, one might conclude the phloem is often not accessed despite the excretion of a stylet sheath. Thus, rather than feeding, stylet sheaths may actually reflect probing or "tasting."

Our results suggest that, as in tomato, potato variety influences oviposition decisions in TPPs. More importantly, we have demonstrated that both variety and the maturity of a plant influence adult TPP probing decisions. This maturity effect on probing is likely because time since planting is broadly associated with plant physiological characteristics. Such characteristics could include leaf thickness (Moran and Buchan 1975, Walker 1988), a factor associated with insect nutrition such as nitrogen (Mattson 1980, Jannson and Smilowitz 1986) or phosphorous level (Xue and Nansen, unpublished data), or even time since disease infection (Gao et al. 2009, Rashed et al. 2013).

In this study, we did not explicitly test phenology, but rather used time since planting as a proxy. In part, this is because it is unclear how greenhouse conditions relate to field conditions for potato growth, even though we examined field-grown plants and obtained similar results. Regardless, it is probable that plant physiology influences suitability for feeding by TPP.

The results presented here have implications for TPP integrated pest management. First, they indicate that TPP behavior will vary among potato varieties. As it is known that susceptibility varies among potato varieties (Munyaneza et al. 2011), this is not an unexpected finding. However, as TPPs can be migratory, populations sometimes expand after invading a field (Munyaneza et al. 2009, Swisher et al. 2013), and planting time can influence disease severity (Goolsby et al. 2012, Munyaneza et al. 2012). Additionally, Davis et al. (2012) have demonstrated that settling behavior is influenced by both CLP infection and time since infection, while also indicating that flowering phenology is correlated with TPP population performance. The combination of these factors has implications for understanding intercrop movement, for area-wide sampling of TPP, and for future studies of host choice behaviors. Second, current management of TPP in potato fields is focused on multiple insecticide applications during the growing season (Gharalari et al. 2009, Butler et al. 2011). Commonly used insecticides include at least one antifeedent (pymetrozine) (Guenthner et al. 2012). However, if in some varieties, feeding is already minimal, its effectiveness may be limited. These results support that concept and also indicate that variety should be considered in other management decisions such as pesticide inputs. For example, treating varieties that are not preferred for oviposition with compounds targeting young stages may not be optimal. Finally, a few important notes on project design. As noted, these bioassays were conducted on excised leaflets and while we found no difference in stylet sheaths between intact and excised plants, a follow-up study on intact plants would be of great assistance for investigations of the specific mechanisms of these choices. Also, these bioassays were all conducted with individuals collected from CLP-positive colonies and plants that were unexposed to TPPs until used in bioassays. Davis et al. (2012) demonstrated choice in TPPs with respect to CLP-infected and uninfected plants, and Nachappa and colleagues (2012) have demonstrated fitness differences between CLP-infected and uninfected TPPs. Thus, these results are only one of multiple permutations that can occur in the field, and may not completely represent the patterns that would be found under some of these other conditions, and many of these deserve investigation.

Acknowledgments

We thank Kathy Vaughn, Nicole Henderson, and Loren Davis for assistance with field collections and colony maintenance. Xavier Martini offered helpful advice on experimental design. Adam Zeilinger provided comments on an earlier version of this manuscript. This work was funded in part by the Texas Department of Agriculture and a USDA-Special Crop Research Initiative Grant #2009-51181-20178. Jeff Koym and Creighton Miller kindly provided tubers for

conducting these experiments. T.X.L. originally collected psyllids that were used in these experiments.

References Cited

Abdullah, N.M.M. 2008. Life history of the Potato psyllid *Bactericera cockerelli* (Homoptera: Psyllidae) in controlled environment agriculture in Arizona. Afr. J. Agric. Res. 3: 60–67.

Backus, E. A., W. B. Hunter, C. N. Arne, and N. Arne. 1988. Technique for staining leafhopper (Homoptera: Cicadellidae) salivary sheaths and eggs within unsectioned plant tissue. J. Econ. Entomol. 81: 1819–1823.

Bar-Yam, S., and D. H. Morse. 2011. Host-plant choice behavior at multiple life-cycle stages: the roles of mobility and early growth in decision-making. Ethology 117: 508–519.

Butler, C. D., F. J. Byrne, M. L. Keremane, R. F. Lee, and J. T. Trumble. 2011. Effects of insecticides on behavior of adult *Bactericera cockerelli* (Hemiptera: Triozidae) and transmission of *Candidatus Liberibacter psyllaurous.* Econ. Entomol. 104: 586–594.

Butler, C. D., and J. T. Trumble. 2012a. The potato psyllid, *Bactericera cockerelli* (Sulc) (Hemiptera: Triozidae): life history, relationship to plant diseases, and management strategies. Terr. Arthropod Rev. 5: 87–111.

Butler, C. D., and J. T. Trumble. 2012b. Spatial dispersion and binomial sequential sampling for the potato psyllid (Hemiptera: Triozidae) on potato. Pest Manag. Sci. 142: 247–257.

Butler, C. D., G. P. Walker, and J. T. Trumble. 2012. Feeding disruption of potato psyllid, *Bactericera cockerelli,* by imidacloprid as measured by electrical penetration graphs. Entomol. Exp. Appl. 142: 247–257.

Clark, K. E., S. E. Hartley, R. M. Brennan, K. MacKenzie, and S. N. Johnson. 2012. Oviposition and feeding behaviour by the vine weevil *Otiorhynchus sulcatus* on red raspberry: effects of cultivars and plant nutritional status. Agric. For. Entomol. 14: 157–163.

Coyle, D. R., K. E. Clark, K. F. Raffa, and S. N. Johnson. 2011. Prior host feeding experience influences ovipositional but not feeding preference in a polyphagous insect herbivore. Entomol. Exp. Appl. 138: 137–145.

Davis, T. S., D. R. Horton, J. E. Munyaneza, and P. J. Landolt. 2012. Experimental infection of plants with an herbivore-associated bacterial endosymbiont influences herbivore host selection behavior. PLoS ONE 7: e49330.

Demirel, N., and W. Cranshaw. 2006. Relative effect of color mulches to potato/tomato Psyllid, *Paratrioza cockerelli* (Sulc) (Homoptera: Psyllidae), on garden tomato plants. J. Entomol. 3: 189–193.

Diaz-Montano, J., and J. T. Trumble. 2013. Behavioral responses of the potato psyllid (Hemiptera: Triozidae) to volatiles from dimethyl disulfide and plant essential oils. J. Insect Behav. 26: 336–351.

Doak, P., P. Kareiva, and J. Kingsolver. 2006. Fitness consequences of choosy oviposition for a time-limited butterfly. Ecology 87: 395–408.

Feeny, P. 1970. Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. Ecology 50: 565–581.

Fordyce, J. A., and C. C. Nice. 2002. Variation in butterfly egg adhesion: adaptation to local host plant senescence characteristics? Ecol. Lett. 6: 23–27.

Freedman, D., and P. Diaconis. 1981. On the histogram as a density estimator:L 2 theory. Zeit. Wahrsheinlichkeitstheorie 57: 453–476.

Futuyma, D. J., and G. Moreno. 1988. The evolution of ecological specialization. Annu. Rev. Ecol. Syst. 207–233.

Gao, F., J. Jifon, X. Yang, and T. Liu. 2009. Zebra chip disease incidence on potato is influenced by timing of potato psyllid infestation, but not by the host plants on which they were reared. Insect Sci. 16: 399–408.

Gharalari, A. H., C. Nansen, D. S. Lawson, J. Gilley, J. E. Munyaneza, and K. Vaughn. 2009. Knockdown mortality, repellency, and residual effects of insecticides for control of adult *Bactericera cockerelli* (Hemiptera: Psyllidae). J. Econ. Entomol. 102: 1032–1038.

Goolsby, J. A, J. J. Adamczyk, J. M. Crosslin, N. N. Troxclair, J. R. Anciso, G. G. Bester, J. D. Bradshaw, E. D. Bynum, L. a Carpio, D. C. Henne, et al. 2012. Seasonal population dynamics of the potato psyllid (Hemiptera: Triozidae) and its associated pathogen "*Candidatus Liberibacter solanacearum*" in potatoes in the southern great plains of North America. J. Econ. Entomol. 105: 1268–76.

Grafton-Cardwell, E. E., L. L. Stelinski, and P. A. Stansly. 2013. Biology and management of Asian citrus psyllid, vector of the huanglongbing pathogens. Annu. Rev. Entomol. 58: 413–32.

Guenthner, J., J. Goolsby, and G. Greenway. 2012. Use and cost of insecticides to control potato psyllids and zebra chip on potatoes. Southwest. Entomol. 37: 263–270.

Haga, E., B. Weber, and S. Jansky. 2012. Examination of potential measures of vine maturity in potato. Am. J. Plant Sci. 3: 495–505.

Hall, D. G., M. L. Richardson, E.-D. Ammar, and S. E. Halbert. 2012. Asian citrus psyllid, *Diaphorina citri* , vector of citrus huanglongbing disease. Entomol. Exp. Appl. 146: 207–223.

Heisswolf, A., E. Obermaier, and H. J. Poethke. 2005. Selection of large host plants for oviposition by a monophagous leaf beetle: nutritional quality or enemy-free space? Ecol. Entomol. 299–306.

Hodkinson, I. D., and M. K. Hughes. 1982. Insect Herbivory. Outlook Study of Ecology. Chapman and Hall, London, United Kingdom.

Hoffman, G. D., and S. Rao. 2011. Oviposition site selection on oats: the effect of plant architecture, plant and leaf age, tissue toughness, and hardness on cereal leaf beetle, *Oulema melanopus.* Entomol. Exp. Appl. 141: 232–244.

Hunter, M. D. 1992. A variable insect-plant interaction: the relationship between tree budburst phenology and population levels of insect herbivores among trees. Ecol. Entomol. 16: 91–95.

Jaenike, J. 1978. On optimal oviposition behavior in phytophagous insects. Theor. Popul. Biol. 14: 350–6.

Jamieson, M. A., and M. D. Bowers. 2011. Soil nitrogen availability and herbivore attack influence the chemical defenses of an invasive plant (*Linaria dalmatica;* Plantaginaceae). Chemoecology 22: 1–11.

Jannson, R. K., and Z. Smilowitz. 1986. Influence of nitrogen on population parameters of potato insects: abundance, population growth, and within-plant distribution of the green peach aphid, *Myzus persicae* (Homoptera: Aphididae). Environ. Entomol. 15: 49–55.

Jefferies, R. A., and H. M. Lawson. 1991. A key for the stages of development of potato. Ann. Appl. Biol. 119: 387–389.

Johnson, S. N., N. E. Birch, P. J. Gregory, and P. J. Murray. 2006. The "mother knows best" principle: should soil insects be included in the preference–performance debate? Ecol. Entomol. 31: 395–401.

Lana, E., R. Johansen, and D. Nelson. 1970. Variation in specific gravity of potato tubers. Am. Potato J. 47: 9–12.

Liu, D., and J. T. Trumble. 2004. Tomato psyllid behavioral responses to tomato plant lines and interactions of plant lines with insecticides. J. Econ. Entomol. 97: 1078–1085.

Martini, X., S. Seibert, S. M. Prager, and C. Nansen. 2012. Sampling and interpretation of psyllid nymph counts in potatoes. Entomol. Exp. Appl. 143: 103–110.

Marwaha, R. S., and R. Kumar. 1987. Relationship between specific gravity and dry matter content of potato tubers. Int. J. Trop. Agric. 5: 227–230.

Mattson, W. J. 1980. Herbivory in relation to plant nitrogen content. Annu. Rev. Ecol. Syst. 11: 119–161.

Mayhew, P. J. 2001. Herbivore host choice and optimal bad motherhood. Trends Ecol. Evol. 16: 165–167.

Moran, V. C., and P. R. Buchan. 1975. Oviposition by the citrus psylla, *Trioza Ertreae* (Homoptera: Psyllidae), in relation to leaf hardness. Entomol. Exp. Appl. 18: 96–104.

Munyaneza, J. E., J. M. Crosslin, and J. L. Buchman. 2009. Seasonal occurrence and abundance of the potato psyllid, *Bactericera cockerelli,* in south central Washington. Am. J. Potato Res. 86: 513–518.

Munyaneza, J. E., J. L. Buchman, and C. C. Pearson. 2011. Susceptibility of selected potato varieties to zebra chip potato disease. Am. J. Potato Res. 88: 435–440.

Munyaneza, J. E., J. L. Buchman, V. G. Sengoda, J. A. Goolsby, A. P. Ochoa, J. Trevino, and G. Schuster. 2012. Impact of potato planting time on incidence of potato zebra chip disease in the lower Rio Grande Valley of Texas. Southwest. Entomol. 37: 253–262.

Murali, K. S., and R. Sukumar. 1993. Leaf flushing phenology and herbivory in a tropical dry deciduous forest, southern India. Oecologia 94: 114–119.

Nachappa, P., A. A. Shapiro, and C. Tamborindeguy. 2012. Effect of "*Candidatus Liberibacter solanacearum*" on fitness of its insect vector, *Bactericera cockerelli* (Hemiptera: Triozidae) on tomato. Phytopathology 102: 1–22.

Nava, D. E., M.L.G. Torres, M.D.L. Rodrigues, J.M.S. Bento, and J.R.P. Parra. 2007. Biology of *Diaphorina citri* (Hem., Psyllidae) on different hosts and at different temperatures. J. Appl. Entomol. 131: 709–715.

Patt, J. M., W. G. Meikle, A. Mafra-Neto, R. Mangan, C. Yang, N. Malik, and J. J. Adamczyk. 2011. Multimodal cues drive host-plant assessment in Asian citrus psyllid (*Diaphorina citri*). Environ. Entomol. 40: 1494–1502.

Pletsch, D.J.J. 1947. The potato psyllid *Paratrioza cockerelli* (Sulc), its biology and control. Mont. State College Agric. Exp. Stn. Bull. 446: 1–95.

Quintero, C., and M. D. Bowers. 2012. Changes in plant chemical defenses and nutritional quality as a function of ontogeny in *Plantago lanceolata* (Plantaginaceae). Oecologia 168: 471–81.

Rashed, A., D. Nash, L. Paetzold, F. Workneh, C. M. Rush, and T. D. Nash. 2013a. Transmission efficiency of *Candidatus Liberibacter solanacearum* and potato zebra chip disease progress in relation to pathogen titer, vector numbers and feeding sites. Phytopathology 102: 1–30.

Rashed, A., C. M. Wallis, L. Paetzold, F. Workneh, and C. M. Rush. 2013b. Zebra chip disease and potato biochemistry: tuber physiological changes in response to "*Candidatus Liberibacter solanacearum*" infection over time. Phytopathology (in press).

Raupp, M. J., and R. F. Denno. 1983. Leaf Age as a predictor of herbivore distribution and abundance, pp. 91–124. *In* Variable Plants and Herbivores in Natural and Managed Systems. Academic, New York, NY.

Scheirs, J., L. De Bruyn, and R. Verhagen. 2000. Optimization of adult performance determines host choice in a grass miner. Proc. R. Soc. London B 267: 2065–9.

Selman, B. J. 1994. The biology of the paropsine eucalyptus beetles of Australia, pp. 555–565. *In* P. H. Jolivet, M. L. Cox, and E. Petitpierre (eds.), Nov. Asp. Biol. Chrysomelidae SE - 43. Springer, Amsterdam, The Netherlands.

Stark, J. C., and S. L. Love. 2003. Potato production systems, p. 426. *In* Potato Production Systems. University of Idaho Agricultural Communications, Moscow Idaho.

Steinbauer, M. J., A. R. Clarke, and J. Madden. 1998. Oviposition preference of a eucalyptus herbivore and the importance of leaf age on interspecific host choice. Ecol. Entomol. 23: 201–206.

Swisher, K. D., J. E. Munyaneza, and J. M. Crosslin. 2013. Temporal and spatial analysis of potato psyllid haplotypes in the United States. Environ. Entomol. 42: 381–393.

Tekalign, T., and P. S. Hammes. 2005. Growth and productivity of potato as influenced by cultivar and reproductive growth. Sci. Hortic. (Amsterdam) 105: 29–44.

Thompson, J. N. 1988. Mini-review: evolutionary ecology of the relationship between oviposition preference and performance of offspring in phytophagous insects. Entomol. Exp. Appl. 47: 3–14.

Tsai, J. H., and Y. H. Liu. 2000. Biology of *Diaphorina citri* (Homoptera: Psyllidae) on four host plants. J. Econ. Entomol. 93: 1721–1725.

Valladares, G., and J. Lawton. 1991. Host-Plant selection in the holly leaf-miner: does mother know best? J. Anim. Ecol. 60: 227–240.

Venables, W. N., and B. D. Ripley. 2002. Modern applied statistics with S., 4th ed. Springer, New York, NY.

Walker, G. P. 1988. The role of leaf cuticle in leaf age preference by bayberry whitefly (Homoptera: Aleyrodidae) on lemon. Ann. Entomol. Soc. Am. 81: 365–369.

Wallis, R. L. 1951. Potato psyllid selection of host plants. J. Econ. Entomol. 44: 815–817.

Wallis, R. L. 1955. Ecological studies on the potato psyllid as a pest of potatoes. U.S. Dep. Agric. Tech. Bull. USDA, Washington, DC.

Wallis, C. M., A. Rashed, A. K. Wallingford, L. Paetzold, F. Workneh, and C. M. Rush. 2013. Similarities and differences in physiological responses to "*Candidatus Liberibacter solanacearum*" infection among different potato cultivars. Phytopathology 104: 1–34.

Wenninger, E. J., L. L. Stelinski, and D. G. Hall. 2009. Roles of olfactory cues, visual cues, and mating status in orientation of *Diaphorina citri* Kuwayama (Hemiptera: Psyllidae) to four different host plants. Environ. Entomol. 38: 225–234.

Werner, B. K., S. L. Love, and B. Shafii. 1998. Comparison of seasonal development of tuber specific gravity among seven potato clones. Am. J. Potato Res. 75: 121–127.

Wiklund, C. 1975. The evolutionary relationship between adult oviposition preferences and larval host plant range in *Papilio machaon* L. Oecologia 18: 185–197.

Yang, X.-B., Y.-M. Zhang, H. Lei, and T.-X. Liu. 2010. Life history and life tables of *Bactericera cockerelli* (Hemiptera: Psyllidae) on potato under laboratory and field conditions in the lower Rio Grande Valley of Texas. J. Econ. Entomol. 103: 1729–1734.

Received 30 September 2013; accepted 21 January 2014.