

Copyright is owned by the Author of the thesis. Permission is given for a copy to be downloaded by an individual for the purpose of research and private study only. The thesis may not be reproduced elsewhere without the permission of the Author.

**Assessing the effect of plant surface on the predatory ability  
of *Orius vicinus*: A potential biological control agent of the  
tomato-potato psyllid (*Bactericera cockerelli*)**

A thesis presented in partial fulfilment of the  
requirements for the degree of

Master of Science  
in  
Zoology

at Massey University, Palmerston North,  
New Zealand

Abel Gamarra Landa  
2019



## Abstract

The tomato-potato psyllid (TPP), *Bactericera cockerelli* (Sulc), is a pest to solanaceous crops (e.g. potato, tomato, peppers, and eggplant) and is associated with economically important plant diseases. Subsequently, chemical control is the preferred management option. However, chemical reliance is associated with a host of issues. The development of biological control methods is vital to implementing Integrated Pest Management (IPM) programs as an alternative to broad-spectrum insecticide usage. The predatory bug *Orius vicinus* (Ribaut) is a potential biological control agent that is capable of consuming all nymphal life stages of TPP.

In order to be a commercially viable management option, potential biological control agents of TPP have to cope with the different morphological plant features of the pest's wide range of host plants. Tomato and capsicum plant surfaces were selected as the experimental surfaces for my thesis because they differ significantly in their substrate morphology. Tomato plant surfaces can be a hostile environment for potential biological control agents due to the negative effect tomato trichomes have on their foraging performance. Alternatively, because capsicum plant surfaces are virtually void of trichomes they appear to be more suitable for effective biological control agent deployment.

I exposed the predatory bug to a variety of TPP nymph densities (10, 20, 30 and 40 individuals) in order to determine the functional response of *O. vicinus*. Furthermore, the predatory bug was exposed to all five TPP nymphal stages simultaneously. The predatory performance of *O. vicinus* was also assessed on experimental arenas varying in complexity (leaflet vs. small plant environments). The functional response was determined to be Type II on both plant surfaces. Nymph consumption at higher prey densities (30 and 40 nymphs) was significantly greater on capsicum than on tomato. Nymph consumption at lower prey densities (10 and 20 nymphs) was only significantly greater on capsicum when the complexity of the experimental arena increased from leaflet to small plant. The influence of *O. vicinus* in nymph dispersal was also assessed. My results revealed that the presence of *O. vicinus* increased the dispersal of nymphs to lower leaf surfaces and that nymph dispersal was significantly greater on capsicum than on tomato.

TPP nymph size preference by *O. vicinus* was determined in my study. I established that the predatory bug is capable of killing all nymphal stages. My study strongly indicated that the predatory bug is more likely to target and consume medium (3<sup>rd</sup> instars) and large nymphs (4<sup>th</sup> and 5<sup>th</sup> instars) over small nymphs (1<sup>st</sup> and 2<sup>nd</sup> instars). I investigated the behaviour of *O. vicinus* adults and TPP nymphs during their interactions via video recordings. The predatory bug spent a significantly greater amount of time investigating TPP nymphs on capsicum than on tomato. There was significantly higher number of attacks recorded on capsicum. The greater killing percentage on tomato suggests that the defensive capabilities of TPP nymphs appear to have been negatively affected by the tomato substrate.

The results from my study indicate that augmentative releases of *O. vicinus*, in the presence of smaller TPP nymphs, could be a viable biological control option on capsicum plants. However, the predatory bug will likely struggle if deployed on tomato plants. Future studies should be conducted in settings such as open field or glasshouses using multiple predatory bugs in the presence of susceptible life stages to assess augmentative release efficiency.

**Keywords:** Biological control, tomato-potato psyllid (TPP), *Bactericera cockerelli*, *Orius vicinus*, functional response, prey preference, plant surface morphology, capsicum, tomato.

## Acknowledgements

This thesis would not have been possible without the input and support from many people. Firstly, I must thank my supervisors Professor Murray Potter and Professor Qiao Wang. They have shown much patience and understanding over the years as I juggled full time work and thesis requirements. Their input, guidance and encouragement have been valuable and appreciated. I must also thoroughly thank Dr Xiong Zhao He, who provided vital statistical analysis expertise and was always on hand to assist me in any way he could.

I would also like to thank the following people who provided vital assistance in some capacity during my thesis. They virtually kept my thesis alive at times. Mike Sim from Bioforce for providing *Orius vicinus* individuals for my colony. Robin Gardner-Gee from Plant and Food Research for providing TPP individuals for my colony. Steve Ray and the staff at the Massey University Plant Growth Unit, for providing vital assistance and maintenance of my experimental plants. Paul Barrett for assisting with any technical issues with the temperature control rooms and providing equipment when needed.

I would also like to thank Diwas Khatri for kindly lending me his video camera for my experiment. Jen Buxton for helping transport plants from the PGU to my lab and Geneva Whitlow–Waa for maintaining my plants alive while I was away from campus. My mother Cynthia Landa and her partner Neil Hawes for providing much appreciated dinners during the experimental phase of my thesis. Finally, the long journey of this thesis would not have been possible without the love and understanding of my lovely partner Laura Volp.



## Table of Contents

<b>Abstract</b>	<b>iii</b>
<b>Acknowledgements</b>	<b>v</b>
<b>Table of Contents</b>	<b>vii</b>
<b>List of Figures</b>	<b>ix</b>
<b>List of Tables</b>	<b>xi</b>
<b>Chapter 1: Introduction</b>	<b>1</b>
1.1 Overview	1
1.2 Tomato-potato psyllid (TPP)	3
1.2.1 Distribution	3
1.2.2 Life history	5
1.2.2.1 Life stages	5
1.2.3 Diseases associated with TPP	7
1.2.3.1 Psyllid yellows	7
1.2.3.2 <i>Candidatus</i> Liberibacter	8
1.2.4 TPP management strategies	10
1.2.4.1 Monitoring TPP	10
1.2.4.2 Insecticides	10
1.2.4.2.1 Biorational insecticides	13
1.2.4.3 Biological control	13
1.2.4.3.1 Entomopathogenic fungi	14
1.2.4.3.2 Parasitoids	14
1.2.4.3.3 Predators	16
1.3 Genus: <i>Orius</i>	19
1.3.1 <i>Orius vicinus</i>	20
1.4 The effect of morphological plant traits on biological control agents	22
1.4.1 Assesment of experimental plant surfaces	25
1.4.1.1 Tomato plant surfaces	25
1.4.1.1 Capsicum plant surfaces	27
1.5 Aims and objectives	28
<b>Chapter 2: The effect of host plant substrate on the biological control potential of <i>Orius vicinus</i> (Ribaut) on <i>Bactericera cockerelli</i> (Sulc) nymphs</b>	<b>31</b>
2.1 Abstract	31
2.2 Introduction	31
2.3 Material and Methods	34
2.3.1 Experimental plants	34
2.3.2 Insect colonies	35
2.3.3 Experimental design	35
2.3.3.1 Leaflet experimental arena	35
2.3.3.2 Plant experimental arena	37
2.3.4 Data analysis	38
2.3.4.1 Leaflet experimental arena	38
2.3.4.2 Plant experimental arena	41
2.4 Results	42
2.4.1 Leaflet experimental arena	42
2.4.2 Plant experimental arena	49



2.5 Discussion	51
<b>Chapter 3: The effect of host plant substrate on the behaviour of <i>Orius vicinus</i> (Ribaut) and <i>Bactericera cockerelli</i> (Sulc) nymphs</b>	<b>55</b>
3.1 Abstract	55
3.2 Introduction	55
3.3 Material and Methods	57
3.3.1 Experimental plants	57
3.3.2 Insect colonies	58
3.3.3 Experimental design	58
3.3.4 Data analysis	61
3.4 Results	62
3.5 Discussion	66
<b>Chapter 4: Conclusion</b>	<b>71</b>
4.1 Objectives and outcomes	71
4.1.1 Objective 1	71
4.1.2 Objective 2	72
4.1.3 Objective 3	72
4.1.4 Objective 4	72
4.2 Future research	73
4.3 Final summary	74
<b>References</b>	<b>75</b>

## List of Figures

<b>Figure 1.1:</b> TPP life stages: egg attached to capsicum leaflet (left); fifth instar TPP nymph on tomato leaflet (middle); and adult TPP on tomato leaflet (right).....	6
<b>Figure 1.2:</b> Adult <i>O. vicinus</i> probing a TPP nymph on capsicum surface (left) and <i>O. vicinus</i> nymph on tomato surface (right).....	21
<b>Figure 2.1:</b> Adult <i>O. vicinus</i> on smooth surfaced capsicum (left) and hairy surfaced tomato (right) leaves.....	35
<b>Figure 2.2:</b> Petri dish containing the raised tomato leaflet uncovered (left) and covered with jar with ventilation holes (right).....	36
<b>Figure 2.3:</b> Uncovered (left) and covered (right) small capsicum plant with all but one leaflet removed.....	38
<b>Figure 2.4:</b> Estimated percentage of TPP nymphs located on the upper surface of capsicum (C) and tomato (T) leaflets after 24 h in the presence (+) and absence (-) of <i>O. vicinus</i> at different prey densities.....	43
<b>Figure 2.5:</b> Percentage of TPP nymphs consumed by <i>O. vicinus</i> on the upper surface of capsicum and tomato leaflets after 24 h. For each density or mean, columns with different letters are significantly different (Kruskal-Wallis Test: $P < 0.05$ ).....	44
<b>Figure 2.6:</b> Percentage of TPP nymphs consumed by <i>O. vicinus</i> on capsicum and tomato leaflets after 24 h. For each density or mean, columns with different letters are significantly different (ANOVA: $P < 0.05$ ).....	44
<b>Figure 2.7:</b> Type II functional response of <i>O. vicinus</i> on capsicum and tomato leaflet surfaces: (A) number of TPP nymphs consumed, and (B) percentage of TPP nymphs consumed.....	46
<b>Figure 2.8:</b> TPP density (TPPD: 10, 20, 30 and 40 nymphs) and size index (TPPSI: small (1), medium (2), and large (3) nymphs) affecting the rate of TPP consumed (ROTTPC) by <i>O. vicinus</i> : (A) Capsicum, $ROTTPC = 0.0148 - 0.0014TPPD + 0.3814TPPSI - 0.0992TPPSI^2$ ( $R^2 = 0.1185$ , $F_{3,236} = 10.57$ , $P < 0.0001$ ); (B) Tomato, $ROTTPC = 0.0459 - 0.0039TPPD + 0.3209TPPSI - 0.0733TPPSI^2$ ( $R^2 = 0.1562$ , $F_{3,236} = 14.57$ , $P < 0.0001$ ).....	48
<b>Figure 2.9:</b> Percentage of TPP nymphs located on the upper leaf surface of capsicum and tomato plants after 24 h. Columns with different letters are significantly different (Kruskal-Wallis Test: $P < 0.05$ ).....	49
<b>Figure 2.10:</b> Percentage of TPP nymphs consumed by <i>O. vicinus</i> on the upper leaflet surface of capsicum and tomato plants after 24 h. Columns with different letters are significantly different (Kruskal-Wallis Test: $P < 0.05$ ).....	50

**Figure 2.11:** Percentage of TPP nymphs consumed by *O. vicinus* on capsicum and tomato experimental arenas after 24 h at the prey density of 10 individuals. Columns with different upper case letters indicate significant differences between experimental arenas within host plants and columns with different lower case letters indicate significant differences between host plants (ANOVA:  $P < 0.05$ ).....50

**Figure 2.12:** Hairless capsicum stem surface (left) and hairy tomato stem surface (right).....53

**Figure 3.1:** Adult TPP on smooth surfaced capsicum (left) and hairy surfaced tomato (right) leaves.....58

**Figure 3.2:** Capsicum leaflet sitting on blutack balls surrounded by water within Petri dish (right). Aerial view of Petri dish within plastic cylinder containing capsicum leaflet (left).....59

**Figure 3.3:** TPP nymphs on tomato surface: (1) first instar, (2) second instar, (3) third instar, (4) fourth instar, and (5) fifth instar.....60

**Figure 3.4:** The mean number of seconds spent by *O. vicinus* performing the observed behaviours on tomato and capsicum surfaces during the 1 h observation period (Wal = Walking; Sea = Searching; Sta = Stationary; Gro = Grooming; Ori = Orienteering; Inv = Investigating; Att = Attacking; Con = Consuming; Oth = Other). For each behaviour, columns with a different letter are significantly different (ANOVA:  $P < 0.05$ )..... 62

**Figure 3.5:** Adult *O. vicinus* probing large sized TPP nymph (left) and adult *O. vicinus* consuming medium sized TPP nymph (right).....69

## List of Tables

<b>Table 2.1:</b> Logistic regression analysis of functional response of <i>O. vicinus</i> to TPP densities.....	45
<b>Table 2.2:</b> Searching efficiency ( $a$ , $h^{-1}$ ) and handling time ( $T_h$ , $h$ ) parameters (P) for Type II functional response of <i>O. vicinus</i> to TPP nymph density on Capsicum (C) and Tomato (T) plants.....	47
<b>Table 3.1:</b> Behavioural parameters for adult <i>O. vicinus</i> .....	60
<b>Table 3.2:</b> Behavioural parameters for TPP nymphs.....	61
<b>Table 3.3:</b> The mean ( $\pm$ SE) number of predator-prey encounters and number of predator attacks observed on capsicum and tomato surfaces.....	63
<b>Table 3.4:</b> The mean ( $\pm$ SE) percentage of attacks resulting in kills observed on capsicum and tomato surfaces.....	63
<b>Table 3.5:</b> The probability ( $\pm$ SE) of <i>O. vicinus</i> initiating an encounter with TPP nymphs based on their size on capsicum, tomato, and combined (capsicum and tomato) surfaces.....	64
<b>Table 3.6:</b> The probability ( $\pm$ SE) of <i>O. vicinus</i> initiating an attack during an encounter with TPP nymph based on their size on capsicum, tomato, and combined (capsicum and tomato) surfaces.....	64
<b>Table 3.7:</b> The probability ( $\pm$ SE) of <i>O. vicinus</i> killing a TPP nymph during an attack based on their size on capsicum, tomato, and combined (capsicum and tomato) surfaces.....	65
<b>Table 3.8:</b> The probability ( $\pm$ SE) of TPP nymph performing defensive behaviours during an encounter with <i>O. vicinus</i> based on their size on capsicum, tomato, and combined (capsicum and tomato) surfaces.....	66
<b>Table 3.9:</b> The probability ( $\pm$ SE) of TPP nymph performing defensive escape behaviours during an encounter with <i>O. vicinus</i> based on their size on capsicum surfaces.....	66



## **Chapter 1: Introduction**

### **1.1 Overview**

Integrated Pest Management (IPM) combines biological, cultural and chemical tactics to reduce pest populations to economically tolerable levels whenever they reach an economic threshold (Tang & Cheke, 2008). IPM programs incorporate economic injury levels, economic thresholds, field monitoring and record keeping, to make pest management decisions (Tang & Cheke, 2008). Studies have revealed that IPM programs are more effective than relying solely on chemical control, which is associated with a host of issues such as environmental damage, development of insecticide resistance and secondary pest problems (Symondson et al., 2002; Tang & Cheke, 2008; Van Lenteren, 2012b). Biological control is a key aspect of the IPM paradigm, and can be defined as the exploitation of the ability of an organism to reduce the population density of another organism (Symondson et al., 2002; Van Lenteren, 2012b).

Biological control can be broken down into the following types: natural, conservation, classical, and augmentative (Van Lenteren, 2012b). Natural biological control can be defined as the reduction of pest organisms by their natural enemies without human intervention (Van Lenteren, 2012b). Conservation biological control occurs when human intervention protects and stimulates the performance of naturally occurring biological control agents (Van Lenteren, 2012b). Classical biological control involves introduction of agents from an exploration area (usually the area of origin of the targeted pest) and their release in the areas where the targeted pest has become a problem (Van Lenteren, 2012b). Augmentative biological control is the mass-rearing and mass release of biological control agents with the purpose of immediately controlling a pest population (Van Lenteren, 2012b). Augmentative control can be an environmentally and economically sound alternative to chemical pest control in certain areas of agriculture such as greenhouses (particularly those that use bees for pollination) (Van Lenteren, 2012b). Biological control agents used in augmentative control programs can be either indigenous or exotic. However, there are costs associated with the importation and release of exotics due to the required environmental assessment of their impact and subsequent registration (Van Lenteren, 2012b). Therefore finding ways

to augment the efficacy of indigenous or established exotic natural enemies is usually the primary option when a new pest is found (Van Lenteren, 2012b).

Arthropods used as biological control agents generally come from four taxonomic groups: Hymenoptera, Acari, Coleoptera and Heteroptera (Van Lenteren, 2012b). A review of multiple biological control studies by Stiling and Cornelissen (2005) found that the majority of biological control agents were generalists whose efficacy tended to be higher than specialists. However, the capability of generalists to affect non-target organisms has to be taken into consideration when assessing their potential as biological control agents (Stiling & Cornelissen, 2005). The majority of studies on biological control agents reviewed by Stiling and Cornelissen (2005) focused on their effectiveness while other areas of interest included their feeding or oviposition behaviour and the biotic effects on the target and/or the agents (e.g. tri-trophic interactions). The success of biological control programs is primarily determined by economic criteria, so potential biological control agents are either deemed to be a potential success or a failure based on their performance in totally or partially controlling a pest population (Stiling & Cornelissen, 2005).

In this chapter, I review literature relevant to my studies. I start with a review of the distribution, life history, history as a recognised plant pest, and potential methods of control of the tomato-potato psyllid (TPP), *Bactericera cockerelli* (Sulc) (Hemiptera: Triozidae). I then review the literature on *Orius vicinus* (Ribaut) (Heteroptera: Anthocoridae) which is a potential biological control agent for TPP, and the effects that plant morphological traits (e.g., foliar pubescence, glandular trichomes, waxy leaf surface, and plant architecture) can have on the performance efficiency and behaviour of biological control agents. I have placed particular focus on tomato and capsicum because they provide the experimental surfaces I used here. I selected these plants because they are important crops grown in glasshouses and because they differ significantly in their substrate morphology. Finally, I then outline my aim and objectives for this thesis.

## 1.2 Tomato-potato psyllid (TPP)

TPP was first described as *Trioza cockerelli* by Karel Sulc in 1909 (Butler & Trumble, 2012a; Horton et al., 2016). In 1911 TPP was reassigned from the genus *Trioza* to *Paratrioza* (Butler & Trumble, 2012a). The genus *Paratrioza* was subsequently synonymized with the genus *Bactericera* in 1997, which also led to TPP changing families from Psyllidae to Triozidae (Burckhard & Lauterer, 1997; Butler & Trumble, 2012a). TPP is also commonly known as either the potato psyllid or the tomato psyllid (Abdullah, 2008).

TPP nymphs and adults are phloem-feeders that are capable of feeding on all plant surfaces (leaves, stems, petioles) (Butler & Trumble, 2012a). TPP infestations have been associated with outbreaks of economically important plant diseases (Butler & Trumble, 2012a). TPP can also affect crops via honeydew accumulation (insect faeces) which can result in sooty mould that can compromise the structure of the plant and may impose an economic cost due to fruit requiring cleaning or being downgraded (Prager et al., 2016). TPP infestations have the potential to inflict significant economic losses to solanaceous crops (e.g. potato, tomato, peppers, and eggplant) in North America, Central America, and New Zealand (Burckhard & Lauterer, 1997; Teulon et al., 2009; Butler & Trumble, 2012a; Munyaneza, 2012). Currently, the combination of chemical solutions and the implementation of cultural control methods such as removal of alternative breeding hosts is the standard control strategy for TPP outbreaks (Butler & Trumble, 2012a). Threshold benchmarks for IPM programs have been proposed, developed and deployed (Goolsby et al., 2007; Butler et al., 2011; Walker et al., 2015a; Prager et al., 2016).

### 1.2.1 Distribution

TPP is believed to be indigenous to the southwestern USA and northern Mexico (Goolsby et al., 2007). They are currently found throughout North and Central America, including USA (Arizona, California, Colorado, Idaho, Kansas, Minnesota, Montana, Nebraska, Nevada, New Mexico, North and South Dakota, Oklahoma, Oregon, Texas, Utah, Washington, and Wyoming), Canada (Alberta, British Columbia, Ontario, Saskatchewan), Mexico, Guatemala, Honduras, Nicaragua and New Zealand



(Burckhard & Lauterer, 1997; Goosby et al., 2007; Butler & Trumble, 2012a; Munyaneza, 2012; Horton et al., 2015). TPP and their associated diseases were reported on Norfolk Island in 2014 and there are concerns it could reach mainland Australia or Tasmania via accidental importation or natural dispersals via airflow from New Zealand (Walker et al., 2015b). Californian capsicums infested with live TPP nymphs are rejected in high numbers by border authorities in Hawaii (Walker et al., 2015b). Costa Rica temporarily banned all imports of potato from Nicaragua once TPP and its associated diseases were discovered. These highlight the threat of this pest to the trade of a country (Munyaneza, 2012).

Through the use of mitochondrial DNA (mtDNA), researchers have discovered four distinct TPP haplotypes within the United States which have been identified as central, western, northwestern and southwestern due to their presence in these regions (Munyaneza, 2015). These haplotypes may potentially differ in their capability to develop and reproduce on various host plants; transmit diseases; their overwintering capabilities; and magnitude of dispersal (Munyaneza, 2015). Previous genetic studies had suggested that TPP populations in North America belonged to two groups, one from western United States (invasive type) and the other from central United States and eastern Mexico (native type) (Liu et al, 2006a; Liu & Trumble, 2007). TPP that invaded New Zealand were believed to have come from the western North American range, in other words the “invasive” type rather than the “native” type (Walker et al., 2015b).

The invasion of TPP into New Zealand may have occurred in the summer of 2005-2006 (Teulon et al., 2009; Butler & Trumble, 2012a). However, the entry pathway remains unclear with the most likely scenario being accidental introduction from the western United States via smuggled primary host plant material into the Auckland region (Teulon et al., 2009; Thomas et al., 2011). TPP populations were established in both the North and South Islands of New Zealand by 2009 (Teulon et al., 2009; Thomas et al., 2011). Widespread distribution is believed to have been achieved by a combination of natural dispersal (e.g. movement from infested crops to nearby crops) and human-mediated dispersal (e.g. infested host plant material and inanimate objects) (Teulon et al., 2009). The affected indoor and outdoor crops included capsicum, tomato, tamarillo and potato (Teulon et al., 2009). TPP infestations and associated diseases resulted in IPM systems within the New Zealand vegetable sector being severely affected due to

increased usage of non-selective chemicals (Teulon & Hill, 2015). Furthermore the export certification of certain crops was momentarily lost (Teulon & Hill, 2015).

### *1.2.2 Life history*

TPP have a host plant range that exceeds 20 plant families and they are capable of completing development on over 40 host species (Butler & Trumble, 2012a). Plant species from the family Solanaceae appear to be the preferred host plants; however, reproduction and development have also been recorded on species from the family Convolvulaceae including sweet potato (Butler & Trumble, 2012a; Munyaneza, 2012; Diaz-Montano & Trumble, 2013). TPP behaviours (including feeding, jumping and leaf abandonment); life parameters (including developmental rates and survivorship); and nymphal densities have been shown to vary between host plants species and even host plant cultivars (Liu & Trumble, 2004; Liu & Trumble, 2005; Goolsby et al., 2007; Yang & Liu, 2009; Yang et al., 2010b; Yang et al., 2013; Thinakaran et al., 2015a; Thinakaran et al., 2015b). The vast host range of TPP complicates the control of this pest due to the different susceptibilities each host plant has to TPP and its associated diseases (Prager et al., 2016). TPP nymphs (particularly from the northwestern haplotype) have the capability of overwintering on certain host plants (e.g. bittersweet nightshade) which are generally outside of agricultural crops, making management difficult (Goolsby et al., 2007; Butler & Trumble, 2012a; Munyaneza, 2015; Horton et al., 2015). Non-crop hosts can act as reservoir hosts which allow for future invasions into crop hosts (Thinakaran et al., 2015a). Despite the overwintering potential of TPP, the main mechanism for TPP presence in agricultural crops is believed to be their capacity to migrate long distances via air currents (Goolsby et al., 2007; Butler & Trumble, 2012a).

#### *1.2.2.1 Life stages*

TPP pass through hemimetabolous metamorphosis and their development is temperature dependent (Butler & Trumble, 2012a). The optimal laboratory temperature for survival, development and oviposition is believed to be 26.7°C, and these life history parameters begin to be negatively affected when temperatures rise beyond 32.2°C (Butler & Trumble, 2012a). Sustained temperatures above 38°C are lethal for eggs and nymphs

(Butler & Trumble, 2012a). Depending on the temperature, a single generation can be completed within three to five weeks (Munyaneza, 2012). Under ideal climatic conditions the rapid development cycle of TPP and the early reproductive capability of females allow for rapid population growth which tends to contain overlapping TPP generations within a growing season (Liu & Trumble, 2005; Lacey et al., 2009; Butler et al., 2011; Butler & Trumble, 2012a; Munyaneza, 2012). In countries and regions such as Mexico and Central America where temperature remains ideal for this species, regardless of the season, and where host plants are always available, it is possible for TPP to reproduce and develop throughout the year (Munyaneza, 2012).

TPP eggs (Figure 1.1) are yellow, oval shaped, 0.3 mm in length, 0.1 mm in width and are attached to the plant surface (generally the leaves) via a 0.2 mm long stalk (Butler & Trumble, 2012a). The egg stage can take anywhere between 3 to 15 days and there is a 1:1 sex ratio (Yang & Liu, 2009; Yang et al., 2010b; Butler & Trumble, 2012a; Yang et al., 2013). The nymph stage (Figure 1.1) consists of five instars, whose length of development may vary depending on host plant and field/laboratory conditions (Yang & Liu, 2009; Yang et al., 2010b; Yang et al., 2013). Host plants can influence the development of life stages with progression from egg to adult under laboratory conditions taking 18.7, 19.6, 24.1 and 26.1 days on tomato, potato, eggplant and capsicum, respectively (Yang & Liu, 2009; Yang et al., 2010b; Yang et al., 2013). Transitions from egg to adult have been found to take longer in field conditions (Yang et al., 2010b; Yang et al., 2013).



**Figure 1.1:** TPP life stages: egg attached to capsicum leaflet (left); fifth instar TPP nymph on tomato leaflet (middle), and adult TPP on tomato leaflet (right).

TPP adults (Figure 1.1) generally emerge with pale green or light amber in colour, eventually darkening to reach their brown/dark green adult coloration (Butler & Trumble, 2012a). Adult length ranges from 1.3mm to 1.9mm (Liu & Trumble, 2007;

Butler & Trumble, 2012a). They can live between 16 and 97 days (Yang & Liu, 2009; Yang et al., 2010b; Butler & Trumble, 2012a; Yang et al., 2013). Females produce a pheromone that attracts males (Guedot et al., 2010). Adults are capable of reaching reproductive maturity within 48 hours from emergence (Guedot et al., 2012). The pre-oviposition period (covering emergence to first egg oviposition) for females can range from 5.9 to 8 days (Abdullah, 2008). Females have the capability to oviposit between 5 to 50 eggs over a 24 hour period (Butler & Trumble, 2012a). Furthermore, females have the ability to oviposit in excess of 1400 eggs in their lifetime (Liu & Trumble, 2005; Thinakaran et al., 2015a). In open field conditions females prefer potato and tomato to pepper, eggplant and silverleaf nightshade for oviposition (Thinakaran et al. 2015b). However, such preferences do not occur in laboratory conditions where adults prefer larger host plants regardless of species (Thinakaran et al., 2015b). Prager et al. (2014) suggest that TPP have host plant preferences influenced by haplotype.

The spatial distribution of TPP adults within crops varies among host plants (Henne et al., 2010b; Butler & Trumble, 2012c; Prager et al., 2013c; Prager et al., 2014). TPP nymphs on potato tended to distribute themselves on the underside of leaves, but, on capsicum no such leaf side preference was found (Butler & Trumble, 2012c; Prager et al., 2013c). TPP were found primarily in the upper two thirds on both potato and capsicum plants (Butler & Trumble, 2012c; Prager et al., 2013c). These spatial distribution differences highlight the importance of developing sampling plans for specific crops (Prager et al., 2014). Adults are active dispersers and are capable of covering extensive distances within crops and therefore infesting multiple plants at relative rapid frequencies (Henne et al., 2010b). Alternatively, Thinakaran et al. (2015b) reported that TPP movement after landing was minimal.

### *1.2.3 Diseases associated with TPP*

#### *1.2.3.1 Psyllid yellows*

TPP was first classified as a pest of agricultural crops following an outbreak of an unidentified disease on potato crops in the late 1920s which was later attributed to the feeding behaviour of TPP nymphs and named 'Psyllid Yellows' (PY) (Butler & Trumble, 2012a). PY infects the entire plant which leads to reduction in growth,

erectness of new foliage, chlorosis of leaves, thickened internodes, aerial tubers, premature senescence and eventually plant death (Liu & Trumble, 2006; Butler & Trumble, 2012a). The nymphal stages of TPP are attributed as the main culprits in the proliferation of PY (Liu & Trumble, 2006; Butler & Trumble, 2012a). Symptoms appear at low and high nymph densities (Liu & Trumble, 2006; Butler & Trumble, 2012a). The presence of crystalline honeydew produced by nymphs can be used as an indicator of TPP infestation (Abdullah, 2008). Adults do not appear to be as capable as nymphs in producing PY (Butler & Trumble, 2012a). Recovery from PY can potentially occur in potato and tomato plants if nymphs are removed within 10 days of infestation (Liu et al., 2006b; Butler & Trumble, 2012a). Therefore, PY is likely the result of an unidentified toxin rather than a pathogenic microorganism (Butler et al., 2012a; Prager et al., 2016).

#### 1.2.3.2 *Candidatus* Liberibacter

The disease ‘Zebra chip’ (ZC) was first documented in the early 1990’s on potato crops in Mexico and later discovered in Texas and other American states (Munyaneza et al., 2007b; Munyaneza et al., 2007b). ZC outbreaks in Mexico and the USA have resulted in massive economic losses (Munyaneza et al., 2007b). ZC is named after the dark brown streaks that appear in chips towards the end of the processing stage (Munyaneza et al., 2007b). ZC symptoms are similar to other TPP caused diseases (e.g. PY) (Munyaneza et al., 2007b). However, differences between PY and ZC symptoms have also been recognized (Secor et al., 2009). The exact cause of ZC went largely undetermined until observations made in the mid 2000’s correlated the abundance of TPP individuals with ZC infected potato crops in Mexico and the USA (Munyaneza et al., 2007b). ZC has now been documented throughout most of the known range of TPP including New Zealand (Secor and Rivera-Varas, 2004; Liefting et al., 2008; Henne et al., 2010a).

While TPP was identified as the transmitting vector of ZC to solanaceous species, the causal agent of ZC was undetermined until 2008 when a phloem- limited, Gram negative, unculturable bacteria from the *Alphaproteobacteria* group named *Candidatus* Liberibacter psyllaourous (syn. *Ca. L. solanacearum*) was identified (Munyaneza et al., 2007a; Hansen et al., 2008; Liefting et al., 2008; Munyaneza et al., 2008; Gao et al.,

2009; Liefting et al., 2009a; Munyaneza et al., 2009d; Munyaneza, 2010; Munyaneza, 2015). Hansen et al. (2008) proposed that a new bacteria species of the genus *Candidatus Liberibacter*, which the authors termed *Ca. L. psyllaourous*, was capable of infecting solanaceous plants and was vectored by TPP. About the same time, a previously undescribed disease was discovered in New Zealand solanaceous crops (capsicum, Cape gooseberry, tamarillo, tomato and potato) and ultimately revealed to be a new species of the *Candidatus Liberibacter* genus which was named *Candidatus Liberibacter solanacearum* (Liefting et al., 2008; Liefting et al., 2009a; Liefting et al., 2009b). Further studies established that *Ca. L. psyllaourous* and *Ca. L. solanacearum* (referenced as CLs from this point on) were the same bacterium (Crosslin & Bester, 2009; Munyaneza et al., 2009a,b,c; Secor et al., 2009; Wen et al., 2009; Crosslin et al., 2010; French-Monar, 2010; Munyaneza, 2015). While CLs infections result in ZC disease in potatoes, the outcome of the infection in tomatoes, peppers/capsicums and eggplants is vein greening disease (Prager et al., 2016). Convolvulaceae species such as sweet potato and bindweed appear to be suitable hosts for TPP but not for CLs (Munyaneza, 2012).

It has now been established that not all TPP colonies carry CLs (Henne et al., 2010a; Henne et al., 2010b). Temperatures below 17°C slow but do not prevent the development of CLs while temperatures above 32°C are known to be detrimental to CLs (Munyaneza et al., 2012). The heat sensitivity of CLs could explain the presence of this bacterium in certain countries and regions (Munyaneza et al., 2012). CLs can be transmitted vertically however the ratio of transmission through the different TPP life stages appears to be influenced by the host plant, e.g. greater on potato reared TPP than on tomato reared TPP (Hansen et al., 2008). The bacterium is generally horizontally transmitted throughout crops by TPP feeding on infected plants and propagating the disease to healthy plants (Munyaneza, 2015). CLs are believed to be transmitted to the plant by nymphs and adults during phloem salivation, meaning that both life stages have to be controlled (Butler et al., 2012; Page-Weir et al., 2011; Echegaray et al., 2016). Adults were reported as being more efficient vectors than nymphs at transmitting CLs to plants (Buchman et al., 2011). The transmission of CLs to tomato and potato plants by an individual can range between less than 10 minutes to 6 hours; generally transmissions to susceptible plants will be achieved after one week of exposure to infected TPP (Hansen et al., 2008; Yang et al., 2010a; Munyaneza, 2010; Butler et al.,

2011; Jorgensen et al., 2013; Prager et al., 2013a; Munyaneza, 2015). The latent period of the bacterium in TPP is roughly two weeks when feeding has occurred on infected potato plants, however it is shorter when feeding has occurred on infected tomato plants potentially due to the greater CLs titer in tomato than potato (Munyaneza, 2015).

#### *1.2.4 TPP management strategies*

##### *1.2.4.1 Monitoring TPP*

Early detection of TPP invasions via ‘direct’ and/or ‘indirect’ sampling techniques increases the probability of implementing management decisions to eradicate/control TPP prior to population establishment and propagation of associated diseases and also assists in the development of economic action thresholds by confirming the efficacy of controls, trends of infestations and population dynamics of secondary pests and natural enemies (Al-Jabr & Cranshaw, 2007; Goolsby et al., 2007; Walker et al., 2011; Martini et al., 2012; Yen et al., 2013; Walker et al., 2013; Yen et al., 2013; Echegaray et al., 2016). A study by Walker et al. (2011) on unsprayed potato crops in Pukekohe revealed that early season crops could avoid being damaged by TPP infestations and confirmed that sticky traps were a good indicator of crop infestation. Furthermore, Walker et al. (2013) developed a sub-sampling method of plants and recommended that crop scouting protocols for TPP infestations be based on sampling 100 middle leaves of 50 randomly selected plants. In order to mitigate the risk of TPP incursions into Australia an ongoing surveillance program using yellow sticky traps was initiated in 2011 in various locations around Tasmania, Victoria, South Australia and Queensland (Walker et al., 2015b).

##### *1.2.4.2 Insecticides*

Economic pressures on farmers to control TPP invasions immediately, because of their high reproductive rates and the threat posed by the suite of associated diseases that they carry, has led to insecticide applications being the most widely used TPP management strategy in the majority of affected regions (Goolsby et al., 2007; Yang et al., 2010a; Butler et al., 2011; Ail-Catlim., et al 2012; Butler & Trumble, 2012a; Munyaneza, 2012; Mauchline & Stannard, 2013; Granados-Echegoyen et al., 2015; Munyaneza, 2015; Prager et al., 2016; Villanueva et al., 2016). TPP management is complicated

because pathogens may be transmitted to the plant at the same time as insecticides are ingested by the insect (Liu & Trumble, 2004; Prager et al., 2013a). TPP death after toxic consumption generally takes longer than the time required by a TPP individual to transmit the pathogen to the plant (Yang et al., 2010a; Butler et al., 2011; Jorgensen et al., 2013; Prager et al., 2013a; Munyaneza, 2015). Prager et al. (2013a) proposed that ZC symptoms were found in their field study despite low TPP pressure and significant effects of insecticide treatments because 100% mortality was not achieved and enough TPP survived to transmit the bacteria. This outcome highlights the difficulty of managing diseases that can be passed on by relative few individuals (Prager et al., 2013a).

A variety of studies have focused on the immediate knockdown and residual effects of products on TPP nymphs and adults (Berry et al., 2009; Gharalari et al., 2009; Page-Weir et al., 2011). The effectiveness of an insecticide may vary depending on the life stage that has been targeted; chemicals that control adults may not be effective against eggs and nymphs and *vice versa* while others can affect all life stages (Page Weir et al., 2011; Butler & Trumble, 2012a; Prager et al 2013a; Prager et al., 2013b ;Munyaneza, 2015; Echegaray et al., 2016). Insecticides will also affect TPP behaviours such as feeding, probing, cleaning, resting and walking in different ways (Butler et al., 2011; Butler et al., 2012). TPP reproduction can also be affected (Echegaray et al., 2016). Insecticides can reduced bacterium transmission by repelling TPP or inhibiting them feeding, but non-target effects and resistance have also been reported (Liu & Trumble, 2007; Berry et al., 2009; Butler et al., 2011; Butler et al., 2012; Liu et al., 2012; Prager et al 2013a; Prager et al 2013b; Cerna et al.,2012; Ail-Catzim et al., 2015; Martinez et al., 2015).

Resistance to insecticides by TPP has been linked to how long and how often certain insecticides have been used in the affected regions (Liu & Trumble, 2007; Prager et al., 2013a; Chavez et al., 2015; Prager et al., 2016). The potential of TPP populations to develop resistance to commonly used chemicals could be mitigated with the introduction of newer insecticides with distinct modes of action (Echegaray et al., 2016). The perception of ineffective TPP control via insecticides has also been proposed to be due to unsatisfactory spray coverage, faulty calibration and ineffective equipment rather than chemical resistance (Chavez et al., 2015). The application method of



insecticides can cause differences in mortality (Gharalari et al., 2009; Prager et al., 2016). Good coverage of plant surfaces is vital for effective results due to TPP adults and nymphs regularly distributing themselves to the underside of leaves (Munyaneza, 2015).

The management of TPP is usually conducted via the calendar based rotation of a small group of insecticides (Goolsby et al., 2007; Liu & Trumble, 2007; Yang et al., 2010a; Butler et al., 2011; Guenthner et al., 2012; Prager et al., 2013a; Echegaray et al., 2016). Rotation of treatments with different modes of action serves as a tool for insecticide resistance management strategy and maximises the impact of natural enemies by deploying the more selective products earlier in the season (Gharalari et al., 2009; Anderson et al., 2013; Wright et al., 2015; Prager et al., 2016). TPP commercial insecticide programs in Northern New Zealand typically involve a greater number of applications in comparison to Southern New Zealand programs due to lower TPP pressure down South (Wright et al., 2015). Following consistent results over six growing seasons in the Pukekohe region Walker et al. (2015a) reported that insecticides are not required before the end of December. The New Zealand potato industry has taken the recommendation from Walker et al. (2015) onboard and growers are now saving up to 10 insecticide sprays per season in early potato crops and using more selective insecticides to minimize effects on natural enemies.

Anderson et al. (2013) proposed that intense insecticide programmes do not guarantee the elimination of ZC risk and they are economically unsustainable. The arrival of TPP into New Zealand disrupted IPM practices for affected solanaceous crops due to the incompatibility of the majority of registered TPP controlling insecticides with existing IPM management plans (Berry et al., 2009; Mauchline & Stannard 2013). Similarly, dramatic increases in TPP populations resulted in pesticide usage increases and disruption of low-input IPM strategies of California and Baja California (Mexico) tomato crops (Liu & Trumble., 2004). Furthermore, growers in potato growing regions in Texas grew their crops without the use of insecticides prior to the appearance of ZC (Guenthner et al., 2012). Subsequently, growers via trial and error attempted to narrow down effective insecticides against TPP that were also least disruptive against beneficial species (Guenthner et al., 2012). Despite the use of multiple applications of insecticides with varied modes of action, yield and quality losses remain a problem for the affected

industries (Guenthner et al., 2012). Organic productions affected by TPP find that compatible insecticides are not abundant and those that are compatible may not provide effective protection on their own (Villanueva et al., 2016). Organic productions may require alternative host plants in order to increase numbers of natural enemies with assistance from the use of organic insecticides (Villanueva et al., 2016).

#### *1.2.4.2.1 Biorational insecticides*

The use of biorational insecticides (e.g. soaps/detergents, essential oils, mineral oils and botanical extracts, wettable sulphur, etc. ) is seen as an approach to maintain a sustainable TPP IPM program (Lacey et al., 2009; Yang et al., 2010a; Lacey et al., 2011; Diaz Montano & Trumble, 2012; Jorgensen et al., 2013; Granados-Echegoyen et al., 2015; Wright et al., 2015). These environmentally sensitive products tend to be active against targeted pest population but also relatively harmless to non-target organisms which will allow the conservation and augmentation of biological control agents and will avoid the use of broad-spectrum insecticides (Yang et al., 2010a; Lacey et al., 2011; Diaz Montano & Trumble, 2012; Jorgensen et al., 2013). Phytotoxicity is a potential adverse effect of biorational insecticides (Yang et al., 2010a; Jorgensen et al., 2013). Biorational products alone might be incapable of being a commercially viable option (Wright et al., 2015). However, mixing biorational insecticides with different traditional effective pesticides can possibly delay the development of resistance and increase their efficacy (Yang et al., 2010a).

#### *1.2.4.3 Biological control*

The reliance of broad-spectrum insecticides can be expensive, environmentally damaging, susceptible to resistance and lethal to natural enemies (Butler et al., 2011; Chavez et al., 2015; Granados-Echegoyen et al., 2015; Munyaneza, 2015; Pineda et al., 2016). Concerns with chemical control dependency and potential resistance suggest there is a need to find alternative solutions (Butler et al., 2011; Chavez et al., 2015; Munyaneza, 2015; Prager et al., 2016). The use of biological control agents in conjunction with selective insecticide programs and other control methods is a prospective solution to deal with the overuse of chemical controls (Symondson et al., 2002; Van Lenteren, 2012b; Prager et al., 2016). TPP has known natural enemies but

the number of studies on potential biological control agents acting on TPP is fairly limited and therefore the number of commercially available biological control agents exclusive to this pest are non-existent (Munyaneza, 2015; Prager et al., 2016). Most commercially available biological control agents are usually marketed towards other pest species that cause issues in similar host plants such as whiteflies, leafminers, thrips, aphids and spider mites (Prager et al., 2016; Bioforce Limited, 2014).

#### *1.2.4.3.1 Entomopathogenic fungi*

Fungi are an effective entomopathogen of Hemiptera due to their ability to penetrate the integument of the insect and not rely on uptake via the piercing and sucking mouthparts (Lacey et al., 2009). Furthermore, their insecticidal activity is usually host specific and can often complement predators and parasitoids (Lacey et al., 2011; Mauchline & Stannard, 2013). Commercially available fungi have been trialled on TPP adults and nymphs in the laboratory and greenhouses with varied success (Lacey et al., 2009; Lacey et al., 2011; Mauchline & Stannard, 2013; Tamayo-Mejía et al., 2014). Environmental factors are vital to entomopathogenic fungi success in field environments particularly in areas where temperatures and relative humidity percentages can fluctuate outside the range of ideal conditions for fungal germination and infection (Lacey et al., 2009; Lacey et al., 2011). Ultraviolet radiation inactivated conidia and was identified as the principal limiting factor of residual activity in entomopathogenic fungus applications (Lacey et al., 2011). The development of greater effective delivery systems such as spraying technology that efficiently targets the lower sides of leaves was proposed by Lacey et al. (2011) as a means to extend the viability of conidia and improve residual activity. Mauchline and Stannard (2013) emphasised the importance of timing spray applications of entomopathogens to periods when greenhouses are at an ideal temperature in order to maximise effectiveness.

#### *1.2.4.3.2 Parasitoids*

The North American parasitoid *Tamarixia triozae* (Burks) (Hymenoptera: Eulophidae) has been observed parasitizing TPP nymphs in Mexico and USA field environments (Rojas et al., 2015; Castillo Carrillo et al., 2016). Mexican *T. triozae* were imported to containment into New Zealand and subsequently granted release approval by the New

Zealand Environmental Protection Agency to manage TPP (Workman & Whiteman, 2009; Environmental Protection Authority, 2016). A variety of studies have been performed on the *T. triozae*-TPP interactions (Martinez et al., 2015; Rojas et al., 2015; Yang et al., 2015; Hernández-Moreno et al., 2017). Yang et al. (2015) reported that *T. triozae* significantly preferred to parasitize larger (fourth and fifth) instar stages over smaller instar stages, potentially due to their greater nutritional content which would increase development and ensure lower mortality rates. When female parasitoids were deployed in, densities greater than one their searching efficiency was greatly reduced (Yang et al., 2015). Rojas et al. (2015) raised the issue that *T. triozae* is not known to target TPP adults that are largely responsible for the infection of plants with ZC disease. Nevertheless, *T. triozae* was deemed to have the potential to be used in augmentative TPP control programs on tomato and bell pepper (Rojas et al., 2015; Yang et al., 2015). The combination of *T. triozae* and entomopathogenic fungi against TPP nymphs has been tested with results revealing that the combination was more effective if the fungus is applied after the parasitoid has parasitized the target rather than before (Tamayo-Mejía et al., 2015; Tamayo-Mejía et al., 2016).

The susceptibility of *T. triozae* to broad spectrum insecticides has led to low parasitism levels being reported in the field (Liu et al., 2012; Martinez et al., 2015; Rojas et al., 2015). However, a variety of insecticides have been identified by Liu et al. (2012) as being likely to be IPM compatible with *T. triozae*. Morales et al. (2015) recommended that the application of selective insecticides may be most effective when the parasitoid is in its pupal stage since this is the least susceptible stage. The apparent sensitivity of the parasitoid towards the tested insecticides in a laboratory environment led Martinez et al. (2015) to propose that the combination of these tools in a TPP IPM program must be evaluated further in a field environment. Liu et al. (2012) concluded that unlike parasitoids reared and tested in cages, vials or dishes, *T. triozae* on a plant can potentially escape the effects of detrimental insecticides by finding refuge in non-contaminated sections of the plant or via insecticide residue degradation due to rainfall. Therefore, laboratory results should not be extrapolated immediately to commercial crop level although they do provide an insight of the potential effects they may have on the parasitoid.

#### 1.2.4.3.3 Predators

Augmentative releases of the parasitoid *T. triozae* are expensive to deploy due to the large numbers required; furthermore, they generally target larger TPP instars, limiting the impact on disease transmission by smaller TPP instars (Rojas et al., 2015; Calvo et al., 2016). *T. triozae* was tested in combination with *Dicyphus hesperus* Knight (Heteroptera: Miridae) on a variety of TPP life stages and the predatory mirid reportedly preferred to prey on unparasitized nymphs rather than parasitized nymphs (de Lourdes Ramírez-Ahuja et al., 2017). The simultaneous release of *D. hesperus* and *T. triozae* was summarised by de Lourdes Ramírez-Ahuja et al. (2017) as having the potential to succeed because each agent targets different TPP life stages but further research into their relationship was required before this interaction can be fully implemented. A variety of studies have been conducted on predatory mirids predating on TPP adults and nymphs (Martinez et al., 2014; Calvo et al., 2016; Pineda et al., 2016). *D. hesperus* and *Engytatus varians* (Distant) (Heteroptera: Miridae) were proposed as potential TPP predators to be deployed in IPM programs (Martinez et al., 2014; Calvo et al., 2016; Pineda et al., 2016). However, precaution is required prior to release because predatory mirids have the capability to injure plants (Martinez et al., 2014; Calvo et al., 2016; Pineda et al., 2016).

The potential of coccinellid species as biological control agents of TPP have also been tested with varying results. For example, O'Connell et al. (2012) tested TPP nymph consumption by *Cryptolaemus montrouzieri* Mulsant, *Cleobora mellyi* Mulsant, and *Scymnus loewii* Mulsant on potato and tomato leaflets. The authors reported that *C. mellyi* consumed the greatest number of nymphs while *S. loewii* consumed the least. The research into the biological control potential of *C. mellyi* was advanced further by Pugh et al. (2015) who investigated TPP consumption in the presence of green peach aphids, potato aphids and whiteflies. The authors reported that no prey preference was found between the aphid species and TPP. However, there was a significant preference of TPP over whiteflies. TPP numbers in potato plants significantly decreased in the presence of *C. mellyi* which subsequently increased the production of tubers by the plants.

Ail-Catzim et al. (2012) reported that the third larval stage of *Chrysoperla carnea* (Stephens) (Neuroptera: Chrysopidae) was likely to be successful in augmentative biological control programs of TPP nymphs. Cerna et al. (2012) identified insecticides that were highly toxic towards *C. carnea* and therefore deemed to be impractical for their implementation in a joint biological/chemical TPP control program. However, the authors also proposed abamectin and endosulfan as candidates for integration with *C. carnea* releases due to their high toxicity towards TPP and low toxicity towards *C. carnea*. Similarly, Ail-Catzim et al. (2015) proposed that abamectin could be employed in cooperation with *C. carnea* in an IPM system. Interestingly, unlike Cerna et al. (2012), bifenthrin was not discarded by Ail-Catzim et al. (2015) and was also proposed to use in an IPM system. Like Cerna et al. (2012), profenofos and imidacloprid were also found to be highly toxic and discarded as an IPM option.

Xu and Zhang (2015) proposed the predatory mite *Amblydromalus limonicus* Garman & McGregor (Acari: Phytoseiidae) as a potential biological control agent of TPP due to its capacity to consume and reproduce on a diet of TPP eggs, first, second and third instar nymphs and psyllid-produced honeydew and also be commercially mass reared. Villanueva et al. (2016) reported that adult *Amblyseius largoensis* (Muma) (Acari: Phytoseiidae) consumed TPP eggs on potato leaf disk. Furthermore, the predatory mite was observed in non-experimental settings predating on TPP nymphs. The authors also identified two further phytoseiid mites *Typhlodromips* near *tennesseensis* (Mesostigmata: Phytoseiidae), and *Typhlodromalus* near *peregrinues* (Mesostigmata: Phytoseiidae) as potential biological control agents for TPP but predatory tests were not conducted. Geary et al. (2016) reported that *Anystis baccarum* L. (Trombidiformes: Anystidae) was capable of attacking and killing large TPP nymphs but proposed that the predatory mite was potentially more suited to attack the egg and smaller nymphal stages of TPP despite not investigating these life stages in their study. Furthermore, the authors reported that the predatory mite appeared to be distracted by the presence of psyllid-produced honeydew leading them to occasionally feed and be satiated on these sugars, leaving the prey alone.

A TPP monitoring study on Pukekohe region potato crops by Walker et al. (2011) revealed that the brown lacewing *Micromus tasmaniae* (Walker) (Neuroptera: Hemerobiidae) and the small hover fly *Melanostoma fasciatum* (Macquart) (Diptera:

Syrphidae) were the most abundant predators. The study also revealed the presence of other predators such as Pacific damsel bug *Nabis kinbergii* Reuter (Hemiptera: Nabidae), 11-spotted ladybird *Coccinella undecimpunctata* L. (Coleoptera: Coccinellidae), and large spotted ladybird *Harmonia conformis* (Boisduval) (Coleoptera: Coccinellidae). Based on their presence in potato crops, MacDonald et al. (2015) investigated the potential of *M. tasmaniae*, *M. fasciatum*, *N. kinbergii*, *C. undecimpunctata*, and *H. conformis* as TPP biological control agents. All the tested predator life stages consumed all of the TPP life stages offered. However, the tested predators did not show any preference for TPP over *Myzus persicae* Sulzer (Hemiptera, Aphididae). The authors concluded that *M. tasmaniae* and *M. fasciatum* have the potential to be effective natural enemies of TPP in crop IPM programs that implement the use of selective insecticides and emphasise the use of conservation biological control methods.

The biological control potential of *Orius tristicolor* (White) (Hemiptera: Anthocoridae) to control TPP in capsicum, tomato and potato Southern Californian crops was investigated by Butler and Trumble (2012b) during a two-year study which combined field study with laboratory feeding tests. *O. tristicolor* was categorized as a potential biological control agent due to its presence on the affected crops (particularly capsicum and tomato) and its ability to attack TPP nymph stages. A subsequent study by Castillo Carrillo et al. (2016) on the abundance of predatory arthropods on bittersweet nightshade, a non-crop host of TPP, found that *O. tristicolor* was one of the most abundant generalist predator species found. Tran (2012) investigated the biological control potential of *O. vicinus* to control TPP in New Zealand. The predatory bug consumed a greater number of egg and smaller nymphal stages in comparison to larger nymphal stages. The predatory bug preferably consumed thrip nymphs over TPP nymphs; however, it continued consuming TPP in the presence of its preferred prey. Tran (2012) concluded that further studies were required to assess the true impact of *O. vicinus* on TPP populations. Tran (2012) identified plant architecture and/or traits as potential factors that may affect the predatory behaviour of *O. vicinus*. Therefore, assessing the predatory bug on crops with varying morphological plant traits will provide further insight into their practical usefulness. Particularly, considering the potential of TPP to inflict economic losses to a wide variety of solanaceous crops, which vary in morphological traits.

### 1.3 Genus: *Orius*

Species from the genus *Orius* (Hemiptera: Anthocoridae) are commonly known as minute pirate bugs or flower bugs (Lattin, 1999; Horton, 2008). There are roughly 70 described *Orius* species that are geographically widespread (found in Oriental, Ethiopian, Palaertic, and Neotropical regions) occupying both natural and disturbed habitats (Horton, 2008). *Orius* spp. attack and consume small soft-bodied arthropods from a variety of taxonomic groups (e.g. thrips, scales, aphids, psyllids, and eggs/small larvae of Lepidoptera, Coleoptera, and Diptera) (Lattin, 1999; Horton, 2008; Gomez-Polo et al., 2013). Consumption of prey is achieved via their piercing-sucking mouthparts, which are in the form of a slender beak/labium (Horton, 2008). *Orius* spp. can also supplement their diet with pollen, which means that they can potentially maintain themselves on this food source when prey populations are low (Lattin, 1999; Horton, 2008; Gomez-Polo et al., 2013). However, their ability to ingest plant juices means that they are also susceptible to systemic insecticide ingestion from root treated plants (Funderburk et al., 2000; Horton, 2008). Nevertheless, several studies have identified compatible insecticides that can be implemented concurrently with *Orius* spp. in IPM programs (Funderburk et al., 2000; Funderburk et al., 2013; Srivastava et al., 2014).

The colonization of crops by *Orius* spp. can occur without human intervention (Veres et al., 2012). However, various *Orius* spp. are produced by commercial insectaries for augmentative biological control programs against economically important pests in annual/perennial row crops, greenhouses and ornamental plants environments (Horton, 2008; Bonte & De Clercq, 2011; Veres et al., 2012). An augmentative biological control programs reviewed by van Lenteren (2012b) found that *Orius* spp. were used in 9 out of 20 programs involving heteropteran species. Control programs using *O. laevigatus* (Fieber) were implemented in 15 to 20 countries worldwide (van Lenteren, 2012b). Furthermore, control programs involving *O. laevigatus* and *O. insidiosus* (Say) were reported to have sold anywhere between a hundred thousand to a million individuals per week (van Lenteren, 2012b). The majority of studies on this family are generally focused around economically important arthropod pests (Horton, 2008). The predatory performance of *Orius* spp. has been trialled on a variety of plants (cucumber, sweet pepper, eggplant, sweet corn, lima bean, French bean, soy bean, tomato, cabbage, wild



grape, strawberry, potato, roses, sweet potato) with a variety of economically important pests (thrips, spider mites, whiteflies, aphids, Lepidoptera larvae and eggs) (Chambers et al., 1993; Coll & Ridgway, 1995; Eigenbrode et al., 1995; Eigenbrode et al., 1996; Coll et al., 1997; Brown et al., 1999; Zsellér & Kiss, 1999; Norton et al., 2001; Gitonga et al., 2002; Shipp & Wang., 2003; Rutledge & O'Neil, 2005; Economou et al., 2006; Hamdan & Abu-Awad, 2007; Chow et al., 2008; Madadi et al., 2008; Lundgren et al., 2009; Chow et al., 2010; Dai et al., 2010; Jalalizand et al., 2011; El-Basha et al., 2012; Fathi, 2014).

### 1.3.1 *Orius vicinus*

*O. vicinus* is widely distributed in the Palaearctic region (particularly in Europe) (Lariviere & Wearing, 1994). It has subsequently been found in western North America (British Columbia, Oregon and Washington) since the 1930s but had previously been misidentified as *O. minutus* (Linnaeus) (Lewis & Lattin, 2010). Despite its vast Northern Hemisphere range its presence in the Southern Hemisphere was unknown until the early 1990s when Lariviere and Wearing (1994) recorded their existence on chemically untreated apple trees in the central Otago region. How and when *O. vicinus* became established in New Zealand remains unknown but it may have arrived earlier than the 1990s but its susceptibility to insecticides may explain why it failed to establish on commercial orchards (Lariviere & Wearing, 1994).

The development of *O. vicinus* from egg to adult will generally take two months (Lariviere & Wearing, 1994). The predatory bug will pass through five nymphal stages (Figure 1.2) which will generally take 16 to 18 days at 25C° (Lariviere & Wearing, 1994). Adults (Figure 1.2) are relatively small and will reach a length between 2.0-2.6 mm (Lariviere & Wearing, 1994). The predatory bug has two to three generations per year within their European range (Wearing & Attfield, 2002). Research in New Zealand indicates that there are usually two generations per year with a potential third generation being possible during warm seasons (Wearing & Attfield, 2002). Females from the second generation overwinter after mating (Wearing & Attfield, 2002).



**Figure 1.2:** Adult *O. vicinus* probing a TPP nymph on capsicum surface (left) and *O. vicinus* nymph on tomato surface (right).

The predatory bug from the Palaearctic region is generally found in fruit trees (particularly apple trees of the Beauty of Boskoop variety, a preference that might be substrate related) and herbaceous plants (e.g. *Chenopodium* and *Herecleum*) (Lariviere & Wearing, 1994). It was also collected from a variety of North American plants by Lewis and Lattin. (2010), implying a vast host range in this region. *O. vicinus* in its natural environments in the Palaearctic region largely targeted aphids, mites, thrips and scale insects (Lariviere & Wearing, 1994; Wearing & Colhoun, 1999; Lewis & Lattin, 2010). North American potential prey consisted of bark lice, psyllids, thrips, aphids and leafhoppers (Lewis & Lattin, 2010). The diet of the predatory bug in New Zealand has been observed to include mites, thrips and leafhoppers (Lariviere & Wearing, 1994; Wearing & Colhoun, 1999).

*O. vicinus* survives on a variety of prey species and a pollen-specific diet in the laboratory (Heitmans et al. 1986). Within a New Zealand context, Wearing and Colhoun (1999) studied the development and adult size of *O. vicinus* on the mites *Aculus schlechtandali* (Nalepa) (Prostigmata: Eriophyidae), *Panonychus ulmi* (Koch) (Trombidiformes: Tetranychidae), and *Tetranychus urticae* Koch (Acari: Tetranychidae), the larvae of the New Zealand flower thrip *Thrips obscuratus* (Crawford) (Thysanoptera: Thripidae) and the apple leaf curling midge *Dasineura mali* (Bouche) (Diptera: Cecidomyiidae). The authors found that the predatory bug fed and completed their development on all prey species. The fastest development time and largest adult size were recorded for the predatory bugs that fed on *T. obscuratus* and the

slowest development and smallest adult size were recorded for predatory bugs fed with *A. schlechtandali*.

Within a biological control context, *O. vicinus* has previously been identified as having the potential to provide control against phytophagous mites (Heitmans et al, 1986). Wearing and Lariviere (1994) also raised the possibility that they could be mass reared and released in greenhouses. Furthermore, Wearing and Lariviere (1994) proposed the deployment of the predatory bug to act as a biological control agent in New Zealand apple and stonefruit orchards. The implementation of integrated organic production systems in New Zealand orchards with their use of selective insecticides or alternative pest management methods such as mating disruption further increased its suitability as a biological control agent (Walker et al., 1997; Walker et al., 1998; Wearing & Colhoun, 1999). A study by Wearing et al. (2010) monitored the woolly apple aphid *Eriosoma lanigerum* (Hausmann) (Hemiptera: Aphididae) and its natural enemies on apple orchards between 1994 and 2000 as pest management transitioned from conventional fruit production (broad spectrum insecticide usage) to integrated fruit production (biological and cultural control along with selective insecticide usage). *O. vicinus* were either absent if organophosphate insecticides were applied or in low numbers if lufenuron (a chitin synthesis inhibitor) was sprayed. However, a significant greater number of *O. vicinus* were found in trees sprayed with the selective insecticide tebufenozide (Wearing et al., 2010). These results coincide with a study by van de Veire et al. (2002) who tested the effects of 22 pesticides on *O. laevigatus* and catalogued tebufenozide as harmless while also suggesting that lufenuron should not be used in conjunction with the predatory bug.

#### **1.4 The effect of morphological plant traits on biological control agents**

The assessment of a potential biological control agent on a targeted pest must consider the effect that the morphological traits of the host plant may have. These traits have the capacity to affect the pest control efficiency of the biological control agents by impeding their movement, reducing their attachment efficiency and providing refugia that allow prey to be completely or partially inaccessible (Clark & Messina, 1998; Cortesero et al., 2000; Reynolds & Cuddington, 2012a; Reynolds & Cuddington, 2012b).

The gross morphology of plants (e.g., overall size, macroscopic shape and connectivity between plant parts) can affect the foraging success of predators and parasitoids (Reynolds & Cuddington, 2012a). Cloyd and Sadof (2000) investigated how plant height, leaf surface area, number of leaves and number of branches impacted the attack rate of the parasitoid *Leptomastix dactylopii* Howard (Hymenoptera: Encyrtidae) on various densities of the citrus mealybug, *Planococcus citri* Risso (Hemiptera: Pseudococcidae). The authors found that the plant height and number of leaves of *Solenostemon scutellarioides* (L.) Codd (Lamiales: Lamiaceae) negatively affected the searching efficiency of the parasitic wasp. Gingras et al. (2002) suggests that the reliance of the parasitoid *Trichogramma evanescens* Westwood (Hymenoptera: Trichogrammatidae) on locomotion over chemical cues and flying to locate the eggs of *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) explains the decrease in their host finding ability and parasitism rate when plant structure connectivity increased (greater number of stems, secondary stems, leaves and buds resulted in more plant connections). Similarly, Gingras et al. (2008) found that *T. turkestanica* Meyer located more *E. kuehniella* eggs on simple (less plant connections) than on complex (greater plant connections) plant structures. The authors suggest that increases in connections also increase the number of pathways and directions a parasitoid can take which lessens host finding efficiency. This effect has been shown in the performance of parasitoids on cabbage, Brussels sprouts and broccoli (Gingras et al, 2003).

Like parasitoids, predators that rely on locomotion as their primary method of searching for prey are also susceptible to the effects of plant morphology. Legrand and Barbosa (2003) reported that the predation rates of *Coccinella septempunctata* Linnaeus on pea aphid, *Acyrtosiphon pisum* Harris (Hemiptera: Aphididae), decreased on structurally more complex hosts (complexity was determined by the number of branch nodes). However, Karaeiva and Sahakian (1990) found contrasting results when they reported that *C. septempunctata* had greater success capturing *A. pisum* on leafless mutant pea plants (with greater junctions) than on normal leafy pea plants (with less junctions). The predator falling off the slippery leaf surfaces was proposed by Karaeiva and Sahakian (1990) as the reason for greater success in the leafless plant. Similarly, Reynolds and Cuddington (2012a) found consumption rates on *A. pisum* for a similar predator *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae), and dissimilar predator *C.*

*carnea* increased in highly branched pea plants and decreased in leafier and less branched pea plants. Different searching strategies and/or consumption capacities were proposed by Reynolds and Cuddington (2012a) as potential reasons why their results differed from Legrand and Barbosa (2003). Prey distribution was also proposed as a reason for the disparity in results. Karaeiva and Sahakian (1990) and Legrand and Barbosa (2003) used the same predator but differed in prey distribution (patchy distribution vs. roughly uniform distribution). Reynolds and Cuddington (2012a) concluded that partial refugia in leafier morphologies could make prey inaccessible to predators and would explain the lower consumption they and Kareiva and Sahakian (1990) reported.

Enemy free spaces can be found in plants that provide refugia for prey to become inaccessible to predators. Clark and Messina (1998) proposed that predation rates of the fourteen-spotted ladybird, *Propylea quatuordecimpunctata* (L), on the Russian wheat aphid, *Diuraphis noxia* (Mordvilko) (Homoptera: Aphididae), were greater on Indian ricegrass than on crested wheatgrass due to the available refugia in the latter being large enough to allow aphids to find shelter but small enough to deny access to the predator. In comparison the refugia available on Indian ricegrass was relatively small and only allowed a certain number of aphids to be completely inaccessible to the predator, which left the majority of available aphids exposed to the predator.

Gassman and Hare (2005) tested four natural enemies of the leaf feeding beetle *Lema daturaphila* Kogan and Goeden (Coleoptera: Chrysomelidae) and the piercing-sucking mirid bug *Tupiocoris notatus* Distant (Hemiptera: Miridae) on Jimsonweed which exhibits two trichome phenotypes: a velvety phenotype (surface is densely covered with short non-glandular trichomes) and a sticky phenotype (surface is less densely covered with glandular trichomes that secrete glucose esters and aliphatic acids). Natural enemies were less effective on sticky surfaces due to their movement being hampered and the authors hypothesized that the negative impact of glandular trichomes on predators might have led to certain herbivores specializing on these plants due to the enemy free space they provided.

Eigenbrode et al. (1996) tested the mobility and predation rates of adult *Hippodamia convergens* Guérin-Menneville (Coleoptera: Coccinellidae), adult *O. insidiosus*, and

larval *C. carnea* on larval populations of the diamondback moth *Plutella xylostella* (L.) (Lepidoptera: Plutellidae) on two cabbage surfaces (normal-wax and glossy) which differed in the amount of crystallized waxes (wax bloom) found on their surfaces. The authors found that predators were less mobile and spent more time grooming on the normal-wax surfaces (extensive wax bloom) due to reduced traction/attachment. Furthermore, the greater number of prey encounters on glossy surfaces (no wax bloom) was attributed to predators experiencing less mobility impediments which increased searching efficiency and thus emphasised a link between mobility and predation.

Fathi (2014) investigated the predation rates of *O. minutus* on *T. urticae* on potato cultivars that differed in leaf trichome densities. The authors found that the predation rates of *O. minutus* were significantly higher on the cultivar with the lowest trichome density. Furthermore, there was no difference in predation rates between the two cultivars with high trichome density. Similarly, Jalalizand et al. (2011) also focused on *T. urticae* predation (via functional response) but using *Orius niger niger* (Hemiptera: Anthocoridae) on cucumber (high trichome density) and strawberry (low trichome density) leaves. The predator handling time was highest and searching efficiency was lowest on cucumber, while the maximum number of prey attacked by the predator was highest on strawberry. The authors attributed this result to the mechanical effect that cucumber trichomes had on the movement and subsequent encounter rate of the predator. Krips et al. (1999) reported that *Phytoseiulus persimilis* Athias-Henriot (Acari: Phytoseiidae) moved faster on the gerbera cultivar surface with the lowest trichome density. Furthermore, the effect of leaf hair density on predation of *T. urticae* eggs by the predatory mite was only significant at low prey densities with no effect at high prey densities.

#### *1.4.1 Assessment of experimental plant surfaces*

##### *1.4.1.1 Tomato plant surfaces*

There are host plant structures that are either partially or completely unsuitable for either predators or parasitoids to maintain pest populations below economic threshold levels. The literature suggests that the stems and foliage of tomato plants can be a hostile environment for potential biological control agents due to the negative effect

tomato non-glandular and glandular trichomes have on the foraging performance of the predator/parasitoid (De Clercq et al, 2000; Kennedy, 2003; Shipp & Wang, 2003; Economou et al, 2006; Koller et al 2007).

Cédola et al. (2001) found that *Neoseiulus californicus* McGregor (Acari: Phytoseiidae) predating on the two-spotted spider mite, *T. urticae*, exhibited poor predatory performance when tested on two tomato hybrids with different glandular trichome densities. De Clercq et al. (2000) reported that the foraging efficiency of *Podisus nigrispinus* Say (Heteroptera: Pentatomidae) on various densities of the beet armyworm *Spodoptera exigua* Hubner (Lepidoptera: Noctuidae) was lowest on tomato surfaces in comparison to other tested host plant surfaces. Verheggen et al. (2009) reported that larvae *Episyrphus balteatus* De Geer (Diptera: Syrphidae) predating on *M. persicae* moved significantly slower on the stems of tomato in comparison to other tested plant surfaces. Furthermore, a significantly greater number of predators were recorded falling off the stem surface of tomato. The authors from these studies concluded that tomato surfaces impeded efficient locomotion.

O'Connell et al. (2012) tested TPP nymph consumption by Coccinellid species on tomato and potato plant surfaces. Adults and fourth instar larvae of *C. mellyi* consumed the greatest number of TPP nymphs on both plant surfaces and showed no difference in performance between plant surfaces. However, *S. loewii* adults performed poorly on tomato surfaces. Behavioural observation results on tomato leaflets revealed that the smaller *S. loewii* spent more time grooming and less time searching for prey while the opposite occurred for the larger *C. mellyi*. The authors concluded that *C. mellyi* had a morphological advantage over *S. loewii* due to their larger size, which enabled greater consumption capacity and reduced the effect of tomato trichomes on their mobility.

The searching behaviour of highly mobile predators like *Orius* spp. may be influenced by the plant surface in which they are released (Coll et al., 1997). The walking speed of adult *O. insidiosus* was found by Coll et al. (1997) to be significantly slower on tomato surfaces than on plant surfaces with lower trichome densities. The authors conducted simulated searching efficiency tests (by overlapping the information gathered from prey distribution maps and predator walking paths) and the results indicated that at low prey densities the rate of encounters would be lowest on tomato surfaces. The activity of *O.*

*niger* Wolff was tested by Economou et al. (2006) on different varieties of tomato cultivars which differed in trichome density. The authors found that the predatory bug spent more time grooming and less time moving on the cultivar with the greatest trichome density. Furthermore, Shipp and Wang (2003) tested the effectiveness of augmentative releases of the predatory bug *O. insidiosus* on greenhouse tomatoes infested with *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae) and found that it failed to reduce the pest to acceptable non-economic loss densities. Monitoring of population densities revealed that *O. insidiosus* failed to establish on tomato crops. A number of dead *O. insidiosus* nymphs were found tangled on the glandular hairs of tomato stems, implying that establishment failure could be related to the impact of tomato surfaces. Alternatively, Hamdan and Abu-Awad (2007) reported that *O. laevigatus* consumed significantly more tobacco whitefly larvae *Bemisia tabacum* (Gennadius) (Hemiptera: Aleyrodidae) on the leaf discs of tomato than on eggplant. It is important to highlight that both tomato and eggplant leaf surfaces are densely covered with trichomes (Kennedy, 2003; Madadi et al., 2008) and that a plant surface with lower trichome densities was not tested in this study.

#### 1.4.1.2 *Capsicum* plant surfaces

Sweet pepper/capsicum surfaces appear to have greater suitability for predators and parasitoids that rely on locomotion to search for prey and hosts. As demonstrated by Hernández-Moreno et al. (2017) who found that *T. triozae* consumed more TPP nymphs on capsicum plants than on tomato plants, attributing this result to the effects of tomato trichomes. Furthermore, Madadi et al. (2007) found that the handling time of *Neoseiulus cucumeris* (Oudemans) (Acari: Phytoseiidae) predating on onion thrips *Thrips tabaci* (Lindeman) (Thysan: Thripidae) was lowest on capsicum than on plant surfaces with greater trichome densities. Choudhury and Copland (2003) found that when the parasitoid wasp *Anagrus atomus* Linnaeus (Hymenoptera: Mymaridae) was exposed to the glasshouse leafhopper, *Hauptidia maroccana* Melichar (Hemiptera, Cicadellidae) they moved fastest on sweet pepper surfaces in comparison to other plant surfaces that ranged in greater trichome densities. Similarly, Sütterlin and van Lenteren (1997) reported that *Encarsia formosa* Gahan (Hymenoptera: Aphelinidae) recorded faster walking speeds on capsicum in comparison to tomato leaves. These studies highlighted



the relationship between trichome density and movement (a key component of searching success).

Despite their apparent suitability for predators and parasitoids, the surfaces of capsicum/peppers can deleteriously affect their predation/parasitism rates. Abdala-Roberts et al. (2014) investigated the abundance of the predatory mite *Amblyseius swirskii* Athias-Henriot (Mesostigmata: Phytoseiidae) and their predation rates of thrips *Frankliniella cephalica* Crawford DL (Thysanoptera: Thripidae) on 17 different pepper (*Capsicum annuum* Linnaeus) varieties that varied in flower number, pollen production and leaf trichome density. Greater *A. swirskii* densities were reported on varieties with an intermediate trichome density. High trichome densities appeared to interfere with *A. swirskii* foraging and influenced the low abundance of the predator on these varieties. The authors concluded that this trait may incur an ecological cost to the host plant by reducing indirect defences and potentially benefiting pests. Leaf surface hairiness could be taken as an indicator that predators/parasitoids may struggle to effectively control a pest population, however, this may not always be the case. Kheradpir et al. (2008) found that consumption of spider mites *T. urticae* by the predacious thrips *Scolothrips longicornis* Priesner (Thysanoptera: Thripidae) was highest on the hairier tomato surface than on the hairless/smooth capsicum surface. The authors suggested that the capsicum surface was too slippery for effective traction which affected the movement of the predator.

Despite of the unsuitability of sweet pepper/capsicum plant surfaces in certain predator-prey interactions they do appear to be suitable for effective *Orius* spp. predation. As demonstrated by *O. albidipennis* (Reuter) on leaf discs (Madadi et al., 2008) and small plants (Madadi et al., 2009). Furthermore, Van de Veire and Degheele (1992) reported that *O. niger* contributed to the population decline of Western flower thrip in Belgian sweet pepper glasshouse crops.

## **1.5 Aims and objectives**

The aim of this thesis was to investigate how the morphological structures of plant surfaces (hairy tomato vs. non-hairy capsicum) can influence the predatory behaviour and efficiency of a potential biological control agent (*O. vicinus*) on an economically

important pest (TPP) that affects a variety of host plants. The objectives of this thesis were to:

1. Determine the effects of plant surface morphology on the TPP nymph consumption capacity of *O. vicinus* (Chapter 2).
2. Assess how the surface structure influences the dispersal of TPP nymphs in the presence and absence of *O. vicinus* (Chapter 2).
3. Determine the TPP nymph size preference of *O. vicinus* (Chapter 2 and Chapter 3).
4. Investigate the behaviour of *O. vicinus* and the defensive behaviours (fight or flight) of TPP nymphs during predator-prey encounters on morphologically dissimilar surfaces (Chapter 3).



## **Chapter 2: The effect of host plant substrate on the biological control potential of *Orius vicinus* (Ribaut) on *Bactericera cockerelli* (Sulc) nymphs.**

### **2.1 Abstract**

Broad-spectrum insecticides are the preferred option for managing invasions to solanaceous crops by the tomato-potato psyllid (TPP) *Bactericera cockerelli* (Sulc). However, chemical reliance is associated with a host of issues. Therefore, the development of alternative management options such as biological control is vital for implementing future Integrated Pest Management (IPM) programs. This chapter investigates the biological control potential of *Orius vicinus* (Ribaut) adults acting on TPP nymphs on morphologically distinct plant surfaces (tomato versus capsicum). The functional response of adult *O. vicinus* simultaneously exposed to all TPP nymphal stages was determined to be Type II on both plant surfaces. The handling time ( $T_h$ ) was significantly longer and the searching efficiency ( $a$ ) was slightly greater on tomato in comparison to capsicum. Nymph consumption at higher prey densities (30 and 40 nymphs) was significantly greater on capsicum than on tomato. Nymph consumption at lower prey densities (10 and 20 nymphs) was only significantly greater on capsicum when the complexity of the experimental arena was increased from leaflet to small plant. The presence of *O. vicinus* increased the dispersal of nymphs to lower leaf surfaces. Nymph dispersal was significantly greater on capsicum than on tomato. *O. vicinus* was capable of attacking and killing all nymphal stages. The predatory bug significantly preferred medium sized nymphs on both surfaces.

### **2.2 Introduction**

The economic impact of tomato-potato psyllid (TPP) *Bactericera cockerelli* (Sulc) invasions to solanaceous crops has led to chemical control being the preferred management option (Liu & Trumble, 2004; Goolsby et al., 2007; Berry et al., 2009; Yang et al., 2010a; Ail-Catzim., et al 2012; Butler & Trumble, 2012a). However, broad-spectrum insecticide usage can be expensive, can cause environmental contamination, and can lead to secondary pest outbreaks due to natural enemies being removed (Van Lenteren & Woets, 1988; Butler et al., 2011). Furthermore, dependency on chemical

control may lead to chemical resistance (Goolsby et al., 2007; Gharalari et al., 2009; Butler et al., 2011; Cerna et al., 2012; Liu et al., 2012; Martinez et al., 2015; Munyaneza, 2015; Barrios-Diaz et al., 2016; Calvo et al., 2016; Prager et al., 2016). Therefore, integrated pest management (IPM) that incorporates biological control methods along with target-specific pesticides and cultural control methods is a prospective long term alternative to broad-spectrum insecticide usage (Liu et al., 2006b; Liu et al., 2012; Martinez et al., 2015; Calvo et al., 2016; Prager et al., 2016).

Butler and Trumble (2012b) identified *Orius tristicolor* (White) (Hemiptera: Anthocoridae) as a potential TPP biological control agent in Southern California solanaceous crops. The predatory bug has also been found on bittersweet nightshade (*Solanum dulcamara* L), a key non-crop host of TPP (Castillo Carrillo et al., 2016). Certain species from the *Orius* genus (Hemiptera: Heteroptera: Anthocoridae) are mass-produced by commercial insectaries for use in augmentative biological control programs that target economically important pests (Horton, 2008; Colomer et al., 2011; Veres et al., 2012; van Lenteren, 2012b; van Lenteren et al., 2017). Commercial insectaries in New Zealand are now mass-producing *Orius vicinus* (Ribaut) (Heteroptera: Anthocoridae) as a biological control agent of various insect pests (e.g. thrips, aphids and spider mites) (Bioforce Limited, 2014). The predatory bug has been observed preying on mites, aphids, thrips, psyllids, leafhoppers and scale insects (Lariviere & Wearing, 1994; Wearing & Colhoun, 1999, Wearing & Attfield, 2002; Lewis & Lattin, 2010; Wearing et al., 2010). Tran's (2012) functional response study found that *O. vicinus* was capable of consuming TPP nymphs (particularly smaller nymphs), suggesting that the predator may have potential for augmentative release programs for TPP management.

The failure of arthropod predators to manage pest densities below economic thresholds has been linked to prey densities rapidly increasing and overwhelming the functional response of the predator (O'Neil, 1997). The functional response describes the relationship between prey density and the number of prey consumed by a predator. The functional response of a predator will generally fit one of the following three types of mathematical models: Type I (linear), Type II (convex) or Type III (sigmoid) (Holling, 1959; Hassell et al., 1977; Colton, 1987; O'Neil, 1997; Gitonga et al., 2002; Lester & Harmsen, 2002; Stewart et al., 2002; Xiao & Fadamiro, 2010). Type II responses are

most commonly observed among arthropod predators and are characterized by the proportion of prey consumed monotonically declining with increasing prey density (Holling, 1959; Beddington 1975; Hassell et al., 1977; O'Neil, 1989; Gitonga et al., 2002; Stewart et al., 2002; Pervez, 2005; Timms et al., 2008; Xiao & Fadamiro, 2010). Type III responses are typically associated with efficient biological control agents (Fernández-arhex & Corley, 2003; Xiao & Fadamiro, 2010). However, potential biological control agents that exhibit Type II responses on targeted pests have been identified (De Clercq et al., 2000; Badii et al., 2004; Timms et al., 2008). The functional response can be broken down into two components: (1) the searching efficiency, which includes aspects of the encounter rate, strike rate and capture efficiency, and (2) the handling time, which includes the effects of recognition, pursuit, capture, ingestion and digestion of prey (Holling, 1959; Thompson, 1975; Spitze, 1985; El Basha et al., 2012).

Functional response and other predatory assessment studies are generally performed in laboratory settings in order to control the experimental arena (Symondson et al., 2002; Timms et al., 2008). Laboratory studies tend to test predators on homogeneous prey populations (Schenk & Bacher, 2002). Subsequently, predation on different instars is investigated separately and the results are generally characterized with different output values (e.g. attack rate and handling time). However, arthropod species undergo considerable changes in size during their lifecycle, which inevitably results in the coexistence of multiple size classes of targeted prey and biological control agents (McArdle & Lawton, 1979; Colton, 1987; Lester & Harmsen, 2002; Rudolf, 2008). Furthermore, predators are typically exposed to artificial environments (i.e. high prey density on a Petri dish with limited or no plant component presence) that generally fail to emulate host plant environments where prey can be harder to access/capture (e.g. leaf/stem texture can influence the searching behaviour of predators and the distribution/dispersal of prey) (Hassell et al., 1977; Everson, 1980; Carter et al., 1984; O'Neil, 1989; Coll et al., 1997; O'Neil, 1997; Messina & Hanks, 1998; Stewart et al., 2002; Mahdian et al., 2007; Davidson et al., 2016).

The host plant plays a pivotal role in predator/prey interactions and thus the morphological characteristics of host plants (e.g. substrate) could influence the predatory performance of a biological control agent in the field (Hassell et al., 1977; Everson, 1980; Cortesero et al., 2000; De Clercq et al., 2000; Mahdian et al., 2007;

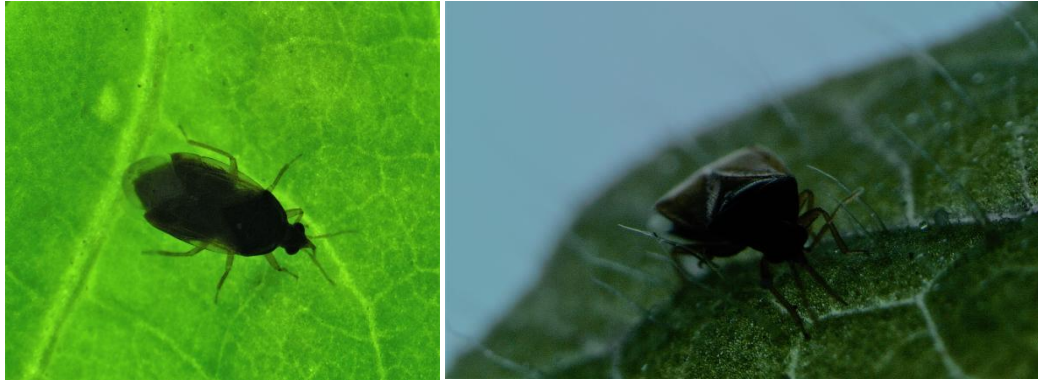
Timms et al., 2008). The interactions between plant, pest, potential biological agent and environment need to be understood in order to formulate and establish an effective biological control program that fits within the IPM paradigm (De Clerq et al., 2000). Furthermore, biological control agents may have to cope with different morphological plant features in order to be a commercially viable management option against pest species that infest a wide range of host plants (Skirvin & Williams, 1999). Therefore, results gained in laboratory environments should be assessed with caution and experimental environments should incorporate as much naturalistic attributes as possible if these are to be used in assessing the true potential of a biological control agent (Everson, 1980; Messina & Hanks, 1998; Stewart et al., 2002; Kumar & Mishra, 2014).

The aim of this study was to investigate the biological control potential of *O. vicinus* on TPP nymphs, with four objectives: (1) to investigate the effect of the morphological structures of the host plant (smooth surfaced capsicum vs. hairy surfaced tomato) on the predatory performance of *O. vicinus*, (2) to assess the effect of the host plant on TPP nymph movement in both the presence and absence of *O. vicinus*, (3) to test TPP nymph size preference by *O. vicinus*, and (4) to compare predatory performance of *O. vicinus* on experimental arenas varying in complexity.

## **2.3 Material and Methods**

### *2.3.1 Experimental plants*

Tomato (*Solanum lycopersicum* cv. Moneymaker) and capsicum (*Capsicum annuum* cv. California Wonder) plants (Figure 2.1) were grown at the Plant Growth Unit (PGU), Massey University, Palmerston North. Seeds were obtained from Egmont Seed Company Ltd, New Plymouth. The experimental plants were chosen due to the impact TPP has on their respective industries and their known differences in leaf surface trichome density (Sutterlin & van Lenteren, 1997; Madadi et al., 2007). When plants were five weeks old, they were transferred to a 25°C controlled temperature room with a photoperiod of 16:8 h (L:D).



**Figure 2.1:** Adult *O. vicinus* on smooth surfaced capsicum (left) and hairy surfaced tomato (right) leaves.

### 2.3.2 *Insect colonies*

TPP nymphs were obtained from a Plant and Food Research, colony and reared on tomato (*S. lycopersicum* cv. Moneymaker) and capsicum (*C. annuum* cv. California Wonder) plants in Massey University, Palmerston North. *O. vicinus* were obtained as 4<sup>th</sup> or 5<sup>th</sup> stage nymphs from Bioforce Ltd, Auckland. The predators were reared in plastic containers (length: 15 cm, height: 9 cm, width: 7 cm) with mesh-covered holes. TPP nymphs were provided as prey on capsicum or tomato leaflets attached to a tube filled with water. Leaflets were replaced daily to ensure constant supply of nymphs to the predators. The leaflets with *O. vicinus* eggs were placed in separate containers in order to ensure the completion of the predatory bug lifecycle. Due to time constraints, adults were not assessed separately by sex in this study. TPP and *O. vicinus* colonies were maintained in a 25C° controlled temperature room with a photoperiod of 16:8 h (L:D). All experiments were carried out under this environmental condition. All insects used in the experiments completed their lifecycle in the experimental environment.

### 2.3.3 *Experimental design*

#### 2.3.3.1 *Leaflet experimental arena: O. vicinus TPP consumption, functional response, prey size preference and TPP movement in absence or presence of a predator*

The leaflet experimental arena consisted of a Petri dish (diameter: 85 mm, depth: 12 mm) covered by a plastic jar (diameter: 85 mm, height: 100 mm) containing ventilation holes on its sides covered with mesh. A capsicum or tomato leaflet was raised off the



base of the Petri dish by an entomological pin (height: 38 mm) and a plastic vial (height: 40 mm) filled with water. The pin and vial were held in place by small balls of blutack<sup>®</sup> (Figure 2.2). The purpose of raising the leaflet from the surface of the Petri dish was to isolate the predator and prey on the leaflet surfaces and to allow predator-prey interactions to take place on upper and lower leaflet surfaces as they would in a natural setting.



**Figure 2.2:** Petri dish containing the raised tomato leaflet uncovered (left) and covered with jar with ventilation holes (right).

Prey densities used in this experiment comprised of nymphs at different developmental stages: 20% small sized (1<sup>st</sup> and 2<sup>nd</sup> instars), 40% medium sized (3<sup>rd</sup> instar), and 40% large sized (4<sup>th</sup> and 5<sup>th</sup> instars). The grouping of nymph sizes and subsequent proportion allocation for densities were incorporated from O'Connell et al. (2012). Nymph stage determination was based on the maximum body width (0.2, 0.3, 0.5, 0.7, and 1.1 mm for 1<sup>st</sup>, 2<sup>nd</sup>, 3<sup>rd</sup>, 4<sup>th</sup>, and 5<sup>th</sup> instars, respectively) (Liu & Trumble, 2007). The average experimental leaf surface area (combining top and bottom surfaces) was measured using Digimizer software to be 27.48 and 25.89 cm, respectively, for capsicum and tomato leaflets.

To assess TPP consumption by *O. vicinus*, TPP nymph size preference by *O. vicinus*, TPP movement in the presence of *O. vicinus*, and the formulation of the functional response, I introduced four densities (10, 20, 30, and 40 individuals) of TPP nymphs onto the upper surface of capsicum and tomato leaflets. A predator adult (3 to 7 days

old) that had been starved for 24 h was then released onto the upper leaflet surface and subsequently removed from the experimental arena after 24 h. A predator was used only once and then discarded. The location (upper surface, lower surface and off leaf) and size (small, medium, and large) of consumed and unconsumed TPP nymphs were recorded. Each treatment had 20 replicates (20 bug adults  $\times$  4 TPP densities  $\times$  2 species of plants = 160 adults).

To determine TPP movement in the absence of *O. vicinus*, I introduced three densities (10, 20, and 30 individuals) of TPP nymphs onto the upper surface of capsicum and tomato leaflets. The numbers of TPP nymphs located on the upper and lower leaflet surfaces were recorded at the following time intervals: 2, 4, 6, 8, 10, 12, and 24 h after introduction. Each treatment had 10 replicates (3 TPP densities  $\times$  2 species of plants  $\times$  10 replicates = 60 trials).

#### *2.3.3.2 Plant experimental arena: O. vicinus TPP consumption and TPP movement in presence of a predator*

The plant experimental arena consisted of a potted plant fitted with a plastic base that separated the plant from the soil in the pot. A plastic cylinder (diameter: 85 mm, height: 200 mm) with mesh-covered holes on its sides covered the plant (Figure 2.3). The plant had all but one of its top leafs removed to ease the recovery of TPP nymphs at the conclusion of the experimental period and to recreate the experimental design of the leaflet experimental arena with augmented naturalistic effect (i.e. leaflet is connected to a stem rather than a plastic vial). Due to the different growth rates between the selected plants, 8-week-old tomato plants and 12-week-old capsicum plants were used. The average stem lengths were measured to be 9.98 and 10.75 cm, respectively, for capsicum and tomato plants.

Ten TPP nymphs (two small sized (1<sup>st</sup> and 2<sup>nd</sup> instars), four medium sized (3<sup>rd</sup> instar) and four large sized (4<sup>th</sup> and 5<sup>th</sup> instars)) were arranged on the upper surface of the leaflet. A predator adult (3 to 7 days old) that had been starved for 24 h was then released at the base of the stem and subsequently removed from the experimental arena after 24 h. A predator was used only once and then discarded. The location (upper leaf surface, lower leaf surface, stem and off plant) of consumed and unconsumed TPP

nymphs was recorded. Each treatment had 30 replicates (30 bug adults  $\times$  2 species of plants = 60 adults).



**Figure 2.3:** Uncovered (left) and covered (right) small capsicum plant with all but one leaflet removed.

#### 2.3.4 Data analysis

All analyses were done using SAS 9.13. Rejection level was set at  $\alpha < 0.05$ .

##### 2.3.4.1 Leaflet experimental arena

###### 2.3.4.1.1 TPP nymph movement in the presence/absence of *O. vicinus* on different leaf surfaces

The effects of *O. vicinus*, plant species and prey densities on TPP nymph movement from the upper to the lower leaf surface were analysed using a mixed linear model (GLM procedure) including the three factors (predator presence, plant species and prey density) and their interactions (Figure 2.4). However, only significant parameters were kept in the final model.

###### 2.3.4.1.2 TPP nymph consumption by *O. vicinus* on different leaf surfaces

A goodness-of-fit test (Shapiro-Wilk test) was used to test for normality. Data on overall TPP nymph consumption by *O. vicinus* was normally distributed after arsine-

square root transformation. Thus an analysis of variance (ANOVA, GLM procedure) was applied to compare the overall percentage of TPP nymphs consumed by predators on the two host plants (Figure 2.6). Data on TPP nymph consumption by *O. vicinus* on upper leaflet surfaces was not normally distributed even after transformation. Therefore, a Kruskal-Wallis Test (NPAR1WAY procedure) was applied to compare the percentages of TPP nymphs consumed by predators on the upper leaflet surfaces on the two host plants (Figure 2.5).

#### 2.3.4.1.3 Functional response of *O. vicinus* to TPP nymphs

##### 2.3.4.1.3.1 Functional response determination

A cubic logistic regression model (Julious, 2001) was initially used to determine the functional response of *O. vicinus* by taking the proportion of consumed TPP nymphs ( $N_a/N_o$ ) as a function of the initial density of hosts ( $N_o$ ):

$$N_a/N_o = \exp(P_0 + P_1N_o + P_2N_o^2 + P_3N_o^3) / [1 + \exp(P_0 + P_1N_o + P_2N_o^2 + P_3N_o^3)] \quad (\text{eq. 1})$$

Where  $N_a$  in this study is the number of TPP nymphs consumed,  $N_o$  is the number of TPP nymphs available,  $P_0$  is the intercept, and  $P_1$ ,  $P_2$ , and  $P_3$  are linear, quadratic and cubic coefficients, respectively, related to the slope of the curve. The slope of the proportion of consumed TPP nymphs near the lowest prey density is characteristic of the functional response. A linear coefficient of  $P_1 = 0$  indicates a Type I functional response; a significant negative linear coefficient of  $P_1 < 0$  shows a Type II functional response, and a significant positive linear coefficient of  $P_1 > 0$  with a significant negative quadratic coefficient of  $P_2 < 0$  demonstrates a Type III functional response (Julious, 2001). However, inclusion of a cubic parameter in the logistic regression model generated non-significant linear and quadratic parameters (results not shown) which were inconsistent with those estimated by the linear and quadratic models (Table 2.1) and could lead to misleading conclusions (Julious, 2001). As a result, only linear and quadratic models were used.

#### 2.3.4.1.3.2 Type II Functional response

Three models have been developed to predict the Type II functional response of predators/parasitoids to prey/host density. The disc model (1) developed by Holling (1959) predicts that predators/parasitoids search systematically for their prey and do not waste any effort in re-searching part of the area:

$$N_a = (aTN_oP_t)/(1+aT_hN_o), (1)$$

Where  $N_a$  is the number of prey consumed/killed or hosts parasitized,  $N_o$  the number of prey or hosts,  $P_t$  is the number of predators/parasitoids (1 in this study),  $T$  is the total time (24 h in this study) available for the predator/parasitoid,  $a$  is the searching efficiency (the rate of prey encounter per unit of prey density by the predator) and  $T_h$  is the handling time (the time spent pursuing, attacking, killing and consuming each prey target).

The general random model (2) (Rogers, 1972) assumes that predators/parasitoids search at random:

$$N_a = N_o[1-\exp(-aTP_t/(1+aT_hN_o))], (2)$$

The general random model is not suitable for most predators because unlike parasitized hosts which can be re-encountered by parasitoids, consumed kills will not remain exposed to further encounters (Rogers, 1972; Kidd and Jervis, 2005). The general random model of predator version is developed by Royama (1971) and Rogers (1972) to take account of gradual prey depletion during the searching period, producing the modified random predator model (3) (Royama, 1971):

$$N_a = N_o[1-\exp(-aP_t(T-T_h(N_o/P_t)))], (3)$$

However, because *O. vicinus* kill their prey by sucking their body fluid, they do not completely consume or remove their prey from the search area. Therefore, the general random model (Rogers, 1972), referred to as the random predator model in this study, is appropriate to determine the Type II functional response of *O. vicinus*. The

performances of the Type II functional response of *O. vicinus* by the disc model (Holling, 1959) and random predator model (Rogers, 1972) were compared (Figure 2.7 and Table 2.2).

Nonlinear least square regression (NLIN procedure) was used to estimate the searching efficiency ( $a$ ) and handling time ( $T_h$ ) in the random predator and disc models of functional response (Table 2.2). The estimated parameters in the nonlinear least square regressions were significantly different from 0 if the 95% confidence interval (CI) did not include 0 (Juliano, 2001). The difference in the searching efficiency ( $a$ ) and handling time ( $T_h$ ) between the two models or between two plant species was compared according to Julious (2004). If the 83.4% CIs overlap, then there is no significant difference in these parameters (Table 2.2).

#### *2.3.4.1.4 TPP nymph size preference by O. vicinus*

TPP nymph size preference by *O. vicinus* at different prey densities was determined using a general linear model (GLM Procedure) with prey size and density as the fixed variables and plant species as the co-variable (Figure 2.8). Analysis of co-variance (ANCOVA) was applied to compare the effect of prey size or density between the two host plants. To enable the performance of linear regression and ANCOVA, 1, 2 and 3 were referred to as the index of prey sizes of small, medium and large nymphs, respectively.

#### *2.3.4.2 Plant experimental arena*

##### *2.3.4.2.1 TPP nymph movement in the presence of O.vicinus*

A goodness-of-fit test (Shapiro-Wilk test) was used to test for normality. Data on TPP nymph movement were not normally distributed even after transformation. Therefore, a Kruskal-Wallis Test (NPAR1WAY procedure) was applied to compare the distribution of TPP nymphs located on upper leaflet surfaces between the two host plants (Figure 2.9).

#### 2.3.4.2.2 TPP nymph consumption by *O. vicinus*

A goodness-of-fit test (Shapiro-Wilk test) was used to test the distribution of data. Data on TPP nymph consumption by *O. vicinus* on upper leaf surfaces were not normally distributed even after transformation. Therefore, a Kruskal-Wallis Test (NPAR1WAY procedure) was applied to compare the percentage of TPP nymphs consumed by predators on the upper leaflet surfaces between the two host plants (Figure 2.10). Data on overall TPP nymph consumption by *O. vicinus* on tomato and capsicum plant and leaflet experimental arenas (density of 10 TPP nymphs) were normally distributed after arsine-square root transformation. Thus analysis of variance (ANOVA, GLM procedure) were applied to compare the percentage of TPP nymphs consumed in the plant arena by *O. vicinus* (capsicum plant results vs. tomato plant results) and to compare the percentage of TPP nymphs consumed by *O. vicinus* between the leaflet and plant arenas on both host plants (capsicum leaflet arena results vs. capsicum plant arena results) (Figure 2.11).

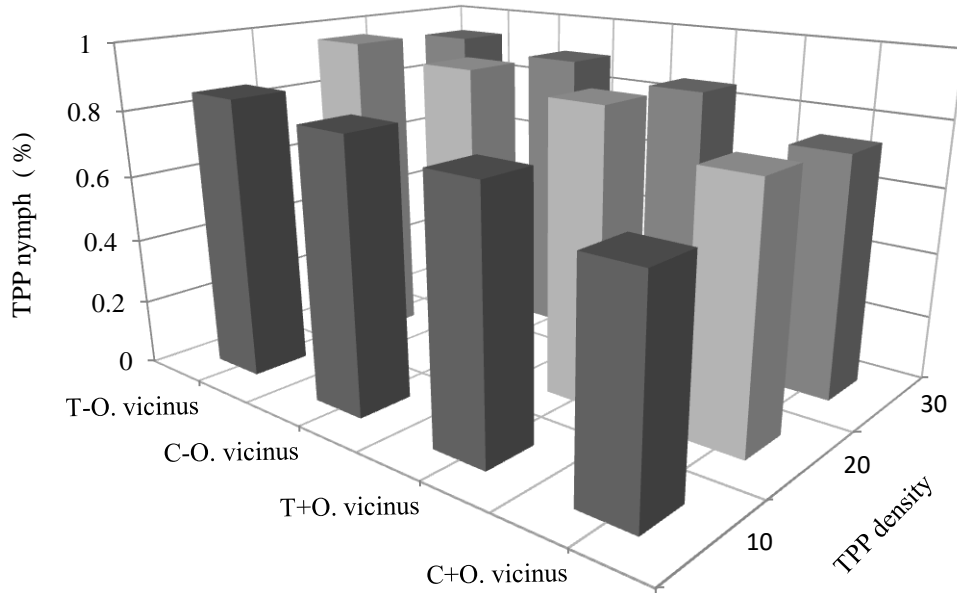
## 2.4 Results

### 2.4.1 Leaflet experimental arena

#### 2.4.1.1 TPP nymph movement in the presence/absence of *O. vicinus* on different leaflet surfaces

The mixed linear model (Figure 2.4) shows that predator presence, plant species and prey density all significantly affected the movement of TPP nymphs. Significantly more TPP nymphs moved from the upper to the lower leaflet surface in the presence of *O. vicinus* regardless of plant species and prey density ( $F_{1,175} = 34.14$ ,  $P < 0.0001$ ). Significantly more TPP nymphs remained on the upper surface of tomato than of capsicum regardless of predator presence or prey density ( $F_{1,175} = 13.28$ ,  $P < 0.0001$ ). Significantly more TPP nymphs occurred on the upper surface of plants when TPP nymph density was higher ( $F_{2,175} = 11.32$ ,  $P < 0.0001$ ). Analysis of the interaction between plant species and predator presence showed no significant difference in the movement of nymphs on the surface of tomato in the presence of the predator. However, there was marginally significantly greater movement of TPP nymphs from

the upper surface of capsicum to the lower surface in the presence of the predator ( $F_{1,174} = 3.89$ ,  $P = 0.0502$ ) (Figure 2.4).

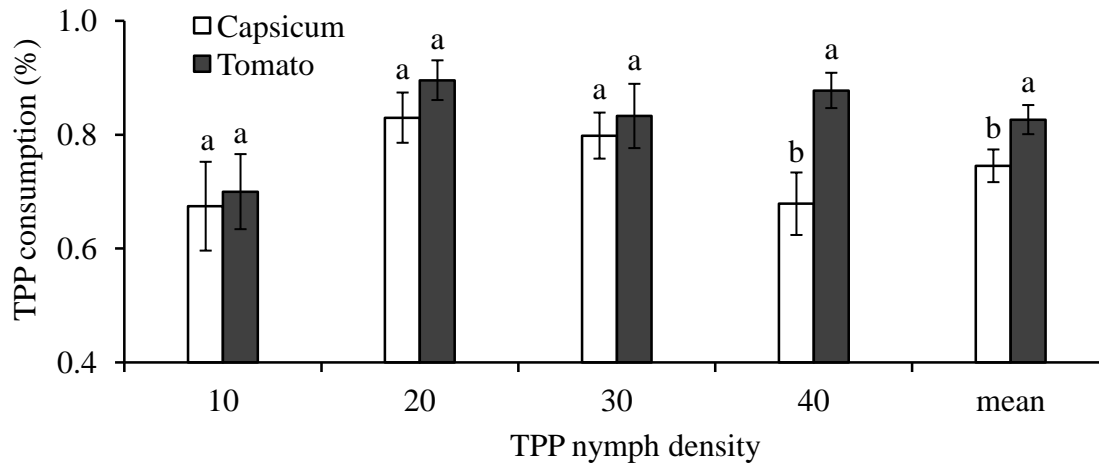


**Figure 2.4:** Estimated percentage of TPP nymphs located on the upper surface of capsicum (C) and tomato (T) leaflets after 24 h in the presence (+) and absence (-) of *O. vicinus* at different prey densities.

#### 2.4.1.2 TPP nymph consumption by *O. vicinus* on leaflet surfaces

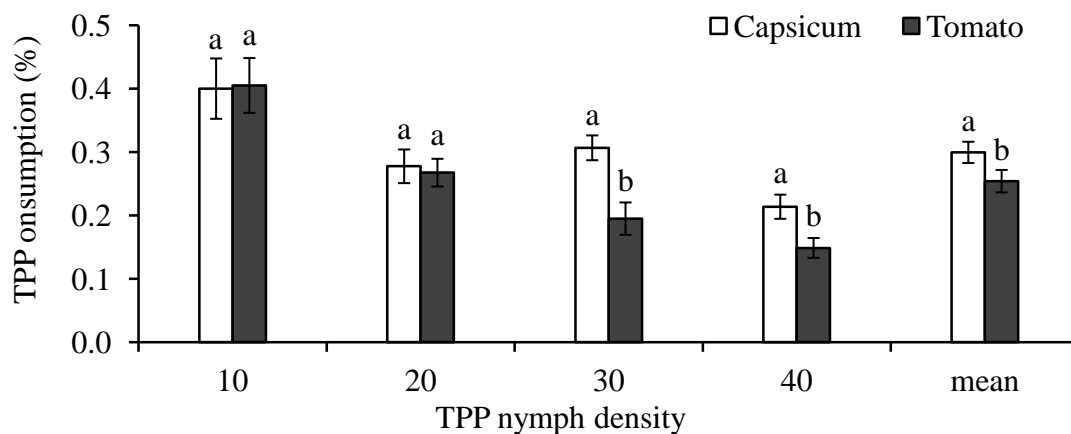
Our results show that after the 24 h experimental time period the percentage of TPP nymphs consumed by *O. vicinus* on the upper leaflet surface was greater, but not significantly so, on tomato leaflets than on capsicum leaflets at the prey densities of 10, 20 and 30 nymphs (Kruskal-Wallis Test:  $\chi^2 = 0.01$ , 1.17 and 1.07, respectively,  $P > 0.05$ ). However, TPP consumption was significantly greater on the upper surface of tomato leaflets than on the upper surface of capsicum leaflets at the prey density of 40 nymphs (ANOVA: Kruskal-Wallis Test:  $\chi^2 = 7.12$ ,  $P < 0.01$ ) and overall mean density (ANOVA: Kruskal-Wallis Test:  $\chi^2 = 5.06$ ,  $P < 0.05$ ) (Figure 2.5).





**Figure 2.5:** Percentage of TPP nymphs consumed by *O. vicinus* on the upper surface of capsicum and tomato leaflets after 24 h. For each density or mean, columns with different letters are significantly different (Kruskal-Wallis Test:  $P < 0.05$ ).

There was no significant difference in the overall consumption percentage of TPP nymphs by *O. vicinus* on capsicum and tomato leaflets at the prey densities of 10 and 20 nymphs (ANOVA:  $F_{1,38} = 0.01$  and  $0.10$ , respectively;  $P > 0.05$ ). However, the consumption percentage was significantly greater on capsicum leaflets than on tomato leaflets at the prey densities of 30 and 40 nymphs (ANOVA:  $F_{1,38} = 11.89$  and  $6.98$ , respectively;  $P < 0.05$ ) and overall mean density (ANOVA:  $F_{1,158} = 4.58$ ,  $P < 0.05$ ) (Figure 2.6).



**Figure 2.6:** Percentage of TPP nymphs consumed by *O. vicinus* on capsicum and tomato leaflets after 24 h. For each density or mean, columns with different letters are significantly different (ANOVA:  $P < 0.05$ ).

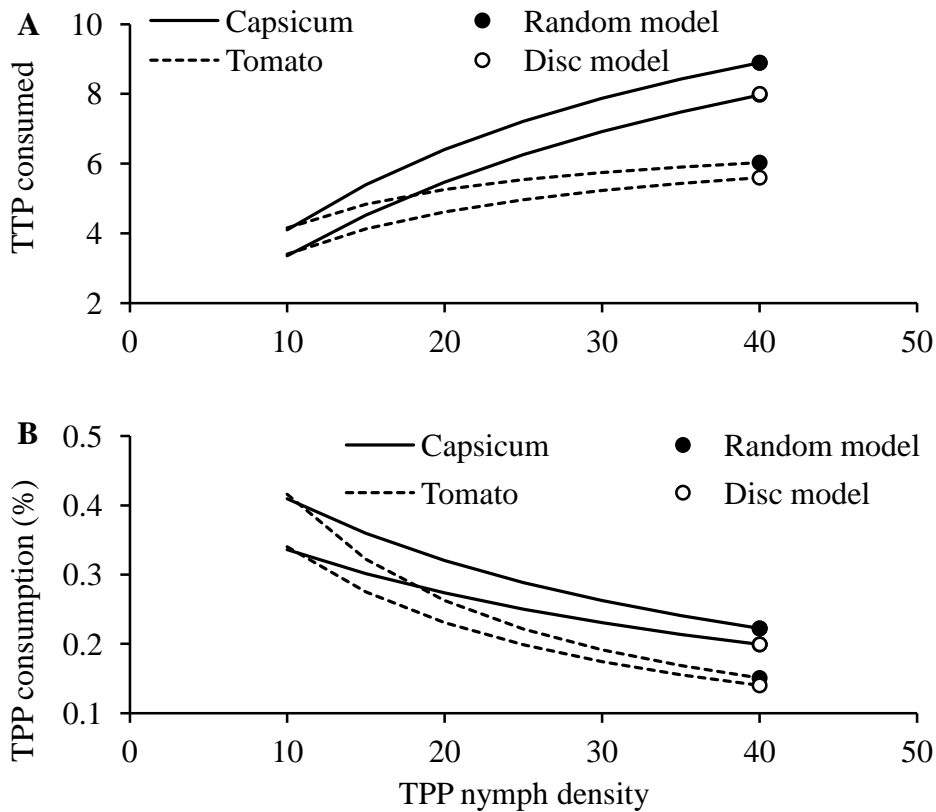
#### 2.4.1.3 Functional response of *O. vicinus* to TPP nymphs

Logistic regression analyses show that the negative linear coefficients for capsicum and tomato were significant (Table 2.1), indicating a Type II functional response on both host plant surfaces.

**Table 2.1:** Logistic regression analysis of functional response of *O. vicinus* to TPP densities.

	Parameters	Estimate	SE	P
Capsicum	Intercept	1.809	0.9543	0.0579
	Linear	-0.3559	0.1405	0.0113
	Quadratic	0.0153	0.0061	0.0121
Tomato	Intercept	0.2933	0.3624	0.4182
	Linear	-0.0749	0.0307	0.0146
	Quadratic	0.0000587	0.0000587	0.3178

Figure 2.7 shows a typical Type II functional response of *O. vicinus* in response to TPP nymph densities. The number of TPP nymphs attacked increased significantly as TPP nymph density increased (capsicum,  $F_{2,78} = 264.02$  and  $263.92$  for random and disc model, respectively,  $P < 0.0001$ ; tomato,  $F_{2,78} = 171.31$  and  $171.28$  for random and disc model, respectively,  $P < 0.0001$ ). As predicted by the functional response models (Figure 2.7), the percentage of TPP nymphs consumed decreased significantly with increasing TPP density ( $F_{1,236} = 3.97$ ,  $P = 0.0475$  for capsicum;  $F_{1,236} = 23.03$ ,  $P < 0.0001$  for tomato). The consumption percentage decreased significantly faster on tomato than on capsicum (Figure 2.8).



**Figure 2.7:** Type II functional response of *O. vicinus* on capsicum and tomato leaflet surfaces: (A) number of TPP nymphs consumed, and (B) percentage of TPP nymphs consumed. The estimated searching efficiency ( $a$ ) and handling time ( $T_h$ ) are listed in Table 2.2.

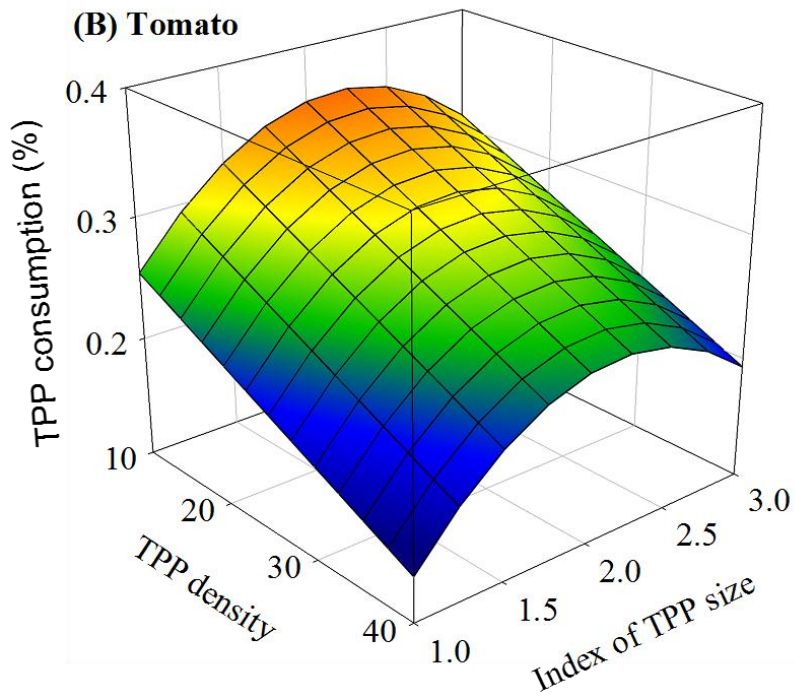
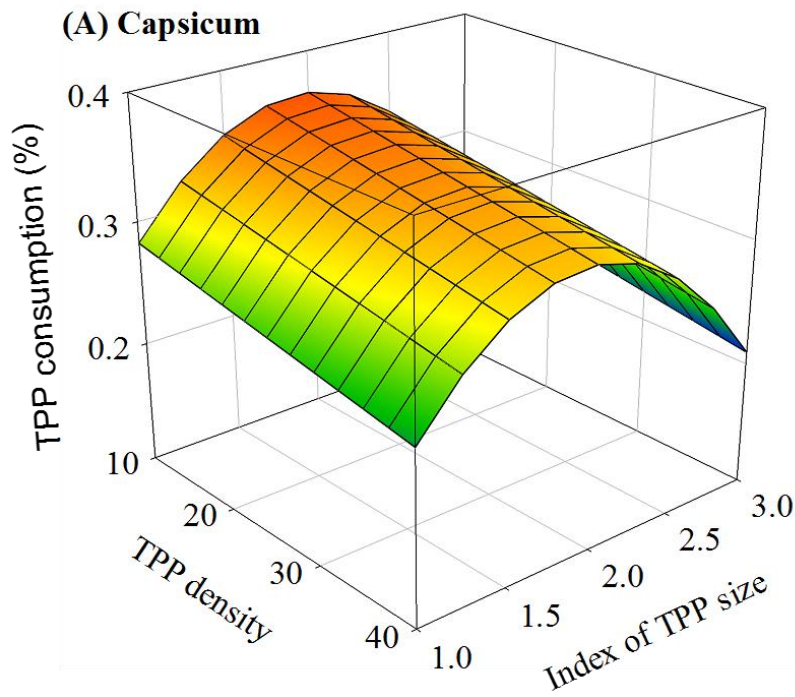
The handling time ( $T_h$ ) of *O. vicinus* was significantly longer on tomato leaflets than on capsicum leaflets with both the random predator and disc models (83.4% CL did not overlap; Table 2.2). However, there was no significant difference in handling time ( $T_h$ ) between the models on each plant species (83.4% CL overlapped; Table 2.2). The searching efficiency ( $a$ ) of *O. vicinus* was higher but not significantly on tomato leaflets than on capsicum leaflets with both the random predator and disc models (83.4% CL did not overlap; Table 2.2). However, there was no significant difference in the searching efficiency ( $a$ ) between the models on each plant species (83.4% CL overlapped; Table 2.2).

**Table 2.2:** Searching efficiency ( $a$ ,  $h^{-1}$ ) and handling time ( $T_h$ ,  $h$ ) parameters (P) for Type II functional response of *O. vicinus* to TPP nymph density on Capsicum (C) and Tomato (T) plants.

Model	Plant	P	Estimated	SE	95% CL		83.4% CL	
Random Model	C	$a$	0.0346	0.0120	0.0106	0.0586	0.0178	0.0514
		$T_h$	1.6638	0.3623	0.9425	2.3851	1.1572	2.1704
	T	$a$	0.0948	0.1037	-0.1117	0.3012	-0.0503	0.2398
		$T_h$	3.4099	0.5195	2.3757	4.4440	2.6835	4.1362
Disc model	C	$a$	0.0237	0.0056	0.0127	0.0348	0.0160	0.0315
		$T_h$	1.6448	0.3572	0.9336	2.3560	1.1453	2.1443
	T	$a$	0.0419	0.0199	0.0023	0.0815	0.0141	0.0697
		$T_h$	3.3813	0.5130	2.3600	4.4025	2.6640	4.0985

#### 2.4.1.4 TPP nymph size preference by *O. vicinus*

My results indicate that *O. vicinus* significantly preferred to consume medium sized TPP nymphs over small and large TPP nymphs, i.e., the rate of TPP nymphs consumed increased significantly when the index of TPP nymph size increased from 1 to 2 ( $F_{1,236} = 24.18$ ,  $P < 0.0001$  for capsicum;  $F_{1,236} = 16.97$ ,  $P < 0.0001$  for tomato) and then decreased significantly when the index of TPP nymph size increased from 2 to 3 ( $F_{1,236} = 26.70$ ,  $P < 0.0001$  for capsicum;  $F_{1,236} = 14.46$ ,  $P = 0.0002$  for tomato) (Figure 2.8). However, there was no significant difference in size preference between plants, i.e., with increasing TPP density the increase (from size index 1 to 2) or decrease (from size index 2 to 3) of *O. vicinus* consumption rate was not significantly different between the two plant species (ANCOVA:  $F_{1,472} = 0.30$ ,  $P = 0.5825$  for increase of consumption rate;  $F_{1,472} = 0.90$ ,  $P = 0.3419$  for decrease of consumption rate).

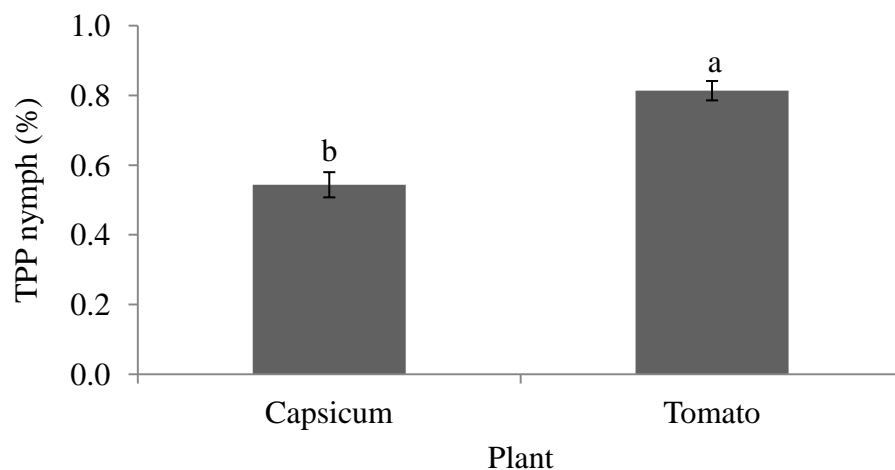


**Figure 2.8:** TPP density (TPPD: 10, 20, 30 and 40 nymphs) and size index (TPPSI: small (1), medium (2), and large (3) nymphs) affecting the rate of TPP consumed (ROTTPC) by *O. vicinus*: (A) Capsicum,  $ROTTPC = 0.0148 - 0.0014TPPD + 0.3814TPPSI - 0.0992TPPSI^2$  ( $R^2 = 0.1185$ ,  $F_{3,236} = 10.57$ ,  $P < 0.0001$ ); (B) Tomato,  $ROTTPC = 0.0459 - 0.0039TPPD + 0.3209TPPSI - 0.0733TPPSI^2$  ( $R^2 = 0.1562$ ,  $F_{3,236} = 14.57$ ,  $P < 0.0001$ ).

## 2.4.2 Plant experimental arena

### 2.4.2.1 TPP nymph movement in the presence of *O. vicinus* on different plant surfaces

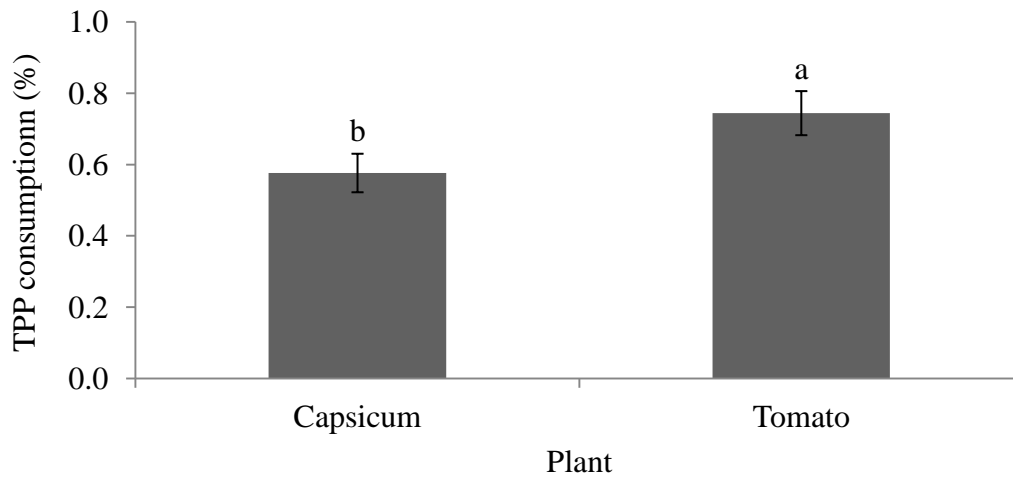
My results show that after 24 h, significantly more TPP nymphs occurred on the upper surface of tomato leaflets than on the upper surface of capsicum leaflets (ANOVA: Kruskal-Wallis Test:  $\chi^2 = 22.20$ ,  $P < 0.05$ ) (Figure 2.9).



**Figure 2.9:** Percentage of TPP nymphs located on the upper leaf surface of capsicum and tomato plants after 24 h. Columns with different letters are significantly different (Kruskal-Wallis Test:  $P < 0.05$ ).

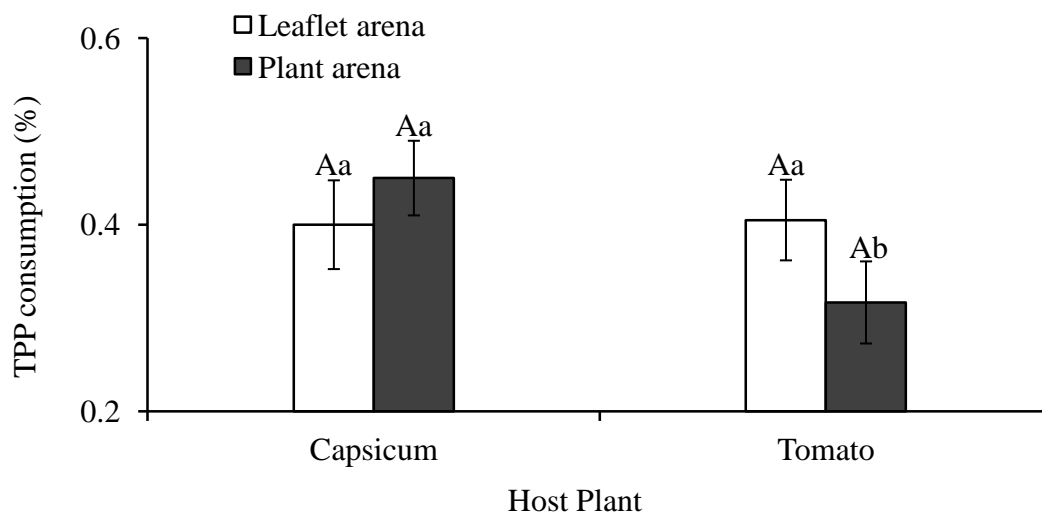
### 2.4.2.2 TPP nymph consumption by *O. vicinus* on different plant surfaces

A significantly higher percentage of TPP nymphs was consumed by *O. vicinus* within 24 h on the upper leaflet surface of tomato than on the upper surface of capsicum (ANOVA: Kruskal-Wallis Test:  $\chi^2 = 5.3$ ,  $P < 0.05$ ) (Figure 2.10).



**Figure 2.10:** Percentage of TPP nymphs consumed by *O. vicinus* on the upper leaflet surface of capsicum and tomato plants after 24 h. Columns with different letters are significantly different (Kruskal-Wallis Test:  $P < 0.05$ ).

I did not find a significant difference in the consumption percentage of TPP nymphs by *O. vicinus* between the leaflet and plant experimental arenas (ANOVA: for capsicum arenas, ANOVA:  $F_{1,48} = 0.64$ ;  $P > 0.05$ ; for tomato arenas,  $F_{1,48} = 2.36$ ;  $P > 0.05$ ) (Figure 2.11). However, the overall percentage of TPP nymphs consumed by *O. vicinus* was significantly greater on capsicum plants than on tomato plants (ANOVA:  $F_{1,58} = 4.99$ ;  $P < 0.05$ ) (Figure 2.11).



**Figure 2.11:** Percentage of TPP nymphs consumed by *O. vicinus* on capsicum and tomato experimental arenas after 24 h at the prey density of 10 individuals. Columns with different upper case letters indicate significant differences between experimental arenas within host plants and columns with different lower case letters indicate significant differences between host plants (ANOVA:  $P < 0.05$ ).

## 2.5 Discussion

The morphological characteristics of plants have the potential to alter the functional response of predators on targeted prey (e.g. from Type II to Type III) (Messina & Hanks, 1998; De Clercq et al., 2000). However, my present study shows that *O. vicinus* exhibited a Type II response on both host plant surfaces (Table 2.1), consistent with findings by Tran (2012). Furthermore, Type II functional responses are a common occurrence among *Orius* spp. and have been found against a variety of prey (Montserrat et al., 2000; Gitonga et al., 2002; Jalalizand et al., 2011). Nonetheless, there have been instances where *Orius* spp have exhibited Type I and Type III responses, but these have tended to be against the egg and early instars stages of the prey (Parajulee et al., 2006; Jalalizand et al., 2011; Tran, 2012).

Hairy plant surfaces in comparison to smoother plant surfaces can mechanically impede the mobility (which can affect prey pursuit and encounter rates) and reactive distance of predators, lowering the searching efficiency, increasing the handling time and subsequently resulting in lower consumption rates (Coll & Ridgway, 1995; Coll et al., 1997; Sutterlin & van Lenteren, 1997; De Clercq et al., 2000; Kennedy, 2003; Madadi et al., 2007; Mahdian, 2007; Jalalizand et al., 2011; Davidson et al., 2016). Alternatively, the searching efficiency may be negatively affected by smoother surfaces due to the predator's inefficiency at effectively attaching themselves to the surface and frequently falling off (Carter et al., 1984). My current study indicates that the handling time was significantly longer on tomato than on capsicum (Table 2.2), supporting previous findings (De Clercq et al., 2007; Mahdian et al., 2007). Contrary to previous reports (Coll & Ridgway, 1995; Mahdian et al., 2007), I show that the searching efficiency was slightly greater (not significantly) on tomato than on capsicum (Table 2.2).

TPP nymph consumption by *O. vicinus* at the higher prey densities of 30 and 40 individuals was significantly greater on capsicum than on tomato leaflets, suggesting that the ability or efficiency of the predator may have been affected by the tomato leaflet surface (Figure 2.6) and supporting previous reports (Coll & Ridgway, 1995; Coll et al., 1997; Cedola et al 2001; Kennedy 2003; Ship & Wang, 2003; Simmons & Gurr, 2004; Simmons & Gurr, 2005; Riddick & Simmons, 2014). Nevertheless, despite



the potential unsuitability of tomato for a variety of biological control agents, several studies have found that certain predators and parasitoids can control pests effectively (Shipp & Wang, 2003; Shipp & Wang, 2006) due to their size (O'Connell et al., 2012) and/or morphological adaptations (Economou et al., 2006; Voight et al., 2007). However, because *Orius* spp. are small sized mobile predators (Lattin et al., 1999; Horton, 2008), they appear to struggle as biological control agents on tomato plants due to their low searching efficiency and slow walking speeds (Coll & Ridgway, 1995; Coll et al., 1997), inability to walk on the surface (van Lenteren, 2012a), failure to establish on greenhouse crops with high numbers found trapped on stem trichomes (Shipp & Wang, 2003), and spending more time grooming than moving in tomato cultivars with high trichome densities (Economou et al., 2006).

Although my leaflet experiment shows that at the lower prey densities of 10 and 20 individuals the host plant did not have an effect on the predation ability or efficiency of *O. vicinus* (Figure 2.6), on small plants (with prey density of 10 individuals) *O. vicinus* consumed significantly more TPP nymphs on capsicum than on tomato plants (Figure 2.11), probably because the complexity between experimental arenas can alter their predatory performance (Hassell et al., 1977; Everson, 1980; O'Neil, 1989; Coll & Ridgway, 1995; O'Neil, 1997; Messina & Hanks, 1998; De Clerq et al., 2000; Timms et al., 2008; Kumar et al., 2011). Here, the location of release of the predator appeared to influence their hunting efficiency, with the predator appearing to be more successful when released directly onto a tomato leaf than when released at the base of the tomato stem. Tomato stem surfaces (Figure 2.12) have high trichome densities (Shipp & Wang, 2003), which may have affected the movement of the predator. This should be evaluated further.

The majority of TPP nymphs were consumed on the top leaflet surfaces on both host plant surfaces (Fig 2.5), probably due to the identical release point for predator and prey on leaflet experiments. However, the lower percentage of top surface consumption and subsequently a greater percentage of lower surface consumption on capsicum leaflets would indicate that *O. vicinus* were more capable of exploring both surfaces of the capsicum leaflet for prey. My results from the small plant experiments also show a similar trend with significantly greater percentages of TPP consumption taking place on the top surface of tomato when compared to capsicum (Figure 2.10). These results

coincide with previous findings on capsicum plants that show *Orius* spp. being capable of searching and subsequently depredating efficiently on excised leaves (Deligeorgidis et al., 2002), on potted plants (Madadi et al 2009), in commercial glasshouses (Higgins, 1992; Van de Veire & Degheele, 1992; Zsellér & Kiss, 1999; Bosco et al., 2008), and in field trials in conjunction with biological insecticides (Funderburk et al., 2000).



**Figure 2.12:** Hairless capsicum stem surface (left) and hairy tomato stem surface (right).

TPP nymphs rarely move once they have settled on a leaflet (Yang et al., 2013). This behavioural characteristic explains why less movement away from the release location (top leaflet surface) was found on both host plant surfaces in the absence of the predator (Figure 2.4). However, the presence of the predator appears to have impeded the nymphs from settling on the leaflets, which resulted in greater numbers moving towards the lower leaflet surfaces on both plants (Figure 2.4). The morphological characteristics of plants can alter the behaviour of prey species (Everson, 1980; Timms et al., 2008). For example, the trichomes of host plants can influence the dispersal of arthropod pests by trapping or impeding their movement (Van Haren et al., 1987; Van Haren et al., 1987; Coll et al., 1997). The host plant morphological influence on prey dispersal in the presence of a predator was observed on tomato surfaces where less TPP nymph movement towards lower surfaces was recorded in both leaflet (Figure 2.4) and small plant experiments (Figure 2.9). These results suggest that TPP nymphs are less hindered by the capsicum surface and therefore able to move to lower surfaces in greater numbers as a means to escape the predator. Subsequently, this would also explain why more kills were recorded on these lower surfaces on capsicum.

The results of this study indicate that *O. vicinus* are capable of attacking and killing all TPP nymphal stages (Figure 2.8). They also highlight the difference in the performance of a predator when they are simultaneously exposed to a variety of prey stages as opposed to being exposed to one or two life stages at a time. Tran (2012) tested the functional response of *O. vicinus* on different TPP life stages (eggs, small 1<sup>st</sup> and 2<sup>nd</sup> instars, medium 3<sup>rd</sup> and 4<sup>th</sup> instars, and large 5<sup>th</sup> instars) and found that when *O. vicinus* was exposed to small sized nymphs they could consumed almost all of the presented nymphs (e.g. average of 21.5 small nymphs consumed out of a density of 32). Furthermore, the size of prey affected the predator's handling time which was longer when large nymphs were handled. Tran (2012) suggests that *O. vicinus* would be most effective against smaller nymphs at low densities. However, the current study demonstrates that when *O. vicinus* was simultaneously exposed to all available nymph sizes, it preferred medium sized nymphs on both surfaces (Figure 2.8). Furthermore, there appeared to be no difference in the proportion of small and large nymphs consumed on capsicum but an apparent bias for large nymphs over small nymphs on tomato (Figure 2.8).

Tomato appears to be an ideal host plant for TPP infestations as demonstrated by the significantly faster developmental time recorded on tomato plants in comparison to capsicum plants (Yang et al., 2013). Therefore, on tomato plants, TPP densities would increase and predation rates would decrease at faster rates, making it less likely that *O. vicinus* would be able to reduce the population below economic thresholds. TPP infestations do not appear to be as severe on capsicum plants as on other solanaceous crops (Yang & Liu, 2009). Therefore, augmentative releases of *O. vicinus* could be a viable option for this pest on capsicum plants. However, although I attempted to mimic field environments as much as possible during my experiments, the predator-prey interactions were still performed within controlled environments. Therefore, further studies are necessary to assess how the predator performs in open field and glasshouses. Overall, my study has provided an insight into a fairly novel predator-prey interaction. My results indicate that *O. vicinus* as a biological control agent of TPP will struggle to be effective on tomato plants, however the predatory bug showed promise on capsicum plants.

### **Chapter 3: The effect of host plant substrate on the behaviour of *Orius vicinus* (Ribaut) and *Bactericera cockerelli* (Sulc) nymphs.**

#### **3.1 Abstract**

The morphological traits of plants can influence the behaviour of biological control agents and the pests they target. Predators are likely to be more mobile than their prey; therefore, negative effects of host plant traits can reduce their predatory efficiency. The prey stage preferences of biological control agents are potentially guided by their nutritional content and handling time required to kill and consume. This chapter investigates the behaviour of *Orius vicinus* (Ribaut) adults and tomato-potato psyllid (TPP) *Bactericera cockerelli* nymphs during their interactions on morphologically dissimilar surfaces (capsicum versus tomato). The predator-prey interactions were video recorded and analysed. The predatory bug was found to spend a significantly greater amount of time investigating TPP nymphs on capsicum than on tomato. There was significantly higher number of attacks recorded on capsicum. The greater killing percentage on tomato suggests that this surface negatively affected the defensive capabilities of TPP nymphs. The predatory bug preferentially targeted large and medium sized nymphs over smaller nymphs.

#### **3.2 Introduction**

The morphological traits of plants can influence the behaviour of biological control agents and the phytophagous pests they target (Everson, 1980; Baur et al., 1991; Coll et al., 1997; Krips et al., 1999; Eisner et al 1998; Kennedy, 2003; Simmons et al, 2003; Eigenbrode, 2004; Simmons & Gurr, 2005; Timms et al., 2008; Riddick & Simmons, 2014). Plant surface trichomes have been shown to negatively affect the dispersal behaviour of prey via entrapment (Van Haren et al., 1987; Kennedy, 2003; Simmons et al, 2003). Host plant resistance to pests mediated by trichome density has been investigated as a potential alternative for pest control. However, compatibility of this method with natural enemies has to be considered (Simmons et al., 2003; Simmons & Gurr, 2004; Simmons & Gurr, 2005; Riddick & Simmons, 2014). Predators and parasitoids tend to be more mobile than their prey and generally cover larger plant

surface areas; therefore, negative effects of host plant traits can reduce mobility, lower prey encounter rates and lessen consumption capacity (Van Haren et al., 1987; Krips et al., 1999; Kennedy, 2003; Gassman & Hare, 2005; Jalalizand et al., 2011; Kheradpir et al., 2013).

Tomato surfaces are known to contain glandular (release sticky exudates) and non glandular trichomes (impeded organisms mechanically) that are capable of limiting movement, thus altering the behaviour of biological control agents (Coll & Ridgway, 1995; Coll et al., 1997; Sutterlin & Van Lenteren, 1997; De Clercq et al, 2000; Cedola & Sanchez, 2003; Choudhury & Copland, 2003; Kennedy, 2003; Shipp & Wang, 2003; Economou et al., 2006; Mulatu et al., 2006; Koller et al., 2007; Riddick & Simmons, 2014). In contrast, the surfaces of capsicum are virtually void of trichomes and therefore do not present the same mechanical impediments as tomato surfaces (Madadi et al, 2007; Madadi et al, 2008; Madadi et al, 2009; Hernández-Moreno et al., 2017). However, capsicum surfaces have been found to negatively affect the searching capacity of biological control agents due to being too slippery for effective traction (Kheradpir et al., 2013). The effect of plant surface morphology appears to be greater in low prey densities where prey encounter rates are lower, rather than high prey densities where prey encounter rates are likely to be higher (Krips et al., 1997). Species from the *Orius* genus (Hemiptera: Anthocoridae) are highly mobile predators, and any impediment to their locomotion is likely to be detrimental to their predatory ability (Coll & Ridgway, 1995; Eigenbrode et al., 1995; Coll et al., 1997).

Tomato-potato psyllid (TPP), *Bactericera cockerelli* (Sulc) (Hemiptera: Triozidae), adults have a preference to settle and establish on tomato over capsicum plants (Thianakaran et al., 2015b). Subsequently, TPP have a faster developmental time on tomato in comparison to capsicum which would explain why infestations tend to be less severe on the latter (Yan & Liu, 2009; Yang et al., 2013). Regardless of host plant preference, TPP nymphs suffer the greatest mortality within the first three instars (Yan & Liu, 2009; Yang et al., 2013). Tran (2012) has demonstrated that *Orius vicinus* (Ribaut) (Heteroptera: Anthocoridae) is capable of consuming all five TPP nymph stages. Furthermore, the predatory bug would be most effective against the TPP egg, first and second instar stages (Tran 2012). The prey stage preferences of biological control agents are potentially guided by their nutritional content and handling time

required to kill and consume (Hamdan & Abu-Awad, 2007; Xiao & Fadamiro, 2010; Yang et al., 2015). Therefore, understanding which life stages are preferentially targeted by biological control agents is valuable in order to synchronize biological control releases in the presence of vulnerable life stages (Shipp & Wang, 2003). For example, *Amblyseius cucumeris* (Oudemans) (Acari: Phytoseiidae) only feed on the first instar larvae of *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae) (Shipp & Wang, 2003), suggesting that all other *F. occidentalis* life stages were not susceptible to the predator and thus could develop and cause damage to affected crops. The authors proposed that *A. cucumeris* be deployed in the presence of the pest's susceptible life stage in order to increase effectiveness.

The aim of this study was to analyze behavioural recordings of *O. vicinus* interactions with TPP nymphs in order to provide further insight into this predator-prey interaction. This study had three objectives: (1) to investigate the behaviour of *O. vicinus* when exposed to morphologically dissimilar surfaces (smooth surfaced capsicum versus hairy surfaced tomato), (2) to examine which TPP nymph sizes *O. vicinus* prefers to prey on, and (3) to evaluate the defensive behaviours (fight or flight) of TPP nymphs when they encounter *O. vicinus*.

### **3.3 Material and Methods**

#### *3.3.1 Experimental plants*

Tomato (*Solanum lycopersicum* cv. Moneymaker) and capsicum (*Capsicum annuum* cv. California Wonder) plants (Figure 3.1) were grown at the Plant Growth Unit (PGU), Massey University, Palmerston North. Seeds were obtained from Egmont Seed Company Ltd, New Plymouth. The experimental plants were chosen due to the impact TPP has on their respective industries and their known differences in leaf surface trichome density (Sutterlin & van Lenteren, 1997; Madadi et al., 2007). When plants were five weeks old, they were transferred to a 25°C controlled temperature room with a photoperiod of 16:8 h (L:D).



**Figure 3.1:** Adult TPP on smooth surfaced capsicum (left) and hairy surfaced tomato (right) leaves.

### 3.3.2 Insect colonies

TPP nymphs were obtained from a Plant and Food Research colony and reared on tomato (*S. lycopersicum* cv. Moneymaker) and capsicum (*C. annuum* cv. California Wonder) plants in Massey University, Palmerston North. *O. vicinus* were obtained as 4<sup>th</sup> or 5<sup>th</sup> stage nymphs from Bioforce Ltd, Auckland. The predators were reared in plastic containers (length: 15 cm, height: 9 cm, width: 7 cm) with mesh-covered holes. TPP nymphs were provided as prey on capsicum or tomato leaflets attached to a tube filled with water. Leaflets were replaced daily to ensure constant supply of nymphs to the predators. The leaflets with *O. vicinus* eggs were placed in separate containers in order to ensure the completion of the predatory bug lifecycle. Due to time constraints, adults were not assessed separately by sex in this study. TPP and *O. vicinus* colonies were maintained in a 25C° controlled temperature room with a photoperiod of 16:8 h (L:D). All experiments were carried out under this environmental condition. All insects used in the experiments completed their lifecycle in the experimental environment.

### 3.3.3 Experimental design

#### 3.3.3.1 Behavioural recordings of *O. vicinus* and TPP interactions on tomato and capsicum leaflet surfaces.

The experiment was performed in the same laboratory conditions used for rearing *O. vicinus* and TPP cultures. The experimental arena consisted of a Petri dish (diameter: 85 mm, depth: 12 mm). Four small balls of blutack<sup>®</sup> were placed on the surface of each

individual Petri dish. One upward-facing capsicum or tomato leaflet was placed on the four blutack<sup>®</sup> balls in order to raise the leaflet off the surface and to maintain the leaflet in a fixed location. Water was poured into the Petri dish surrounding the leaflet to keep the predator and prey on the leaf surface. The experimental arena was covered by a plastic cylinder (diameter: 85 mm, height: 100 mm) (Figure 3.2). A Sony Handycam, DCR-SR85 was positioned above the experimental enclosure in order to record each trial.

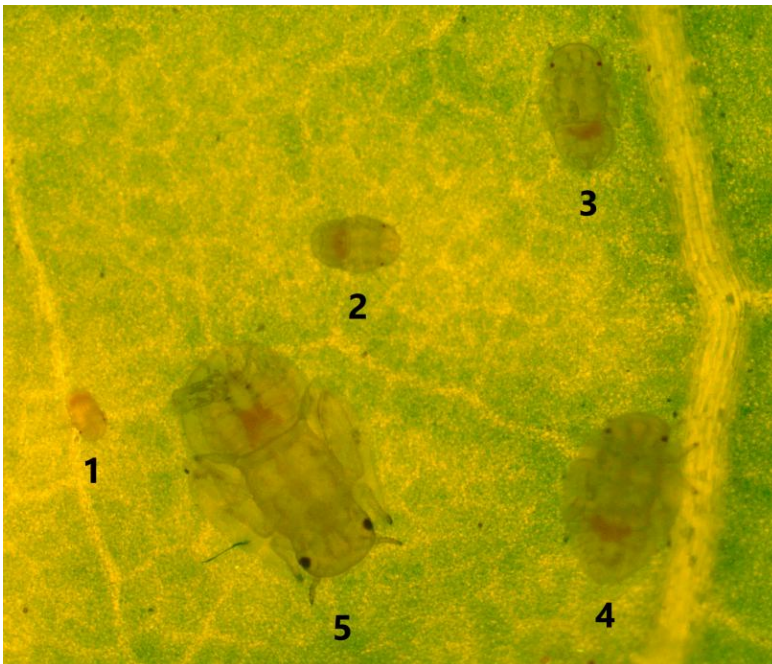


**Figure 3.2:** Capsicum leaflet sitting on blutack balls surrounded by water within Petri dish (right). Aerial view of Petri dish within plastic cylinder containing capsicum leaflet (left).

Twelve TPP nymphs consisting of four small (1<sup>st</sup> and 2<sup>nd</sup> instars), four medium (3<sup>rd</sup> instars) and four large sized nymphs (4<sup>th</sup> and 5<sup>th</sup> instars) were introduced on the top surface of the leaflet (Figure 3.3). Adult *O. vicinus* (3 to 10 days old) were starved for 24 h prior to being introduced into the experimental arena. One adult was released on the top surface of the leaflet per experimental trial. Each individual predator was tested once and discarded. The experimental trials were recorded for 1 hour and began 15 minutes after the predator was introduced onto the leaf surface (allowing the predator time to settle into its new environment) or as soon as a predator-prey encounter occurred. Trials were replicated 12 times on both host plants. The duration of *O. vicinus* behaviours (Table 3.1) and the defensive behavioural responses of TPP nymphs (Table 3.2) were recorded in seconds. Defensive behavioural responses were only recorded during predator/prey interactions. The number of observed encounters (the predator investigates but does not attack), attacks (the predator initiates an attack), and successful



attacks (the predator kills prey) performed by the predator on the three prey size classes were recorded.



**Figure 3.3:** TPP nymphs on tomato surface: (1) first instar, (2) second instar, (3) third instar, (4) fourth instar, and (5) fifth instar.

**Table 3.1:** Behavioural parameters for adult *O. vicinus*.

Behaviour	Description
Walking	Predator moves forward across the leaf surface
Searching	Predator touches plant surface with mouthparts and/or antenna while moving forward across the surface
Orientating	Predator pivots on the leaf surface without advancing in any particular direction
Stationary	Predator stands motionless
Grooming	Predator makes rapid movements with its fore and hind legs across its body surface and antenna
Investigating	Predator initiates encounter with prey by investigating target without attacking
Attack	Predator attacks prey during encounter
Consumption	Predator feeds on prey following successful attack
Other	Behaviour not covered by the definitions above (i.e. flying)

**Table 3.2:** Behavioural parameters for TPP nymphs.

Behaviour	Description
Fighting	Prey fights back during an encounter by swinging body violently from side to side
Escape	Prey moves away from a predator during encounter
None	Prey stands motionless during encounter

#### 3.3.4 Data analysis

All analyses were done using SAS 9.13. Rejection level was set at  $\alpha < 0.05$ .

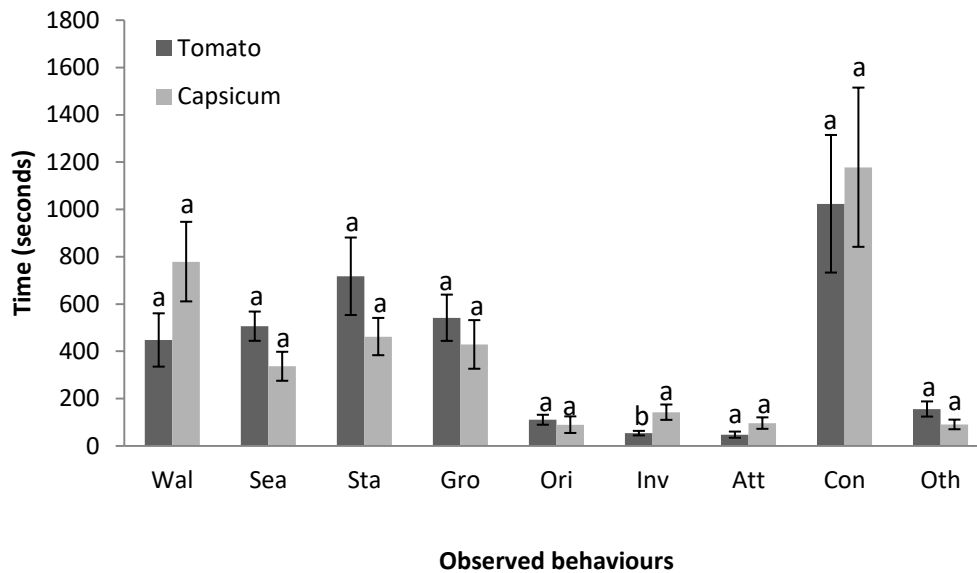
A goodness-of-fit test (Shapiro-Wilk test) was used to test the distribution of data. Data on *O. vicinus* walking, searching, stationary, grooming, attack, other behaviours, overall TPP nymph encounters and overall TPP nymph attacks were normally distributed. Data on *O. vicinus* consumption, investigation, and orienteering behaviours were normally distributed after natural log transformation. Thus, an analysis of variance (ANOVA, GLM procedure) was applied to compare the difference in *O. vicinus* behaviour time allocation (Figure 3.4), total observed TPP nymph encounters, and total observed TPP nymph attacks (Table 3.3) between the two host plants. Data on *O. vicinus* attack success were not normally distributed even after arsine-square-root transformation. Therefore, a Kruskal-Wallis Test (NPAR1WAY procedure) was employed to compare the attack success rate of *O. vicinus* between two host plants (Table 3.4).

The probability of prey size preference by *O. vicinus* for encountering (Table 3.5), attacking (Table 3.6) and killing (Table 3.7) TPP nymphs was determined using a generalized linear mixed model (GLIMMIX Procedure) with binary distribution. The probability of TPP nymphs of different sizes exhibiting fighting (Table 3.8) and escape behaviours (Table 3.9) during encounters with *O. vicinus* was also determined using a generalized linear mixed model (GLIMMIX Procedure) with binary distribution.

### 3.4 Results

#### 3.4.1 *O. vicinus* behaviour time allocation

There was no significant difference between capsicum and tomato surfaces in the overall time allocated by *O. vicinus* for walking, searching, stationary, grooming, orienteering, other behaviours (ANOVA:  $F_{1,22} = 2.68, 3.79, 1.97, 0.63, 0.26, 2.96$  respectively,  $P > 0.05$ ), attacking (ANOVA:  $F_{1,21} = 1.33, P > 0.05$ ), and consumption (ANOVA:  $F_{1,15} = 0.61, P > 0.05$ ), except for the overall time allocated by *O. vicinus* for investigating TPP nymphs which was significantly greater on capsicum surface than on tomato surface (ANOVA:  $F_{1,22} = 6.07, P < 0.05$ ) (Figure 3.4).



**Figure 3.4:** The mean number of seconds spent by *O. vicinus* performing the observed behaviours on tomato and capsicum surfaces during the 1 h observation period (Wal = Walking; Sea = Searching; Sta = Stationary; Gro = Grooming; Ori = Orienteering; Inv = Investigating; Att = Attacking; Con = Consuming; Oth = Other). For each behaviour, columns with a different letter are significantly different (ANOVA:  $P < 0.05$ ).

#### 3.4.2 *O. vicinus* overall encounter, attack and attack success

There was no significant difference between capsicum and tomato surfaces in *O. vicinus* encounters with TPP nymphs (ANOVA:  $F_{1,22} = 3.64, P > 0.05$ ) (Table 3.3). *O. vicinus* attacked a significantly greater number of TPP nymphs during encounters on capsicum surface than on tomato surface (ANOVA:  $F_{1,22} = 6.13, P < 0.05$ ) (Table 3.3). There was

no significant difference between capsicum and tomato surfaces in attack success on TPP nymphs (Kruskal-Wallis Test:  $\chi^2 = 2.11$ ,  $P > 0.05$ ) (Table 3.4).

**Table 3.3:** The mean ( $\pm$ SE) number of predator-prey encounters and number of predator attacks observed on capsicum and tomato surfaces.

Plant	Encounters	Attacks
Capsicum	7.75 $\pm$ 1.2799a	4.25 $\pm$ 0.78937a
Tomato	5.00 $\pm$ 0.66287a	2.08 $\pm$ 0.37856b

Means within a column followed by a different letter are significantly different (ANOVA:  $P < 0.05$ ).

**Table 3.4:** The mean ( $\pm$ SE) percentage of attacks resulting in kills observed on capsicum and tomato surfaces.

Plant	Successful Attacks %
Capsicum	0.3525 $\pm$ 0.11882a
Tomato	0.5682 $\pm$ 0.11722a

Mean followed by the same letter are not significantly different (Kruskal-Wallis Test:  $P > 0.05$ ).

### 3.4.3 Prey size preference probability

The probability on capsicum of *O. vicinus* initiating an encounter with small sized nymphs was significantly lower than for medium and large sized nymphs ( $F_{1,130} = 3.9$ , 10.75, respectively,  $P < 0.05$ ). There was no significant difference between medium and large sized nymph encounters on capsicum ( $F_{1,130} = 2.04$ ,  $P > 0.05$ ) (Table 3.5). The probability on tomato of *O. vicinus* initiating an encounter with small sized nymphs was significantly lower than large sized nymphs ( $F_{1,130} = 4.88$ ,  $P < 0.05$ ). There was no significant difference in encounter probability on tomato surfaces between large sized and medium sized nymphs ( $F_{1,130} = 0.18$ ,  $P > 0.05$ ) and medium sized and small sized nymphs ( $F_{1,130} = 3.3$ ,  $P > 0.05$ ) (Table 3.5). The probability from pooled surface (combining capsicum and tomato) results of *O. vicinus* initiating an encounter with small sized nymphs was significantly lower than medium and large sized nymphs ( $F_{1,262} = 7.19$  and 15.16, respectively,  $P < 0.05$ ). There was no significant difference between medium and large sized nymph encounters ( $F_{1,262} = 1.73$ ,  $P > 0.05$ ) (Table 3.5).

**Table 3.5:** The probability ( $\pm$ SE) of *O. vicinus* initiating an encounter with TPP nymphs based on their size on capsicum, tomato, and combined (capsicum and tomato) surfaces.

Nymph Size	Capsicum	Tomato	Combined
Small	0.208 $\pm$ 0.05968b	0.1866 $\pm$ 0.05797b	0.1973 $\pm$ 0.04166b
Medium	0.3957 $\pm$ 0.07254a	0.3535 $\pm$ 0.07234ab	0.3746 $\pm$ 0.05134a
Large	0.5417 $\pm$ 0.07399a	0.3954 $\pm$ 0.07415a	0.4686 $\pm$ 0.05306a

Probability within a column followed by a different letter are significantly different (GLIMMIX:  $P < 0.05$ ).

There was no significant difference on either host plant and from pooled plant surface results in the probability of *O. vicinus* initiating an attack following an encounter with a particular size of nymph (capsicum,  $F_{1,41} = 0.01$ , 1.5 and 1.49; tomato,  $F_{1,31} = 0.11$ , 0.16 and 0.02; pooled plant results,  $F_{1,74} = 0.06$ , 0.36 and 0.06, respectively, for large nymphs vs. medium nymphs, large nymphs vs. small nymphs and medium nymphs vs. small nymphs,  $P > 0.05$ ) (Table 3.6).

**Table 3.6:** The probability ( $\pm$ SE) of *O. vicinus* initiating an attack during an encounter with TPP nymph based on their size on capsicum, tomato, and combined (capsicum and tomato) surfaces.

Nymph Size	Capsicum	Tomato	Combined
Small	0.3885 $\pm$ 0.1569a	0.5556 $\pm$ 0.1656a	0.4737 $\pm$ 0.1145a
Medium	0.6303 $\pm$ 0.114a	0.5294 $\pm$ 0.1211a	0.5833 $\pm$ 0.08217a
Large	0.6197 $\pm$ 0.099a	0.4737 $\pm$ 0.1145a	0.5556 $\pm$ 0.07407a

Probability within a column followed by a different letter are significantly different (GLIMMIX:  $P < 0.05$ ).

There was no significant difference on capsicum in the probability of *O. vicinus* killing a TPP nymph during an attack with a particular size of nymph ( $F_{1,18} = 2.37$ , 3.94 and 0.01, respectively, for large nymphs vs. medium nymphs, large nymphs vs. small nymphs and medium nymphs vs. small nymphs,  $P > 0.05$ ) (Table 3.7). The probability on tomato of *O. vicinus* killing a large sized nymph during an attack was significantly lower than medium sized nymphs ( $F_{1,10} = 5.89$ ,  $P < 0.05$ ). There was no significant difference in the probability of *O. vicinus* killing a small sized nymph in comparison to medium and large sized nymphs ( $F_{1,10} = 1.42$  and 1.17, respectively,  $P > 0.05$ ) (Table 3.7). The probability from the pooled plant surface results of *O. vicinus* killing a large sized nymph during an attack was significantly lower than small sized nymphs and medium sized nymphs ( $F_{1,30} = 3.99$  and 9.63 respectively,  $P < 0.05$ ). There was no

significant difference in the probability of killing medium sized nymphs in comparison to small sized nymphs ( $F_{1,30} = 0.25$ ,  $P > 0.05$ ) (Table 3.7).

**Table 3.7:** The probability ( $\pm$ SE) of *O. vicinus* killing a TPP nymph during an attack based on their size on capsicum, tomato, and combined (capsicum and tomato) surfaces.

Nymph Size	Capsicum	Tomato	Combined
Small	0.5257 $\pm$ 0.2655a	0.6264 $\pm$ 0.3067ab	0.5772 $\pm$ 0.1855a
Medium	0.5036 $\pm$ 0.1513a	0.9268 $\pm$ 0.08777a	0.6781 $\pm$ 0.1114a
Large	0.1301 $\pm$ 0.08811a	0.2227 $\pm$ 0.1736b	0.1727 $\pm$ 0.08308b

Probability within a column followed by a different letter are significantly different (GLIMMIX:  $P < 0.05$ ).

#### 3.4.4 TPP nymph defensive behaviour probability following encounter with *O. vicinus*

The probability on capsicum of large sized nymphs exhibiting defensive fighting behaviours during encounters with *O. vicinus* was significantly greater than small sized nymphs ( $F_{1,41} = 4.47$ ,  $P < 0.05$ ). There was no significant difference in nymphs exhibiting defensive fighting behaviours between large and medium sized nymphs ( $F_{1,41} = 1.72$ ,  $P > 0.05$ ) and medium and small sized nymphs ( $F_{1,41} = 1.37$ ,  $P > 0.05$ ) (Table 3.8). There was no significant difference on tomato in the probability of a particular size of nymph exhibiting defensive fighting behaviours during encounters with *O. vicinus* ( $F_{1,31} = 1.2$ , 0.49 and 0.04, respectively, for large nymphs vs. medium nymphs, large nymphs vs. small nymphs and medium nymphs vs. small nymphs,  $P > 0.05$ ) (Table 3.8). The probability from pooled plant surface results of large sized nymphs exhibiting defensive fighting behaviours during encounters with *O. vicinus* was significantly greater than small sized nymphs ( $F_{1,74} = 4.34$ ,  $P < 0.05$ ). There was no significant difference in nymphs exhibiting defensive fighting behaviours between large and medium sized nymphs ( $F_{1,74} = 2.99$ ,  $P > 0.05$ ) and medium and small sized nymphs ( $F_{1,74} = 0.54$ ,  $P > 0.05$ ) (Table 3.8).

**Table 3.8:** The probability ( $\pm$ SE) of TPP nymph performing defensive behaviours during an encounter with *O. vicinus* based on their size on capsicum, tomato, and combined (capsicum and tomato) surfaces.

Nymph Size	Capsicum	Tomato	Combined
Small	0.1976 $\pm$ 0.1273b	0.3333 $\pm$ 0.1571a	0.2632 $\pm$ 0.101b
Medium	0.4205 $\pm$ 0.1165ab	0.2941 $\pm$ 0.1105a	0.3611 $\pm$ 0.08005ab
Large	0.6205 $\pm$ 0.09879a	0.4737 $\pm$ 0.1145a	0.5556 $\pm$ 0.07407a

Probability within a column followed by a different letter are significantly different (GLIMMIX:  $P < 0.05$ ).

There was no significant difference on capsicum in the probability of a particular size of nymph exhibiting escape behaviours during encounters with *O. vicinus* ( $F_{1,41} = 0.22$ , 0.92 and 1.57, respectively, for large nymphs vs. medium nymphs, large nymphs vs. small nymphs and medium nymphs vs. small nymphs,  $P > 0.05$ ) (Table 3.9). There was only one escape event (performed by large sized nymph) recorded on tomato surfaces and therefore no results could be formulated.

**Table 3.9:** The probability ( $\pm$ SE) of TPP nymph performing defensive escape behaviours during an encounter with *O. vicinus* based on their size on capsicum surfaces.

Nymph Size	Capsicum
Small	0.2977 $\pm$ 0.1457a
Medium	0.1057 $\pm$ 0.07106a
Large	0.154 $\pm$ 0.07166a

Probability with the same letter are not significantly different (GLIMMIX:  $P > 0.05$ ).

### 3.5 Discussion

The results from my study indicated that plant substrates did not significantly alter the behavioural activity of *O. vicinus* (Figure 3.4). The lack of difference in time allocated for locomotion (walking and searching) was unexpected because the searching behaviour of biological control agents has been reported as altering on different plant substrates (Coll et al., 1997; Messina & Hanks, 1998; Simmons & Gurr, 2005; Madadi et al., 2007). Dense trichome substrates such as tomato are known to decrease locomotion and increase behaviours such as resting and grooming which result in lower prey encounters (Eigenbrode et al., 1996; De Clercq et al., 2000; Gassman & Hare 2005; Economou et al., 2006; O'Connell et al., 2012). For example, O'Connell et al. (2012) found that *Scymnus loewii* Mulsant (Coleoptera: Coccinellidae) adults spent less

time searching on tomato surfaces than on potato surfaces. Subsequently, *S. loewii* recorded greater consumption rates after 24 hours on potato than on tomato which the authors associated with the greater searching time allocation on potato. Furthermore, related congeneric species, *Orius niger* Wolff (Hemiptera: Anthocoridae), spent more time grooming and less time moving on the tomato cultivar with the greatest surface trichome density (Economou et al., 2006). Increased grooming could be a result of arthropods attempting to remove the sticky exudates released from glandular trichome tips (Economou et al., 2006; Riddick & Simmons, 2014). However, my results indicate that the lack of trichomes on capsicum did not significantly reduce the allocated stationary and grooming time in comparison to tomato (Figure 3.4).

The predatory bug spent a significantly greater amount of time investigating TPP nymphs on capsicum than on tomato (Figure 3.4). Furthermore, there was a significantly higher number of attacks recorded on capsicum (Table 3.3). This result suggests that the predatory bug may be more efficient on capsicum than on tomato in finding prey to investigate and attack. *Orius insidiosus* (Say) (Hemiptera: Anthocoridae) was found to search less efficiently on tomato surfaces than on bean or pepper (Coll & Ridgway, 1995). Furthermore, Coll et al. (1997) reported that *O. insidiosus* spent 50% of their time near the leaf vein area of tomato, therefore restricting their foraging capability to a specific section of the available surface area. The authors reported that the distribution of prey and the searching patterns of *O. insidiosus* overlapped the least on tomato foliage in comparison to bean and corn foliage (Coll et al., 1997).

The distance covered and the walking speeds of the predatory bug were not calculated due to the constraints of this study. However, the predatory bug was observed during the experimental trials to move quicker and less cumbersome on capsicum than on tomato. Comparatively, the walking speed of *O. insidiosus* was slowest on tomato surfaces (Coll et al., 1997). While, parasitoids produced higher walking speeds on capsicum surfaces (Sutterlin & Van Lenteren, 1997; Choudhury & Copland, 2003). There was no difference in time allocated to walking by *Phytoseiulus persimilis* Athias-Henriot (Acari: Phytoseiidae) on gerbera cultivars with low and high trichome densities (Krips et al., 1997). However, the predatory mite recorded faster walking speeds on the lower trichome density surface which led to greater coverage of the surface area. Eigenbrode et al. (1996) reported that *O. insidiosus* covered available surfaces less



effectively in substrates in which they had greater struggles to move fluidly. Less surface coverage has been found to result in lower predation rates (Krips et al., 1997). My results suggest that the significantly greater amount of prey attacked by *O. vicinus* on capsicum is a result of the predatory bug covering a greater amount of available surface area in the allocated time due to reduced interference from this surface.

Despite the greater number of attacks being recorded on capsicum, the percentage of killed nymphs after an attack by *O. vicinus* was greater on tomato than on capsicum (Table 3.4), resulting in the number of kills recorded on tomato (13 kills in 12 trials) and on capsicum (10 kills in 12 trials) being almost equal. The predatory bug preferentially targeted large and medium sized nymphs over smaller nymphs (Table 3.5). This selection is likely driven by the greater nutritional content of larger nymphs (Yang et al., 2015). However, attacks on larger nymphs were more likely to result in defensive fighting behaviours being exhibited (Table 3.8) and a lower kill probability (Table 3.7). This result is not surprising as Tran (2012) had reported that *O. vicinus* handling time of TPP nymphs increased as prey size increased with the predatory bug showing to be least capable of killing the 5<sup>th</sup> instar stage. Furthermore, Xu and Zhang (2015) reported that consumption of TPP nymphs increased in difficulty for the predatory mite *Amblydromalus limonicus* Garman & McGregor (Acari: Phytoseiidae) as instars became larger. The results of this study further established that *O. vicinus* are capable of attacking and killing all TPP nymph stages and highlights the importance of assessing the performance of a predator when they are exposed to a variety of life stages. Tran (2012) assessed consumption of TPP life stages separately and established that smaller nymph stages were the most susceptible to *O. vicinus*. However, my results demonstrated that the predatory bug is least likely to initiate an encounter with smaller sized nymphs when all nymph sizes are available (Table 3.5).

The greater killing percentage on tomato (Table 3.4) suggests that the defensive capabilities of TPP nymphs appear to have been negatively affected by the tomato substrate. The predatory bug typically probed the targeted nymph's carapace during an attack, with kills typically occurring once access to the softer underside of the prey was attained (Figure 3.5). Geary et al. (2016) reported that late TPP instars reacted defensively to attacks by *Anystis baccarum* L. (Trombidiformes: Anystidae) by sealing themselves to the surface of box thorn leaves. The effectiveness of this defensive

strategy may have been diminished by the surface of tomato allowing *O. vicinus* easier access to the underside. Interestingly, the defensive fighting behaviours (swinging body side to side) observed in this study were not reported by Geary et al. (2016), this might be due to the behaviour not being catalogued or they simply did not occur in that particular predator-prey-plant interaction. Furthermore, the lack of escape behaviours observed on tomato in comparison to capsicum suggests that the higher trichome density on this substrate impeded attacked nymphs from attempting to escape (Table 3.9). Plant substrates have been known to influence the movement and dispersal of prey (Eigenbrode et al., 1995; Eisner et al., 1998; Simmons et al., 2003). Tomato surfaces in particular have previously been shown to negatively impact the dispersal of the predatory mite *T. urticae* (Van Haren et al., 1987).



**Figure 3.5:** Adult *O. vicinus* probing large sized TPP nymph (left) and adult *O. vicinus* consuming medium sized TPP nymph (right).

*O. vicinus* allocated the greatest amount of time to the consumption of prey on both surfaces (Figure 3.4). Long consumption times may negatively affect the consumption capacity of the predatory bug, particularly if they target medium and large sized nymphs. For example, predatory mites consume relatively few large TPP nymphs due to their long feeding times (Xu & Zhang, 2015; Geary et al., 2016). Tran (2012) reported that *O. vicinus* had the capacity to consume a greater number of small TPP nymphs than large TPP nymphs after a 24 hour period. Macdonald et al. (2015) also tested consumption of TPP life stages separately and reported that *Melanostoma fasciatum* (Macquart) (Diptera: Syrphidae), *Micromus tasmaniae* (Walker) (Neuroptera: Hemerobiidae) and *Coccinella undecimpunctata* L. (Coleoptera: Coccinellidae) consumed a greater number of small (2<sup>nd</sup> and 3<sup>rd</sup> instars) nymphs than large (4<sup>th</sup> and 5<sup>th</sup> instars) nymphs. However, *Harmonia conformis* (Boisduval) (Coleoptera:

Coccinellidae) was reported to consume similar numbers of small and large nymphs which implied that after 24 h this predator was not satiated. *O. vicinus* are relatively small predators (Lariviere & Wearing, 1994), and the size of a predator has been shown to influence their consumption capacity as demonstrated by O'Connell et al. (2012) and Timms et al. (2008) in coccinellids and Xiao and Fadamiro (2016) in phytoseiids. However, predators with low consumption capacity can still be useful provided they are argumentatively released in appropriate circumstances (Cocuzza & De Clercq, 1997; Van de Veire & Degheele; Shipp & Wang, 2003; Shipp & Wang, 2006; Van Lenteren, 2012b; Geary et al., 2016). Timing the release of biological control agents to the presence of susceptible prey stages is vital for successful controls (Shipp & Wang, 2003).

In the present study I provided novel information on a predator-prey interaction on morphologically distinct surfaces. The results from this study imply that the behaviour of the predatory bug was affected by the plant surface which led to a greater amount of attacks on capsicum surfaces. However, the plant surface also appeared to affect the defensive capabilities of TPP nymphs which translated to a greater killing percentage on tomato and relatively equal number of kills between surfaces. Furthermore, the results from this study emphasized that *O. vicinus* would not target the most susceptible prey stage when all life stages were present. Ultimately, my results suggest that augmentative releases of *O. vicinus* in the presence of susceptible smaller life stage will be more successful on capsicum than on tomato given the significantly greater number of attacks recorded on capsicum. However, *O. vicinus* have only been tested individually therefore further studies are required to assess if the predatory bug's performance will be reduced or enhanced when deployed in densities greater than one.

## Chapter 4: Conclusion

The aim of this thesis was to assess how the morphological structures of plant surfaces (hairy tomato versus non-hairy capsicum) can influence the predatory behaviour and efficiency of *Orius vicinus* (Ribaut) acting on tomato-potato psyllid (TPP), *Bactericera cockerelli* (Sulc) nymphs.

### 4.1 Objectives and outcomes

#### 4.1.1 Objective 1: Determination of the effects of surface morphology on the capacity of *O. vicinus* to consume TPP nymphs.

Despite the morphological differences in the experimental plant surfaces, *O. vicinus* exhibited a type II functional response on both plant surfaces. The effect of the plant surface on the consumption capacity of the predator was apparent at high prey densities with greater consumption recorded on capsicum leaf surfaces than on tomato leaf surfaces (Figure 2.6). However, the effect of the plant surface at low prey densities (Figure 2.6) only became apparent once the complexity of the experimental arena increased by testing the predatory bug on small plants and changing the release location of the predator further away from prey (Figure 2.11). Previous studies have determined that plant surface morphology affects predation at low prey densities (Krips et al., 1997) and that complexity of experimental arenas can alter predatory performance (Hassell et al., 1977; Everson, 1980; O'Neil, 1989; Coll & Ridgway, 1995; O'Neil, 1997; Messina & Hanks, 1998; De Clerq et al., 2000; Timms et al., 2008; Kumar et al., 2011). The results from the small plant experiment indicate that the predatory bug would struggle in fully-grown tomato plants, particularly if the predator is not released directly on the prey. Similarly, a related congeneric species, *Orius insidiosus* (Say) failed to reduce *Frankliniella occidentalis* (Pergande) on greenhouse tomato crops (Shipp & Wang, 2003).

#### *4.1.2 Objective 2: Examination of the effects of the surface structure on the dispersal of TPP nymphs in the presence and absence of O. vicinus.*

The presence of the predatory bug appeared to alter TPP nymph behaviour by disrupting their settling behaviour and causing greater dispersal from the upper leaf surface to the lower leaf surface (Figure 2.4). Plant surface morphology influenced nymph dispersal, with greater numbers moving to the lower leaf surface of capsicum in the leaflet (Figure 2.4) and small plant experiments (Figure 2.9). Furthermore, the lack of escape behaviours observed on tomato leaflet surfaces during TPP nymph interactions with the predatory bug provides further evidence that tomato surface morphology influenced TPP nymph movement (Chapter 3).

#### *4.1.3 Objective 3: Determination of TPP nymph size preference by O. vicinus.*

The results from my study further established that *O. vicinus* is capable of killing all nymphal stages. Biological control agents should ideally be released in synchronicity with susceptible life stages (Shipp & Wang, 2003). Tran (2012) reported that the predatory bug would be most effective against smaller nymphal stages. However, my study strongly indicated in both the 24 h study (Figure 2.8) and the behavioural recording study (Table 3.5) that the predatory bug is more likely to target and consume medium (3<sup>rd</sup> instars) and large nymphs (4<sup>th</sup> and 5<sup>th</sup> instars) over small nymphs (1<sup>st</sup> and 2<sup>nd</sup> instars). This is potentially due to the greater nutritional content of larger sized nymphs (Yang et al., 2015). Therefore, my results indicate that *O. vicinus*, should be released in the almost exclusive presence of smaller sized nymphs in order to maximise the pest management capacity of the predatory bug.

#### *4.1.4 Objective 4: Investigation into the behaviour of O. vicinus and the defensive behaviours (fight or flight) of TPP nymphs during predator-prey encounters on morphologically dissimilar surfaces.*

At first glance, the results from behavioural recordings (Figure 3.4) did not indicate that plant substrates significantly altered the behavioural activity of the predatory bug on the experimental plant surfaces. Nonetheless, the significantly greater amount of time the predatory bug spent investigating TPP nymphs (Figure 3.4) and the significantly greater

number of attacks (Table 3.3) on capsicum surfaces suggested that the predatory bug was not as effective at searching for prey on tomato. However, the predatory bug had greater attacking success on tomato (Table 3.4) which resulted in an almost equal number of kills recorded on each plant surface (Chapter 3). This outcome, can be explained by the medium and large size TPP nymph preference of the predatory bug (Table 3.5). The defensive capabilities of TPP nymphs increase as they get larger which increases the handling difficulty for the predator (Tran, 2012; Xu & Zhang, 2015). The tomato surface appeared to negatively affect the defensive capabilities of TPP nymphs, as shown by the lower probability of defensive fighting behaviours of medium and large sized TPP nymphs occurring on this surface (Table 3.8) and the lack of escape behaviours observed during trials (Chapter 3). On the other hand, TPP nymphs appear to be more likely to effectively defend themselves against the predatory bug on capsicum surfaces by either fighting (Table 3.8) or escaping (Table 3.9). Ultimately, this could also explain why TPP nymph consumption was almost equal at low prey densities during the 24 h consumption capacity study (Figure 2.6).

## 4.2 Future research

Despite attempting to recreate naturalistic settings, the experimental arenas were largely controlled environments and the predatory bugs were individually tested. The results from this study established that *O. vicinus* would not target the most susceptible prey stage (1<sup>st</sup> and 2<sup>nd</sup> instars as established by Tran (2012)) when all life stages were present. Therefore, future studies should be: (1) conducted in settings such as open field or glasshouses, (2) deploy multiple predatory bugs to assess augmentative release efficiency, and (3) deploy predators in naturalistic environments in the presence of susceptible life stages. Furthermore, *O. vicinus* are highly susceptible to broad-spectrum insecticides (Lariviere & Wearing, 1994). Therefore, the use of *O. vicinus* in conjunction with selective insecticide programs should be evaluated in order to assess their compatibility and efficiency in managing TPP infestations.

### 4.3 Final summary

Tomato is an ideal host plant for TPP infestations (Yang et al., 2013). Furthermore, TPP adults have a preference to settle and establish on tomato over capsicum plants (Thianakaran et al., 2015b). TPP densities increase at faster rates on tomato plants making it less likely that *O. vicinus* would be able to reduce the population below economic thresholds (Yang et al., 2013). However, TPP infestations do not appear to be as severe on capsicum plants (Yang & Liu, 2009). The results from my study indicate that augmentative releases of *O. vicinus*, in the presence of smaller TPP nymphs, could be a viable biological control option on capsicum plants to potentially reduce TPP populations to below economic thresholds. However the predatory bug will likely struggle if deployed on tomato plants.

## References

- Abdala-Roberts, L., Berny-Mieryteran, J. C., Mooney, K. A., Moguel-Ordonez, Y. B., & Tut-Pech, F. (2014). Plant traits mediate effects of predators across pepper (*Capsicum annuum*) varieties. *Ecological Entomology*, 39(3), 361-370.
- Abdullah, N. M. (2008). Life history of the potato psyllid *Bactericera cockerelli* (Homoptera: Psyllidae) in controlled environment agriculture in Arizona. *African Journal of Agricultural Research*, 3(1), 060-067.
- Ail-Catzim, C., Flores-Davila, M., Cerna-Chavez, E., Badii-Zabeh, M., Landeros-Flores, J., Ochoa-Fuentes, Y., & Aguirre-Urbe, L. (2012). Functional response of different larval instars of *Chrysoperla carnea* (Stephens) (Neuroptera: Chrysopidae) on nymphs of *Bactericera cockerelli* (Sulc) (Homoptera: Psyllidae). *Revista de la Facultad de Ciencias Agrarias, Universidad Nacional de Cuyo*, 44(2), 279-288.
- Ail-Catzim, C. E., Cerna-Chávez, E., Landeros-Flores, J., Ochoa-Fuentes, Y., García-López, A. M., & González, R. E. R. (2015). Efecto de Insecticidas Sobre la Mortalidad y Depredación de *Chrysoperla carnea* (Neuroptera: Chrysopidae). *Southwestern Entomologist*, 40(3), 565-574.
- Al-Jabr, A. M., & Cranshaw, W. S. (2007). Trapping tomato psyllid, *Bactericera cockerelli* (Sulc) (Homoptera: Psyllidae), in greenhouses. *Southwestern Entomologist*, 32(1), 25-30.
- Anderson, J. A., Walker, G. P., Alspach, P. A., Jeram, M., & Wright, P. J. (2013). Assessment of susceptibility to zebra chip and *Bactericera cockerelli* of selected potato cultivars under different insecticide regimes in New Zealand. *American Journal of Potato Research*, 90(1), 58-65.
- Badii, M. H., Hernández-Ortiz, E., Flores, A. E., & Landeros, J. (2004). Prey stage preference and functional response of *Euseius hibisci* to *Tetranychus urticae* (Acari: Phytoseiidae, Tetranychidae). *Experimental & Applied Acarology*, 34(3-4), 263.
- Barrios-Díaz, B., Arellano-Fuentes, M. E., Vázquez-Huerta, G., Manuel, J., Barrios-Díaz, R. B. A., & del Rosario Hernández-Tapia, M. (2016). Control Alternativo de Paratrioza (*Bactericera cockerelli* Sulc.) en Chile Serrano (*Capsicum annuum* L.). *Entomología Mexicana*, 3, 146-152.



- Baumann, P. (2005). Biology of bacteriocyte-associated endosymbionts of plant sap-sucking insects. *The Annual Review of Microbiology*, 59, 155-189.
- Baur, R., Binder, S., & Benz, G. (1991). Nonglandular leaf trichomes as short-term inducible defense of the grey alder, *Alnus incana* (L.), against the chrysomelid beetle, *Agelastica alni* L. *Oecologia*, 87(2), 219-226.
- Beddington, J. R. (1975). Mutual interference between parasites or predators and its effect on searching efficiency. *The Journal of Animal Ecology*, 44(1), 331-340.
- Berry, N. A., Walker, M. K., & Butler, R. C. (2009). Laboratory studies to determine the efficacy of selected insecticides on tomato/potato psyllid. *New Zealand Plant Protection*, 62, 145-151.
- Bioforce Limited (2014). *Orius for Thrips, Aphid and Spider Mite Control*. Retrieved from <http://www.bioforce.net.nz/products/Orius.html>.
- Bonte, M., & De Clercq, P. (2011). Influence of predator density, diet and living substrate on developmental fitness of *Orius laevigatus*. *Journal of Applied Entomology*, 135(5), 343-350.
- Bosco, L., Giacometto, E., & Tavella, L. (2008). Colonization and predation of thrips (Thysanoptera: Thripidae) by *Orius* spp. (Heteroptera: Anthocoridae) in sweet pepper greenhouses in Northwest Italy. *Biological Control*, 44(3), 331-340.
- Brown, A. S., Simmonds, M. S. J., & Blaney, W. M. (1999). Influence of species of host plants on the predation of thrips by *Neoseiulus cucumeris*, *Iphiseius degenerans* and *Orius laevigatus*. *Entomologia Experimentalis et Applicata*, 92(3), 283-288.
- Buchman, J. L., Sengoda, V. G., & Munyaneza, J. E. (2011). Vector transmission efficiency of liberibacter by *Bactericera cockerelli* (Hemiptera: Triozidae) in zebra chip potato disease: effects of psyllid life stage and inoculation access period. *Journal of Economic Entomology*, 104(5), 1486-1495.
- Burckhardt, D., & Lauterer, P. (1997). A taxonomic reassessment of the trioqid genus *Bactericera* (Hemiptera: Psylloidea). *Journal of Natural History*, 31(1), 99-153.
- Butler, C. D., Byrne, F. J., Keremane, M. L., Lee, R. F., & Trumble, J. T. (2011). Effects of insecticides on behavior of adult *Bactericera cockerelli* (Hemiptera: Triozidae) and transmission of *Candidatus Liberibacter psyllaureus*. *Journal of Economic Entomology*, 104(2), 586-594.

- Butler, C. D., & Trumble, J. T. (2012a). The potato psyllid, *Bactericera cockerelli* (Sulc) (Hemiptera: Triozidae): life history, relationship to plant diseases, and management strategies. *Terrestrial Arthropod Reviews*, 5(2), 87-111.
- Butler, C. D., & Trumble, J. T. (2012b). Identification and Impact of natural enemies of *Bactericera cockerelli* (Hemiptera: Triozidae) in Southern California. *Journal of Economic Entomology*, 105(5), 1509-1519.
- Butler, C. D., & Trumble, J. T. (2012c). Spatial dispersion and binomial sequential sampling for the potato psyllid (Hemiptera: Triozidae) on potato. *Pest Management Science*, 68(6), 865-869.
- Butler, C. D., Walker, G. P., & Trumble, J. T. (2012). Feeding disruption of potato psyllid, *Bactericera cockerelli*, by imidacloprid as measured by electrical penetration graphs. *Entomologia Experimentalis et Applicata*, 142(3), 247-257.
- Calvo, F. J., Torres-Ruiz, A., Velázquez-González, J. C., Rodríguez-Leyva, E., & Lomeli-Flores, J. R. (2016). Evaluation of *Dicyphus hesperus* for biological control of sweet potato whitefly and potato psyllid on greenhouse tomato. *BioControl*, 61(4), 415-424.
- Campbell Grant, E. H., Lowe, W. H., & Fagan, W. F. (2007). Living in the branches: population dynamics and ecological processes in dendritic networks. *Ecology Letters*, 10(2), 165-175.
- Carter, M. C., Sutherland, D., & Dixon, A. F. G. (1984). Plant structure and the searching efficiency of coccinellid larvae. *Oecologia*, 63(3), 394-397.
- Castillo Carrillo, C. I., Fu, Z., Jensen, A. S., & Snyder, W. E. (2016). Arthropod pests and predators associated with bittersweet nightshade, a noncrop host of the potato psyllid (Hemiptera: Triozidae). *Environmental Entomology*, 45(4), 873-882.
- Cédola, C. V., Sánchez, N. E., & Liljesthröm, G. G. (2001). Effect of tomato leaf hairiness on functional and numerical response of *Neoseiulus californicus* (Acari: Phytoseiidae). *Experimental & Applied Acarology*, 25(10-11), 819-831.
- Cédola, C. V., & Sánchez N. E. (2003). Effect of tomato pubescence on development, survival and fecundity of *Tetranychus urticae* Koch and *Neoseiulus californicus* (McGregor) (Acari: Tetranychidae, Phytoseiidae). *Acarologia*, 3, 255-260.
- Cerna, E., Ail, C., Landeros, J., Sánchez, S., Badii, M., Aguirre, L., & Ochoa, Y. (2012). Comparación de la toxicidad y selectividad de insecticidas para la plaga

- Bactericera cockerelli* y su depredador *Chrysoperla carnea*. *Agrociencia*, 46(8), 783-793.
- Chambers, R. J., Long, S., & Helyer, N. L. (1993). Effectiveness of *Orius laevigatus* (Hem.: Anthocoridae) for the control of *Frankliniella occidentalis* on cucumber and pepper in the UK. *Biocontrol Science and Technology*, 3(3), 295-307.
- Chávez, E. C., Bautista, O. H., Flores, J. L., Uribe, L. A., & Fuentes, Y. M. O. (2015). Insecticide-resistance ratios of three populations of *Bactericera cockerelli* (Hemiptera: Psylloidea: Triozidae) in regions of northern Mexico. *Florida Entomologist*, 98(3), 950-953.
- Choudhury, D. A. M., & Copland, M. J. W. (2003). Influence of plant structural complexity on the searching behaviour of the egg parasitoid *Anagrus atomus* (Linnaeus) (Hymenoptera: Mymaridae). *Pakistan Journal of Biological Sciences*, 6(5), 455-460.
- Chow, A., Chau, A., & Heinz, K. M. (2008). Compatibility of *Orius insidiosus* (Hemiptera: Anthocoridae) with *Amblyseius (Iphiseius) degenerans* (Acari: Phytoseiidae) for control of *Frankliniella occidentalis* (Thysanoptera: Thripidae) on greenhouse roses. *Biological Control*, 44(2), 259-270.
- Chow, A., Chau, A., & Heinz, K. M. (2010). Compatibility of *Amblyseius (Typhlodromips) swirskii* (Athias-Henriot) (Acari: Phytoseiidae) and *Orius insidiosus* (Hemiptera: Anthocoridae) for biological control of *Frankliniella occidentalis* (Thysanoptera: Thripidae) on roses. *Biological Control*, 53(2), 188-196.
- Clark, T. L., & Messina, F. J. (1998). Plant architecture and the foraging success of ladybird beetles attacking the Russian wheat aphid. *Entomologia Experimentalis et Applicata*, 86(2), 153-161.
- Cloyd, R. A., & Sadof, C. S. (2000). Effects of plant architecture on the attack rate of *Leptomastix dactylopii* (Hymenoptera: Encyrtidae), a parasitoid of the citrus mealybug (Homoptera: Pseudococcidae). *Environmental Entomology*, 29(3), 535-541.
- Cocuzza, G. E., De Clercq, P., Lizzio, S., Van De Veire, M., Tirry, L., Degheele, D., & Vacante, V. (1997). Life tables and predation activity of *Orius laevigatus* and *O. albidipennis* at three constant temperatures. *Entomologia Experimentalis et Applicata*, 85(3), 189-198.

- Coll, M., & Ridgway, R. L. (1995). Functional and numerical responses of *Orius insidiosus* (Heteroptera: Anthocoridae) to its prey in different vegetable crops. *Annals of the Entomological Society of America*, 88(6), 732-738.
- Coll, M., Smith, L. A., & Ridgway, R. L. (1997). Effect of plants on the searching efficiency of a generalist predator: the importance of predator-prey spatial association. *Entomologia Experimentalis et Applicata*, 83(1), 1-10.
- Colomer, I., Aguado, P., Medina, P., Heredia, R. M., Fereres, A., Belda, J. E., & Viñuela, E. (2011). Field trial measuring the compatibility of methoxyfenozide and flonicamid with *Orius laevigatus* Fieber (Hemiptera: Anthocoridae) and *Amblyseius swirskii* (Athias-Henriot) (Acari: Phytoseiidae) in a commercial pepper greenhouse. *Pest Management Science*, 67(10), 1237-1244.
- Colton, T. F. (1987). Extending functional response models to include a second prey type: an experimental test. *Ecology*, 68(4), 900-912.
- Cortesero, A. M., Stapel, J. O., & Lewis, W. J. (2000). Understanding and manipulating plant attributes to enhance biological control. *Biological Control*, 17(1), 35-49.
- Crosslin, J. M., & Bester, G. (2009). First Report of ‘*Candidatus Liberibacter psyllaureus*’ in Zebra Chip Symptomatic Potatoes from California. *Plant Disease*, 93(5), 551-551.
- Crosslin, J. M., Munyaneza, J. E., Brown, J. K., & Liefting, L. W. (2010). A history in the making: potato zebra chip disease associated with a new psyllid-borne bacterium a tale of striped potatoes. *APSnet Features*, 110, 2010.
- Dai, H., Wang, Y., Du, Y., & Ding, J. (2010). Effects of plant trichomes on herbivores and predators on soybeans. *Insect Science*, 17(5), 406-413.
- Davidson, M. M., Nielsen, M. C., Butler, R. C., & Silberbauer, R. B. (2016). Prey consumption and survival of the predatory mite, *Amblydromalus limonicus*, on different prey and host plants. *Biocontrol Science and Technology*, 26(5), 722-726.
- De Clercq, P., Mohaghegh, J., & Tirry, L. (2000). Effect of Host Plant on the Functional Response of the Predator *Podisus nigrispinus* (Heteroptera: Pentatomidae). *Biological Control*, 18(1), 65-70.
- de Lourdes Ramírez-Ahuja, M., Rodríguez-Leyva, E., Lomeli-Flores, J. R., Torres-Ruiz, A., & Guzmán-Franco, A. W. (2017). Evaluating combined use of a parasitoid and a zoophytophagous bug for biological control of the potato psyllid, *Bactericera cockerelli*. *Biological Control*, 106, 9-15.

- Deligeorgidis, P. N. (2002). Predatory effect of *Orius niger* (Wolff) (Hem., Anthocoridae) on *Frankliniella occidentalis* (Pergande) and *Thrips tabaci* Lindeman (Thysan., Thripidae). *Journal of Applied Entomology*, 126(2-3), 82-85.
- Diaz-Montano, J., & Trumble, J. T. (2013). Behavioral responses of the potato psyllid (Hemiptera: Triozidae) to volatiles from dimethyl disulfide and plant essential oils. *Journal of Insect Behavior*, 26(3), 336-351.
- Echegaray, E. R., Vinchesi, A. C., Rondon, S. I., Alvarez, J. M., & McKinley, N. (2016). Potato psyllid (Hemiptera: Triozidae) response to insecticides under controlled greenhouse conditions. *Journal of Economic Entomology*, 110(1), 142-149.
- Economou, L. P., Lykouressis, D. P., & Barbetaki, A. E. (2006). Time allocation of activities of two heteropteran predators on the leaves of three tomato cultivars with variable glandular trichome density. *Environmental Entomology*, 35(2), 387-393.
- Eigenbrode, S. D., Moodie, S., & Castagnola, T. (1995). Predators mediate host plant resistance to a phytophagous pest in cabbage with glossy leaf wax. *Entomologia Experimentalis et Applicata*, 77(3), 335-342.
- Eigenbrode, S. D., Castagnola, T., Roux, M. B., & Steljes, L. (1996). Mobility of three generalist predators is greater on cabbage with glossy leaf wax than on cabbage with a wax bloom. *Entomologia Experimentalis et Applicata*, 81(3), 335-343.
- Eigenbrode, S. D. (2004). The effects of plant epicuticular waxy blooms on attachment and effectiveness of predatory insects. *Arthropod Structure & Development*, 33(1), 91-102.
- Eisner, T., Eisner, M., & Hoebeke, E. R. (1998). When defense backfires: detrimental effect of a plant's protective trichomes on an insect beneficial to the plant. *Proceedings of the National Academy of Sciences*, 95(8), 4410-4414.
- El-Basha, N. A., Salman, M. S., & Osman, M. A. (2012). Functional response of *Orius albidipennis* (Hemiptera: Anthocoridae) to the two-spotted spider Mite *Tetranychus urticae* (Acari: Tetranychidae). *Journal of Entomology*, 9, 248-256.
- Environmental Protection Authority. (2016). *An application to release Tamarixia triozae as a biological control for the tomato potato psyllid (Bactericera cockerelli)*. Retrieved from <https://www.epa.govt.nz/assets/FileAPI/hsno->

- Everson, P. (1980). The relative activity and functional response of *Phytoseiulus persimilis* (Acarina: Phytoseiidae) and *Tetranychus urticae* (Acarina: Tetranychidae): the effect of temperature. *The Canadian Entomologist*, 112(01), 17-24.
- Fathi, S. A. A. (2014). Efficiency of *Orius minutus* for control of *Tetranychus urticae* on selected potato cultivars. *Biocontrol Science and Technology*, 24(8), 936-949.
- Fernández-arhex, V., & Corley, J. C. (2003). The functional response of parasitoids and its implications for biological control. *Biocontrol Science and Technology*, 13(4), 403-413.
- French-Monar, R. D., Patton III, A. F., Douglas, J. M., Abad, J. A., Schuster, G., Wallace, R. W., & Wheeler, T. A. (2010). First report of “*Candidatus Liberibacter solanacearum*” on field tomatoes in the United States. *Plant Disease*, 94(4), 481-481.
- Funderburk, J., Stavisky, J., & Olson, S. (2000). Predation of *Frankliniella occidentalis* (Thysanoptera: Thripidae) in field peppers by *Orius insidiosus* (Hemiptera: Anthocoridae). *Environmental Entomology*, 29(2), 376-382.
- Funderburk, J., Srivastava, M., Funderburk, C., & McManus, S. (2013). Evaluation of imidacloprid and cyantraniliprole for suitability in conservation biological control program for *Orius insidiosus* (Hemiptera: Anthocoridae) in field pepper. *The Florida Entomologist*, 96(1), 229-231.
- Gao, F., Jifon, J., Yang, X., & Liu, T. X. (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 Science*, 16(5), 399-408.
- Gassmann, A. J., & Hare, J. D. (2005). Indirect cost of a defensive trait: variation in trichome type affects the natural enemies of herbivorous insects on *Datura wrightii*. *Oecologia*, 144(1), 62-71.
- Geary, I. J., Merfield, C. N., Hale, R. J., Shaw, M. D., & Hodge, S. (2016). Predation of nymphal tomato potato psyllid, *Bactericera cockerelli* (Šulc) (Hemiptera: Triozidae), by the predatory mite, *Anystis baccarum* L.(Trombidiformes: Anystidae). *New Zealand Entomologist*, 39(2), 110-116.
- Gharalari, A. H., Nansen, C., Lawson, D. S., Gilley, J., Munyaneza, J. E., & Vaughn, K. (2009). Knockdown mortality, repellency, and residual effects of insecticides for

- control of adult *Bactericera cockerelli* (Hemiptera: Psyllidae). *Journal of Economic Entomology*, 102(3), 1032-1038.
- Gingras, D., Dutilleul, P., & Boivin, G. (2002). Modeling the impact of plant structure on host-finding behavior of parasitoids. *Oecologia*, 130(3), 396-402.
- Gingras, D., Dutilleul, P., & Boivin, G. (2003). Effect of plant structure on host finding capacity of lepidopterous pests of crucifers by two *Trichogramma* parasitoids. *Biological Control*, 27(1), 25-31.
- Gingras, D., Dutilleul, P., & Boivin, G. (2008). Effect of plant structure on searching strategy and searching efficiency of *Trichogramma turkestanica*. *Journal of Insect Science*, 8(1), 28.
- Gitonga, L. M., Overholt, W. A., Löhr, B., Magambo, J. K., & Mueke, J. M. (2002). Functional response of *Orius albidipennis* (Hemiptera: Anthocoridae) to *Megalurothrips sjostedti* (Thysanoptera: Thripidae). *Biological Control*, 24(1), 1-6.
- Gomez-Polo, P., Alomar, O., Castañé, C., Riudavets, J., & Agustí, N. (2013). Identification of *Orius* spp. (Hemiptera: Anthocoridae) in vegetable crops using molecular techniques. *Biological Control*, 67(3), 440-445.
- Goolsby, J. A., Adamczyk, J., Bextine, B., Lin, D., Munyaneza, J. E., & Bester, G. (2007). Development of an IPM program for management of the potato psyllid to reduce incidence of zebra chip disorder in potatoes. *Subtropical Plant Science*, 59, 85-94.
- Granados-Echegoyen, C., Pérez-Pacheco, R., Bautista-Martínez, N., Alonso-Hernández, N., Sánchez-García, J. A., Martínez-Tomas, S. H., & Sánchez-Mendoza, S. (2015). Insecticidal effect of botanical extracts on developmental stages of *Bactericera cockerelli* (Sulc) (Hemiptera: Triozidae). *Southwestern Entomologist*, 40(1), 97-110.
- Guédot, C., Horton, D. R., & Landolt, P. J. (2010). Sex attraction in *Bactericera cockerelli* (Hemiptera: Triozidae). *Environmental Entomology*, 39(4), 1302-1308.
- Guédot, C., Horton, D. R., & Landolt, P. J. (2012). Age at reproductive maturity and effect of age and time of day on sex attraction in the potato psyllid *Bactericera cockerelli*. *Insect Science*, 19(5), 585-594.

- Guenther, J., Goolsby, J., & Greenway, G. (2012). Use and cost of insecticides to control potato psyllids and zebra chip on potatoes. *Southwestern Entomologist*, 37(3), 263-270.
- Hamdan, A. J., & Abu-Awad, I. (2007). Effect of host plants on predator prey relationship between predatory bug, *Orius laevigatus* (Fiber) [Hemiptera: Anthocoridae] and tobacco whitefly, *Bemisia tabaci* (Gennadius) [Homoptera: Aleyrodidae]. *An-Najah University Journal for Research*, 21, 86-99.
- Hansen, A. K., Trumble, J. T., Stouthamer, R., & Paine, T. D. (2008). A new huanglongbing species, “*Candidatus Liberibacter psyllaeus*,” found to infect tomato and potato, is vectored by the psyllid *Bactericera cockerelli* (Sulc). *Applied and Environmental Microbiology*, 74(18), 5862-5865.
- Hassell, M. P., Lawton, J. H., & Beddington, J. R. (1977). Sigmoid functional responses by invertebrate predators and parasitoids. *The Journal of Animal Ecology*, 249-262.
- Heitmans, W. R. B., Overmeer, W. P. J., & Van Der Geest, L. P. S. (1986). The role of *Orius vicinus* Ribaut (Heteroptera; Anthocoridae) as a predator of phytophagous and predacious mites in a Dutch orchard. *Journal of Applied Entomology*, 102(1-5), 391-402.
- Henne, D. C., Workneh, F., Wen, A., Price, J. A., Pasche, J. S., Gudmestad, N. C., & Rush, C. M. (2010a). Characterization and epidemiological significance of potato plants grown from seed tubers affected by zebra chip disease. *Plant Disease*, 94(6), 659-665.
- Henne, D. C., Workneh, F., & Rush, C. M. (2010b). Movement of *Bactericera cockerelli* (Heteroptera: Psyllidae) in relation to potato canopy structure, and effects on potato tuber weights. *Journal of Economic Entomology*, 103(5), 1524-1530.
- Hernández-Moreno, S., Pérez-Panduro, A., Lomeli-Flores, J. R., Rodríguez-Leyva, E., Bueno-Aguilar, G., & Tovar, J. C. (2017). Aptitud Biológica de *Tamarixia triozae* Mediada por la Planta Hospedera. *Southwestern Entomologist*, 42(1), 225-236.
- Higgins, C. J. (1992). Western flower thrips (Thysanoptera: Thripidae) in greenhouses: population dynamics, distribution on plants, and associations with predators. *Journal of Economic Entomology*, 85(5), 1891-1903.



- Hodkinson, I. D. (2009). Life cycle variation and adaptation in jumping plant lice (Insecta: Hemiptera: Psylloidea): a global synthesis. *Journal of Natural History*, 43(1-2), 65-179.
- Holling, C. S. (1959). Some characteristics of simple types of predation and parasitism. *The Canadian Entomologist*, 91(7), 385-398.
- Horton, D.R., (2008). Minute pirate bugs (Hemiptera: Anthocoridae). In: Capinera, J.L. (Ed.), *Encyclopedia of Entomology* (2<sup>nd</sup> ed., pp. 2402-2412), Vol. 3. Springer Netherlands.
- Horton, D. R., Cooper, W. R., Munyaneza, J. E., Swisher, K. D., Echegaray, E. R., Murphy, A. F., Rondon, S. I., Wohleb, C. H., Waters, T. D., & Jensen, A. S. (2015). A new problem and old questions: potato psyllid in the Pacific Northwest. *American Entomologist*, 61(4), 234-244.
- Horton, D. R., Lewis, T. M., Garczynski, S. F., Thomsen-Archer, K., & Unruh, T. R. (2016). Morphological and genetic reappraisal of the *Orius* Fauna of the Western United States (Hemiptera: Heteroptera: Anthocoridae). *Annals of the Entomological Society of America*, 109(2), 319-334.
- Jalalizand, A., Modaresi, M., Tabeidian, S. A., & Karimy, A. (2011). Functional response of *Orius niger niger* (Hemiptera: Anthocoridae) to *Tetranychus urticae* (Acari: Tetranychidae): effect of host plant morphological feature. *IPCBEE*, 9, 92-96.
- Jorgensen, N., Butler, R. C., & Vereijssen, J. (2013). Biorational insecticides for control of the tomato potato psyllid. *New Zealand Plant Protection*, 66, 333-340.
- Juliano, S. A. (2001). Nonlinear curve fitting: predation and functional response curves. *Design and Analysis of Ecological Experiments*, 2, 178-196.
- Julious, S. A. (2001), Nonlinear curve fitting: predation and functional response curves, In S. M. Scheiner & J. Gurevitch (Eds.). *Design and Analysis of Ecological Experiment* (pp. 159-182). London, United Kingdom: Chapman and Hall.
- Julious, S. A. (2004). Sample sizes for clinical trials with normal data. *Statistics in Medicine*, 23(12), 1921-1986.
- Kareiva, P., & Sahakian, R. (1990). Tritrophic effects of a simple architectural mutation in pea plants. *Nature*, 345(6274), 433.
- Kennedy, G. G. (2003). Tomato, pests, parasitoids, and predators: tritrophic interactions involving the genus *Lycopersicon*. *Annual Review of Entomology*, 48(1), 51-72.

- Kheradpir, N., Rezapanah, M., Kamali, K. & Fathipour, Y. (2013). Host plant affects the predation and oviposition rate of the predaceous thrips of spider mites, *Scolothrips longicornis*. *Munis Entomology & Zoology*, 8(1): 285-293.
- Kidd, N. A. C., & Jervis, M. A. (2005). Population dynamic. In M. A. Jervis (Ed.), *Insects as Natural Enemies: A Practical Perspective* (pp. 435-523). Dordrecht, the Netherlands: Springer.
- Koller, M., Knapp, M., & Schausberger, P. (2007). Direct and indirect adverse effects of tomato on the predatory mite *Neoseiulus californicus* feeding on the spider mite *Tetranychus evansi*. *Entomologia Experimentalis et Applicata*, 125(3), 297-305.
- Krips, O. E., Kleijn, P. W., Willems, P. E. L., Gols, G. J. Z., & Dicke, M. (1999). Leaf hairs influence searching efficiency and predation rate of the predatory mite *Phytoseiulus persimilis* (Acari: Phytoseiidae). In J. Bruin, L. P. S. Van der Geest, & M. W. Sabelis (Eds.), *Ecology and Evolution of the Acari*, (pp. 389-398). Dordrecht, the Netherlands: Springer.
- Kumar, B., & Mishra, G. (2014). Functional response and predatory interactions in conspecific and heterospecific combinations of two congeneric species (Coleoptera: Coccinellidae). *European Journal of Entomology*, 111(2), 257.
- Lacey, L. A., De La Rosa, F., & Horton, D. R. (2009). Insecticidal activity of entomopathogenic fungi (Hypocreales) for potato psyllid, *Bactericera cockerelli* (Hemiptera: Triozidae): development of bioassay techniques, effect of fungal species and stage of the psyllid. *Biocontrol Science and Technology*, 19(9), 957-970.
- Lacey, L. A., Liu, T. X., Buchman, J. L., Munyaneza, J. E., Goolsby, J. A., & Horton, D. R. (2011). Entomopathogenic fungi (Hypocreales) for control of potato psyllid, *Bactericera cockerelli* (Šulc) (Hemiptera: Triozidae) in an area endemic for zebra chip disease of potato. *Biological Control*, 56(3), 271-278.
- Lattin, J. D. (1999). Bionomics of the Anthocoridae. *Annual Review of Entomology*, 44(1), 207-231
- Lariviere, M. C., & Wearing, C. H. (1994). *Orius vicinus* (Ribaut) (Heteroptera: Anthocoridae), a predator of orchard pests new to New Zealand. *New Zealand Entomologist*, 17(1), 17-21.

- Legrand, A., & Barbosa, P. (2003). Plant morphological complexity impacts foraging efficiency of adult *Coccinella septempunctata* L. (Coleoptera: Coccinellidae). *Environmental Entomology*, 32(5), 1219-1226.
- Lehman, R. S. (1930). Some observations on the life history of the tomato psyllid (*Paratrioza cockerelli* Sulc.) (Homoptera). *Journal of the New York Entomological Society*, 307-312.
- Lester, P. J., & Harmsen, R. (2002). Functional and numerical responses do not always indicate the most effective predator for biological control: an analysis of two predators in a two-prey system. *Journal of Applied Ecology*, 39(3), 455-468.
- Lewis, T. M., & Lattin, J. D. (2010). *Orius* (Heterorhynchus) *vicinus* (Ribaut) (Hemiptera: Heteroptera: Anthracoridae) in western North America, a correction of the past. *Proceedings of the Entomological Society of Washington*, 112(1), 69-80.
- Liefting, L. W., Perez-Egusquiza, Z. C., Clover, G. R. G., & Anderson, J. A. D. (2008). A new 'Candidatus Liberibacter' species in *Solanum tuberosum* in New Zealand. *Plant Disease*, 92(10), 1474-1474.
- Liefting, L. W., Sutherland, P. W., Ward, L. I., Paice, K. L., Weir, B. S., & Clover, G. R. (2009a). A new 'Candidatus Liberibacter' species associated with diseases of solanaceous crops. *Plant Disease*, 93(3), 208-214.
- Liefting, L. W., Weir, B. S., Pennycook, S. R., & Clover, G. R. (2009b). 'Candidatus Liberibacter solanacearum', associated with plants in the family Solanaceae. *International Journal of Systematic and Evolutionary Microbiology*, 59(9), 2274-2276.
- Liu, D., & Trumble, J. T. (2004). Tomato psyllid behavioral responses to tomato plant lines and interactions of plant lines with insecticides. *Journal of Economic Entomology*, 97(3), 1078-1085.
- Liu, D., & Trumble, J. T. (2005). Interactions of plant resistance and insecticides on the development and survival of *Bactericera cockerelli* [Sulc] (Homoptera: Psyllidae). *Crop Protection*, 24(2), 111-117.
- Liu, D., & Trumble, J. T. (2006). Ovipositional preferences, damage thresholds, and detection of the tomato-potato psyllid *Bactericera cockerelli* (Homoptera: Psyllidae) on selected tomato accessions. *Bulletin of Entomological Research*, 96(02), 197-204.
- Liu, D., Trumble, J. T., & Stouthamer, R. (2006a). Genetic differentiation between eastern populations and recent introductions of potato psyllid (*Bactericera*

- cockerelli*) into western North America. *Entomologia Experimentalis et Applicata*, 118(3), 177-183.
- Liu, D., Johnson, L., & Trumble, J. T. (2006b). Differential responses to feeding by the tomato/potato psyllid between two tomato cultivars and their implications in establishment of injury levels and potential of damaged plant recovery. *Insect Science*, 13(3), 195-204.
- Liu, D., & Trumble, J. T. (2007). Comparative fitness of invasive and native populations of the potato psyllid (*Bactericera cockerelli*). *Entomologia Experimentalis et Applicata*, 123(1), 35-42.
- Liu, T. X., Zhang, Y. M., Peng, L. N., Rojas, P., & Trumble, J. T. (2012). Risk assessment of selected insecticides on *Tamarixia triozae* (Hymenoptera: Eulophidae), a parasitoid of *Bactericera cockerelli* (Hemiptera: Triozidae). *Journal of Economic Entomology*, 105(2), 490-496.
- Lundgren, J. G., Wyckhuys, K. A., & Desneux, N. (2009). Population responses by *Orius insidiosus* to vegetational diversity. *BioControl*, 54(1), 135-142.
- MacDonald, F. H., Connolly, P. G., Larsen, N. J., & Walker, G. P. (2015). The voracity of five insect predators on *Bactericera cockerelli* (Sülc) (Hemiptera: Triozidae) (tomato potato psyllid; TPP). *New Zealand Entomologist*, 1-8.
- Madadi, H., Enkegaard, A., Brodsgaard, H. F., Kharrazi-Pakdel, A., Mohaghegh, J., & Ashouri, A. (2007). Host plant effects on the functional response of *Neoseiulus cucumeris* to onion thrips larvae. *Journal of Applied Entomology*, 131(9-10), 728-733.
- Madadi, H., Enkegaard, A., Brodsgaard, H. F., Kharrazi-Pakdel, A., Ashouri, A., & Mohaghegh-Neishabouri, J. (2008). *Orius albidipennis* (Heteroptera: Anthocoridae): Intraguild predation of and prey preference for *Neoseiulus cucumeris* (Acari: Phytoseiidae) on different host plants. *Entomologica Fennica*, 19(1), 32.
- Madadi, H., Enkegaard, A., Brødsgaard, H. F., Kharrazi-Pakdel, A., Ashouri, A., & Mohaghegh-Neishabouri, J. (2009). Interactions between *Orius albidipennis* (Heteroptera: Anthocoridae) and *Neoseiulus cucumeris* (Acari: Phytoseiidae): Effects of host plants under microcosm condition. *Biological Control*, 50(2), 137-142.
- McArdle, B. H., & Lawton, J. H. (1979). Effects of prey-size and predator-instar on the predation of *Daphnia* by *Notonecta*. *Ecological Entomology*, 4(3), 267-275.

- Mahdian, K., Tirry, L., & De Clercq, P. (2007). Functional response of *Picromerus bidens*: effects of host plant. *Journal of Applied Entomology*, 131(3), 160-164.
- Martínez, A. M., Baena, M., Figueroa, J. I., Estal, P. D., Medina, M., Guzmán-Lara, E., & Pineda, S. (2014). Primer registro de *Engytatus varians* (Distant) (Hemiptera: Heteroptera: Miridae) en México y su depredación sobre *Bactericera cockerelli* (Šulc) (Hemiptera: Triozidae): una revisión de su distribución y hábitos. *Acta Zoológica Mexicana*, 30(3), 617-624.
- Martinez, A. M., Chavarrieta, J. M., Morales, S. I., Caudillo, K. B., Figueroa, J. I., Diaz, O., Bujanos, R., Gomez, B., Vinuela, E., & Pineda, S. (2015). Behavior of *Tamarixia triozae* females (Hymenoptera: Eulophidae) attacking *Bactericera cockerelli* (Hemiptera: Triozidae) and effects of three pesticides on this parasitoid. *Environmental Entomology*, 44(1), 3-11.
- Mauchline, N. A., & Stannard, K. A. (2013). Evaluation of selected entomopathogenic fungi and bio-insecticides against *Bactericera cockerelli* (Hemiptera). *New Zealand Plant Protection*, 66, 324-332.
- Messina, F. J., & Hanks, J. B. (1998). Host plant alters the shape of the functional response of an aphid predator (Coleoptera: Coccinellidae). *Environmental Entomology*, 27(5), 1196-1202.
- Montserrat, M., Albajes, R., & Castañé, C. (2000). Functional response of four heteropteran predators preying on greenhouse whitefly (Homoptera: Aleyrodidae) and western flower thrips (Thysanoptera: Thripidae). *Environmental Entomology*, 29(5), 1075-1082.
- Mulatu, B., Applebaum, S. W., & Coll, M. (2006). Effect of tomato leaf traits on the potato tuber moth and its predominant larval parasitoid: a mechanism for enemy-free space. *Biological Control*, 37(2), 231-236.
- Munyaneza, J. E., Goolsby, J. A., Crosslin, J. M., & Upton, J. E. (2007a). Further evidence that zebra chip potato disease in the lower Rio Grande Valley of Texas is associated with *Bactericera cockerelli*. *Subtropical Plant Science*, 59, 30-37.
- Munyaneza, J. E., Crosslin, J. M., & Upton, J. E. (2007b). Association of *Bactericera cockerelli* (Homoptera: Psyllidae) with “zebra chip,” a new potato disease in Southwestern United States and Mexico. *Journal of Economic Entomology*, 100(3), 656-663.
- Munyaneza, J. E., Buchman, J. L., Upton, J. E., Goolsby, J. A., Crosslin, J. M., Bester, G., Godfrey, P. M., & Sengoda, V. G. (2008). Impact of different potato psyllid

- populations on zebra chip disease incidence, severity, and potato yield. *Subtropical Plant Science*, 60, 27-37.
- Munyaneza, J. E., Sengoda, V. G., Crosslin, J. M., Garzón-Tiznado, J. A., & Cardenas-Valenzuela, O. G. (2009a). First report of “*Candidatus Liberibacter solanacearum*” in pepper plants in Mexico. *Plant Disease* 93(10), 1076-1076.
- Munyaneza, J. E., Sengoda, V. G., Crosslin, J. M., Garzón-Tiznado, J. A., & Cardenas-Valenzuela, O. G. (2009b). First report of “*Candidatus Liberibacter solanacearum*” in tomato plants in Mexico. *Plant Disease*, 93(10), 1076-1076.
- Munyaneza, J. E., Sengoda, V. G., Crosslin, J. M., De la Rosa-Lozano, G., & Sanchez, A. (2009c). First report of '*Candidatus Liberibacter psyllaurens*' in potato tubers with Zebra Chip disease in Mexico. *Plant Disease*, 93(5), 552-552.
- Munyaneza, J. E., Crosslin, J. M., & Buchman, J. L. (2009d). Seasonal occurrence and abundance of the potato psyllid, *Bactericera cockerelli*, in South Central Washington. *American Journal of Potato Research*, 86(6), 513.
- Munyaneza, J. E. (2010). Psyllids as vectors of emerging bacterial diseases of annual crops. *Southwestern Entomologist*, 35(3), 471-477.
- Munyaneza, J. E. (2012). Zebra chip disease of potato: biology, epidemiology, and management. *American Journal of Potato Research*, 89(5), 329-350.
- Munyaneza, J. E., Sengoda, V. G., Buchman, J. L., & Fisher, T. W. (2012). Effects of temperature on ‘*Candidatus Liberibacter solanacearum*’ and zebra chip potato disease symptom development. *Plant Disease*, 96(1), 18-23.
- Munyaneza, J. E. (2015). Zebra chip disease, *Candidatus Liberibacter*, and potato psyllid: A global threat to the potato industry. *American Journal of Potato Research*, 92(2), 230-235.
- Nachappa, P., Shapiro, A. A., & Tamborindeguy, C. (2012). Effect of ‘*Candidatus Liberibacter solanacearum*’ on fitness of its insect vector, *Bactericera cockerelli* (Hemiptera: Triozidae), on tomato. *Phytopathology*, 102(1), 41-46.
- Norton, A. P., English-Loeb, G., & Belden, E. (2001). Host plant manipulation of natural enemies: leaf domatia protect beneficial mites from insect predators. *Oecologia*, 126(4), 535-542.
- O’Connell, D. M., Wratten, S. D., Pugh, A. R., & Barnes, A. M. (2012). ‘New species association’ biological control? Two coccinellid species and an invasive psyllid pest in New Zealand. *Biological Control*, 62(2), 86-92.

- O'Neil, R. J. (1989). Comparison of laboratory and field measurements of the functional response of *Podisus maculiventris* (Heteroptera: Pentatomidae). *Journal of the Kansas Entomological Society*, 62(2), 148-155.
- O'Neil, R. J. (1997). Functional response and search strategy of *Podisus maculiventris* (Heteroptera: Pentatomidae) attacking Colorado potato beetle (Coleoptera: Chrysomelidae). *Environmental Entomology*, 26(6), 1183-1190.
- Page-Weir, N. E. M., Jamieson, L. E., Chhagan, A., Connolly, P. G., & Curtis, C. (2011). Efficacy of insecticides against the tomato/potato psyllid (*Bactericera cockerelli*). *New Zealand Plant Protection*, 64, 276-281.
- Parajulee, M. N., Shrestha, R. B., Leser, J. F., Wester, D. B., & Blanco, C. A. (2006). Evaluation of the functional response of selected arthropod predators on bollworm eggs in the laboratory and effect of temperature on their predation efficiency. *Environmental Entomology*, 35(2), 379-386.
- Pervez, A. (2005). Functional responses of coccinellid predators: an illustration of a logistic approach. *Journal of Insect Science*, 5(5), 1-6.
- Pineda, S., Medina, M., Figueroa, J. I., Henry, T. J., Mena, L. V., Chavarrieta, J. M., Gomez, B., Valdez, J. M., Lobit, P., & Martínez, A. M. (2016). Life history, diagnosis, and biological aspects of *Engytatus varians* (Hemiptera: Miridae), a predator of *Bactericera cockerelli* (Hemiptera: Triozidae). *Biocontrol Science and Technology*, 26(8), 1073-1086.
- Prager, S. M., Vindiola, B., Kund, G. S., Byrne, F. J., & Trumble, J. T. (2013a). Considerations for the use of neonicotinoid pesticides in management of *Bactericera cockerelli* (Šulk) (Hemiptera: Triozidae). *Crop Protection*, 54, 84-91.
- Prager, S. M., Vindiola, B., Kund, G. S., Byrne, F. J., & Trumble, J. T. (2013b). An update on resistance and the use of neonicotinoids to manage Zebra Chip and potato psyllids. In F. Workneh & C. M. Rush (Eds.), *Proceedings of the 13th Annual SCRI Zebra Chip Reporting Session* (pp. 72-75). San Antonio, TX.
- Prager, S. M., Butler, C. D., & Trumble, J. T. (2013c). A sequential binomial sampling plan for potato psyllid (Hemiptera: Triozidae) on bell pepper (*Capsicum annum*). *Pest Management Science*, 69(10), 1131-1135.
- Prager, S. M., Esquivel, I., & Trumble, J. T. (2014). Factors influencing host plant choice and larval performance in *Bactericera cockerelli*. *PLoS One*, 9(4), e94047.

- Prager, S., Kund, G., & Trumble, J. (2016). Low-input, low-cost IPM program helps manage potato psyllid. *California Agriculture*, 70(2), 89-95.
- Pugh, A. R., O'Connell, D. M., & Wratten, S. D. (2015). Further evaluation of the southern ladybird (*Cleobora mellyi*) as a biological control agent of the invasive tomato–potato psyllid (*Bactericera cockerelli*). *Biological Control*, 90, 157-163.
- Reynolds, P. G., & Cuddington, K. (2012a). Effects of plant gross morphology on predator consumption rates. *Environmental Entomology*, 41(3), 508-515.
- Reynolds, P. G., & Cuddington, K. (2012b). Effects of Plant Gross Morphology on Predator Searching Behaviour. *Environmental Entomology*, 41(3), 516-522.
- Riddick, E. W., & Simmons, A. M. (2014). Do plant trichomes cause more harm than good to predatory insects? *Pest Management Science*, 70(11), 1655-1665.
- Rogers, D. (1972). Random search and insect population models. *The Journal of Animal Ecology*, 41, 369-383.
- Rojas, P., Rodríguez-Leyva, E., Lomeli-Flores, J. R., & Liu, T. X. (2015). Biology and life history of *Tamarixia triozae*, a parasitoid of the potato psyllid *Bactericera cockerelli*. *BioControl*, 60(1), 27-35.
- Royama, T. (1971). A comparative study of models for predation and parasitism. *Researches on Population Ecology*, 13, 1-91.
- Rudolf, V. H. (2008). Consequences of size structure in the prey for predator–prey dynamics: the composite functional response. *Journal of Animal Ecology*, 77(3), 520-528.
- Rutledge, C. E., & O'Neil, R. J. (2005). *Orius insidiosus* (Say) as a predator of the soybean aphid, *Aphis glycines* Matsumura. *Biological Control*, 33(1), 56-64.
- Schenk, D., & Bacher, S. (2002). Functional response of a generalist insect predator to one of its prey species in the field. *Journal of Animal Ecology*, 71(3), 524-531.
- Secor, G. A., & Rivera-Varas, V. V. (2004). Emerging diseases of cultivated potato and their impact on Latin America. *Revista Latinoamericana de la Papa (Suplemento)*, 1, 1-8.
- Secor, G. A., Rivera, V. V., Abad, J. A., Lee, I. M., Clover, G. R. G., Liefting, L. W., Li, X., & De Boer, S. H. (2009). Association of '*Candidatus Liberibacter solanacearum*' with zebra chip disease of potato established by graft and psyllid transmission, electron microscopy, and PCR. *Plant Disease*, 93(6), 574-583.
- Shipp, J. L., & Wang, K. (2003). Evaluation of *Amblyseius cucumeris* (Acari: Phytoseiidae) and *Orius insidiosus* (Hemiptera: Anthocoridae) for control of



- Frankliniella occidentalis* (Thysanoptera: Thripidae) on greenhouse tomatoes. *Biological Control*, 28(3), 271-281.
- Shipp, J. L., & Wang, K. (2006). Evaluation of *Dicyphus hersperus* (Heteroptera: Miridae) for biological control of *Frankliniella occidentalis* (Thysanoptera: Thripidae) on greenhouse tomato. *Journal of Economic Entomology*, 99(2), 414-420.
- Simmons, A. T., Gurr, G. M., McGrath, D., Nicol, H. I., & Martin, P. M. (2003). Trichomes of *Lycopersicon* spp. and their effect on *Myzus persicae* (Sulzer) (Hemiptera: Aphididae). *Australian Journal of Entomology*, 42(4), 373-378.
- Simmons, A. T., & Gurr, G. M. (2004). Trichome-based host plant resistance of *Lycopersicon* species and the biocontrol agent *Mallada signata*: are they compatible? *Entomologia Experimentalis et Applicata*, 113(2), 95-101.
- Simmons, A. T., & Gurr, G. M. (2005). Trichomes of *Lycopersicon* species and their hybrids: effects on pests and natural enemies. *Agricultural and Forest Entomology*, 7(4), 265-276.
- Skirvin, D. J., & Williams, M. D. C. (1999). Differential effects of plant species on a mite pest (*Tetranychus urticae*) and its predator (*Phytoseiulus persimilis*): implications for biological control. *Experimental & Applied Acarology*, 23(6), 497-512.
- Spitze, K. (1985). Functional response of an ambush predator: *Chaoborus americanus* predation on *Daphnia pulex*. *Ecology*, 938-949.
- Srivastava, M., Funderburk, J., Olson, S., Demirozer, O., & Reitz, S. (2014). Impacts on natural enemies and competitor thrips of insecticides against the western flower thrips (Thysanoptera: Thripidae) in fruiting vegetables. *Florida Entomologist*, 337-348.
- Stewart, C. D., Braman, S. K., & Pendley, A. F. (2002). Functional response of the azalea plant bug (Heteroptera: Miridae) and a green lacewing *Chrysoperla rufilabris* (Neuroptera: Chrysopidae), two predators of the azalea lace bug (Heteroptera: Tingidae). *Environmental Entomology*, 31(6), 1184-1190.
- Stiling, P., & Cornelissen, T. (2005). What makes a successful biocontrol agent? A meta-analysis of biological control agent performance. *Biological Control*, 34(3), 236-246.

- Sütterlin, S., & van Lenteren, J. C. (1997). Influence of Hairiness of *Gerbera jamesonii* Leaves on the Searching Efficiency of the Parasitoid *Encarsia formosa*. *Biological Control*, 9(3), 157-165.
- Symondson, W. O. C., Sunderland, K. D., & Greenstone, M. H. (2002). Can generalist predators be effective biocontrol agents? *Annual Review of Entomology*, 47(1), 561-594.
- Tamayo-Mejía, F., Tamez-Guerra, P., Guzmán-Franco, A. W., Gomez-Flores, R., & Cruz-Cota, L. R. (2014). Efficacy of entomopathogenic fungi (Hypocreales) for *Bactericera cockerelli* (Sulc.) (Hemiptera: Triozidae) control in the laboratory and field. *Southwestern Entomologist*, 39(2), 271-283.
- Tamayo-Mejía, F., Tamez-Guerra, P., Guzmán-Franco, A. W., & Gomez-Flores, R. (2015). Can *Beauveria bassiana* Bals. (Vuill) (Ascomycetes: Hypocreales) and *Tamarixia triozae* (Burks) (Hymenoptera: Eulophidae) be used together for improved biological control of *Bactericera cockerelli* (Hemiptera: Triozidae)? *Biological Control*, 90, 42-48.
- Tamayo-Mejía, F., Tamez-Guerra, P., Guzmán-Franco, A. W., & Gomez-Flores, R. (2016). Developmental stage affects survival of the ectoparasitoid *Tamarixia triozae* exposed to the fungus *Beauveria bassiana*. *Biological Control*, 93, 30-36.
- Tang, S., & Cheke, R. A. (2008). Models for integrated pest control and their biological implications. *Mathematical Biosciences*, 215(1), 115-125.
- Teulon, D. A. J., Workman, P. J., Thomas, K. L., & Nielsen, M. C. (2009). *Bactericera cockerelli*: incursion, dispersal and current distribution on vegetable crops in New Zealand. *New Zealand Plant Protection*, 62, 136-144.
- Teulon, D. A. J., & Hill, M. G. (2015). Responding to the establishment of new pests and diseases: What can be learnt from tomato potato psyllid and *Candidatus Liberibacter solanacearum* in New Zealand. *New Zealand Plant Protection*, 68, 76-84.
- Thinakaran, J., Yang, X. B., Munyaneza, J. E., Rush, C. M., & Henne, D. C. (2015a). Comparative biology and life tables of “*Candidatus Liberibacter solanacearum*”-infected and-free *Bactericera cockerelli* (Hemiptera: Triozidae) on potato and silverleaf nightshade. *Annals of the Entomological Society of America*, 108(4), 459-467.

- Thinakaran, J., Pierson, E. A., Longnecker, M., Tamborindeguy, C., Munyaneza, J. E., Rush, C. M., & Henne, D. C. (2015b). Settling and ovipositional behavior of *Bactericera cockerelli* (Hemiptera: Triozidae) on solanaceous hosts under field and laboratory conditions. *Journal of Economic Entomology*, 108(3), 904-916.
- Thomas, K. L., Jones, D. C., Kumarasinghe, L. B., Richmond, J. E., Gill, G. S. C., & Bullians, M. S. (2011). Investigation into the entry pathway for tomato potato psyllid *Bactericera cockerelli*. *New Zealand Plant Protection*, 64, 259-268.
- Thompson, D. J. (1975). Towards a predator-prey model incorporating age structure: the effects of predator and prey size on the predation of *Daphnia magna* by *Ischnura elegans*. *The Journal of Animal Ecology*, 907-916.
- Timms, J. E., Oliver, T. H., Straw, N. A., & Leather, S. R. (2008). The effects of host plant on the coccinellid functional response: Is the conifer specialist *Aphidecta oblitterata* (L.) (Coleoptera: Coccinellidae) better adapted to spruce than the generalist *Adalia bipunctata* (L.) (Coleoptera: Coccinellidae)? *Biological Control*, 47(3), 273-281.
- Tran, L. T. (2012). *Population phenology, life table and forecasting models of tomato-potato psyllid (Bactericera cockerelli) and the efficiency of a selected natural enemy for its control* (Unpublished doctoral thesis). Lincoln University, Christchurch, New Zealand.
- Van de Veire, M., & Degheele, D. (1992). Biological control of the western flower thrips, *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae), in glasshouse sweet peppers with *Orius* spp. (Hemiptera: Anthocoridae). A comparative study between *O. niger* (Wolff) and *O. insidiosus* (Say). *Biocontrol Science and Technology*, 2(4), 281-283.
- Van de Veire, M., Sterk, G., Van der Staaij, M., Ramakers, P. M. J., & Tirry, L. (2002). Sequential testing scheme for the assessment of the side-effects of plant protection products on the predatory bug *Orius laevigatus*. *BioControl*, 47(1), 101-113.
- Van Haren, R. J. F., Steenhuis, M. M., Sabelis, M. W., & De Ponti, O. D. (1987). Tomato stem trichomes and dispersal success of *Phytoseiulus persimilis* relative to its prey *Tetranychus urticae*. *Experimental & Applied Acarology*, 3(2), 115-121.
- Van Lenteren, J. C., & Woets, J. V. (1988). Biological and integrated pest control in greenhouses. *Annual Review of Entomology*, 33(1), 239-269.

- Van Lenteren, J. C. (2012a). Can recently found Brazilian hemipteran predatory bugs control *Tuta absoluta*? *IOBC-WPRS Bulletin*, 80, 63-67.
- Van Lenteren, J. C. (2012b). The state of commercial augmentative biological control: plenty of natural enemies, but a frustrating lack of uptake. *BioControl*, 57(1), 1-20.
- Van Lenteren, J. C., Bolckmans, K., Köhl, J., Ravensberg, W. J., & Urbaneja, A. (2017). Biological control using invertebrates and microorganisms: plenty of new opportunities. *BioControl*, 1-21.
- Veres, A., Tóth, F., Kiss, J., Fetykó, K., Orosz, S., Lavigne, C., Otto, S., & Bohan, D. (2012). Spatio-temporal dynamics of *Orius* spp. (Heteroptera: Anthocoridae) abundance in the agricultural landscape. *Agriculture, Ecosystems & Environment*, 162, 45-51.
- Verheggen, F. J., Capella, Q., Schwartzberg, E. G., Voigt, D., & Haubruge, E. (2009). Tomato-aphid-hoverfly: a tritrophic interaction incompatible for pest management. *Arthropod-Plant Interactions*, 3(3), 141-149.
- Villanueva, R. T., Esparza-Diaz, G., & Welbourn, C. W. (2016). Phytoseiids as potential natural enemies of potato psyllids in organic potato production in South Texas, USA. *Journal of the Acarological Society of Japan*, 25(1), 137-145.
- Voigt, D., Gorb, E., & Gorb, S. (2007). Plant surface–bug interactions: *Dicyphus errans* stalking along trichomes. *Arthropod-Plant Interactions*, 1(4), 221-243.
- Walker, J. T. S., Hodson, A. J., Wearing, C. H., Bradley, S. J., Shaw, P. W., Tomkins, A. R., Burnip, G. M., Stiefel, H. R., & Batchelor, T. A. (1997). Integrated fruit production for New Zealand pipfruit: evaluation of pest management in a pilot programme. In M. O’Callaghan (Ed.), *Proceedings of the 50<sup>th</sup> NZ Plant Protection Conference* (pp. 258-263). Lincoln, NZ: The New Zealand Plant Protection Society Inc.
- Walker, J. T. S., Wearing, C. H., Bradley, S. J., Shaw, P. W., Burnip, G. M., Tomkins, A. R., Richardson, C., & Hodson, A. J. (1998). Integrated fruit production (IFP) for New Zealand pipfruit: evaluation of pest management recommendations. In M. O’Callaghan (Ed.), *Proceedings of the 51<sup>st</sup> NZ Plant Protection Conference* (pp. 166-172). Hamilton, NZ: The New Zealand Plant Protection Society Inc.

- Walker, G. P., MacDonald, F. H., Larsen, N. J., & Wallace, A. R. (2011). Monitoring *Bactericera cockerelli* and associated insect populations in potatoes in South Auckland. *New Zealand Plant Protection*, 64, 269-275.
- Walker, G. P., MacDonald, F. H., Larsen, N. J., Wright, P. J., & Wallace, A. R. (2013). Sub-sampling plants to monitor tomato-potato psyllid (*Bactericera cockerelli*) and associated insect predators in potato crops. *New Zealand Plant Protection*, 66, 341-348.
- Walker, G. P., MacDonald, F. H., Wright, P. J., Puketapu, A. J., Gardner-Gee, R., Connolly, P. G., & Anderson, J. A. (2015a). Development of action thresholds for management of *Bactericera cockerelli* and Zebra Chip disease in potatoes at Pukekohe, New Zealand. *American Journal of Potato Research*, 92(2), 266-275.
- Walker, P. W., Allen, G. R., Tegg, R. S., White, L. R., & Wilson, C. R. (2015b). The tomato potato psyllid, *Bactericera cockerelli* (Šulc, 1909) (Hemiptera: Trioziidae): a review of the threat of the psyllid to Australian solanaceous crop industries and surveillance for incursions in potato crops. *Austral Entomology*, 54(3), 339-349.
- Wearing, C. H., & Larivière, M. C. (1994). Otago bugs-A windfall for orchardists. *Orchardist of New Zealand (April)*, 54, 58.
- Wearing, C. H., & Colhoun, K. (1999). Development of *Orius vicinus* (Ribaut) (Heteroptera: Anthocoridae) on different prey. *Biocontrol Science and Technology*, 9(3), 327-334.
- Wearing, C. H., & Attfield, B. (2002). Phenology of the predatory bugs *Orius vicinus* (Heteroptera: Anthocoridae) and *Sejanus albisignata* (Heteroptera: Miridae) in Otago, New Zealand, apple orchards. *Biocontrol Science and Technology*, 12(4), 481-492.
- Wearing, C. H., Attfield, B. A., & Colhoun, K. (2010). Biological control of woolly apple aphid, *Eriosoma lanigerum* (Hausmann), during transition to integrated fruit production for pipfruit in Central Otago, New Zealand. *New Zealand Journal of Crop and Horticultural Science*, 38(4), 255-273.
- Wen, A., Mallik, I., Alvarado, V. Y., Pasche, J. S., Wang, X., Li, W., Levy, L., Lin, H., Scholthof, H. B., Mirkov, T. E., Rush, C. M., & Gudmestad, N. C. (2009). Detection, distribution, and genetic variability of 'Candidatus Liberibacter' species associated with zebra complex disease of potato in North America. *Plant Disease*, 93(11), 1102-1115.

- Workman, P. J., & Whiteman, S. A. (2009). Importing *Tamarixia triozae* into containment in New Zealand. *New Zealand Plant Protection*, 62, 412-412.
- Wright, P. J., Gardner-Gee, R., Walker, G. P., & Hedderley, D. I. (2015). Effect of sulphur foliar applications on the tomato-potato psyllid (*Bactericera cockerelli*) in a potato crop. *New Zealand Journal of Crop and Horticultural Science*, 43(1), 59-67.
- Xiao, Y., & Fadamiro, H. Y. (2010). Functional responses and prey-stage preferences of three species of predacious mites (Acari: Phytoseiidae) on citrus red mite, *Panonychus citri* (Acari: Tetranychidae). *Biological Control*, 53(3), 345-352.
- Xu, Y., & Zhang, Z. Q. (2015). *Amblydromalus limonicus*: a “new association” predatory mite against an invasive psyllid (*Bactericera cockerelli*) in New Zealand. *Systematic and Applied Acarology*, 20(4), 375-382.
- Yang, X. B., & Liu, T. X. (2009). Life history and life tables of *Bactericera cockerelli* (Homoptera: Psyllidae) on eggplant and bell pepper. *Environmental Entomology*, 38(6), 1661-1667.
- Yang, X. B., Zhang, Y. M., Hua, L., Peng, L. N., Munyaneza, J. E., Trumble, J. T., & Liu, T. X. (2010a). Repellency of selected biorational insecticides to potato psyllid, *Bactericera cockerelli* (Hemiptera: Psyllidae). *Crop Protection*, 29(11), 1320-1324.
- Yang, X. B., Zhang, Y. M., Hua, L., & Liu, T. X. (2010b). 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. *Journal of Economic Entomology*, 103(5), 1729-1734.
- Yang, X. B., Zhang, Y. M., Henne, D. C., & Liu, T. X. (2013). Life tables of *Bactericera cockerelli* (Hemiptera: Triozidae) on tomato under laboratory and field conditions in southern Texas. *Florida Entomologist*, 904-913.
- Yang, X. B., Campos-Figueroa, M., Silva, A., & Henne, D. C. (2015). Functional response, prey stage preference, and mutual interference of the *Tamarixia triozae* (Hymenoptera: Eulophidae) on tomato and bell pepper. *Journal of Economic Entomology*, 108(2), 414-424.
- Yen, A. L., Madge, D. G., Berry, N. A., & Yen, J. D. (2013). Evaluating the effectiveness of five sampling methods for detection of the tomato potato

psyllid, *Bactericera cockerelli* (Šulc) (Hemiptera: Psylloidea: Triozidae).  
*Australian Journal of Entomology*, 52(2), 168-174.

Zsellér, I. H., & Kiss, E. F. (1999). Control of *Frankliniella occidentalis* and TSWV in capsicum crops in Hungary. *EPPO Bulletin*, 29(1-2), 63-67.