

Lincoln University Digital Thesis

Copyright Statement

The digital copy of this thesis is protected by the Copyright Act 1994 (New Zealand).

This thesis may be consulted by you, provided you comply with the provisions of the Act and the following conditions of use:

- you will use the copy only for the purposes of research or private study
- you will recognise the author's right to be identified as the author of the thesis and due acknowledgement will be made to the author where appropriate
- you will obtain the author's permission before publishing any material from the thesis.

**Population phenology, life table and forecasting models of
tomato-potato psyllid (*Bactericera cockerelli*) and the efficiency of
a selected natural enemy for its control**

A thesis submitted in partial fulfillment of the
requirements for the Degree of Doctor of Philosophy

at

Lincoln University

by

Luc The Tran

Lincoln University 2012

Scientific publications from this thesis

Chapter 2

Tran, L.T., S.P. Worner, R.J. Hale, and D.A.J. Teulon. 2012. Estimating development rate and thermal requirements of *Bactericera cockerelli* (Hemiptera: Triozidae) reared on potato and tomato by using linear and nonlinear models. *Environ. Entomol.* 41(5): 1190-1198.

Presentations from this thesis

Tran, L.T., and S.P. Worner. 2011. Population phenology of tomato-potato psyllid (TPP) *Bactericera cockerelli* (Homoptera: Psyllidae) and the efficiency of selected natural enemies for its control. Potato Industry R & D Research Committee Meeting, 3rd March 2011, Palmerston North, New Zealand.

Tran, L.T., S.P. Worner, and D.A.J. Teulon. 2011. Temperature related development of tomato and potato psyllid (TPP) (*Bactericera cockerelli*) and predation efficiency of *Orius vicinus*: how to use what we know? Plant Protection Society Mini Symposium Tomato Potato Psyllid and Liberibacter in Solanaceous crops, 11 August Rotorua, New Zealand.

Tran, L.T., and S.P. Worner. 2012. Temperature related development of tomato and potato psyllid (TPP) (*Bactericera cockerelli*) and predation efficiency of *Orius vicinus*: how can we use what we know? Vegetables NZ Conference 18th April 2012, Pukekohe, New Zealand.

Tran, L.T., S.P. Worner, D.A.J. Teulon, G. Walker, and N. Berry. 2012. Population dynamics of tomato-potato psyllid (TPP) (*bactericera cockerelli*). Psyllid Conference: 26th and 27th July 2012 - Ellerslie Events Centre, Auckland, New Zealand.

Tran, L., S. Worner, J. Vereijissen, and D. Teulon. 2012. Population dynamics of tomato and potato psyllid (*Bactericera cockerelli*). SCRI Zebra Chip Annual Reporting Session Oct. 30 – Nov. 2, 2012, San Antonio, TX, USA.

Abstract of a thesis submitted in partial fulfilment of the
requirements for the Degree of Ph.D.

**Population phenology, life table and forecasting models of tomato-potato psyllid
(*Bactericera cockerelli*) and the efficiency of a selected natural enemy for its control**

by

Luc The Tran

The tomato-potato psyllid (TPP), *Bactericera cockerelli* (Sulc) (Hemiptera: Triozidae) is an economically important crop pest that not only causes damage through its feeding but also transmits the bacterium, “*Candidatus Liberibacter solanacearum*”, which causes zebra chip disease in potato. TPP is also associated with psyllid yellows disease of potato, tomato and capsicum. Both zebra chip and psyllid yellows cause significant yield losses, plant mortality, decreased quality, and increased control-related costs. This insect invaded New Zealand in early 2006 and has now spread through most of the country. Laboratory and field experiments were conducted to determine the population development, phenology and life history parameters of the tomato-potato psyllid and to investigate aspects of its control, particularly in relation to using developmental parameters for preliminary forecasting models and investigate the efficacy and impact of a selected natural enemy.

The temperature-dependent development of TPP was studied in the laboratory at seven constant temperatures (from 8 to 31°C) on potato and tomato. Developmental time in days for all stages on both host species were inversely proportional to temperature between 8 and 27°C but increased at 31°C. The lower developmental thresholds for total development of TPP were 7.1°C and 7.5°C reared on potato and tomato, respectively; and thermal constants of 358 and 368 degree days for TPP reared on potato and tomato, respectively. The optimum temperatures of TPP were estimated as 26.9°C and 27.1°C reared on potato and

tomato, respectively. The upper temperature thresholds were estimated as 33.9°C and 34.1°C reared on potato and tomato, respectively.

Life table parameters can be used to compare the population growth potential of this insect on different host plants, under different environmental conditions. These parameters can be used to project the population growth and stage differentiation for decision making for control of this species or for designing future studies on population dynamics. Life table parameters of TPP reared on potato were determined in laboratory conditions at $25 \pm 1^\circ\text{C}$, 50-60% RH, and at a photoperiod of 16:8 (L: D) h. A life table was constructed based on results obtained under unlimited food supply and a natural enemy free environment. The mean developmental periods for the egg stage, nymphal stage, and total development were 6.08, 16.94, and 23.02 days, respectively. The intrinsic rate of increase, the finite rate of increase, the net reproduction rate, the mean generation time, the life expectancy, the doubling time, and the fecundity of TPP were determined. The implications of these findings are discussed.

Orius vicinus (Ribaut) has been reported to predate red spider mite, leafhopper, and thrips and is being investigated as a possible biological control agent for a range of pests in New Zealand. Because *B. cockerelli* is one of the prey of *O. vicinus*, it is of scientific interest to determine its potential for biological control of TPP. The functional response of the adult stage of the predatory bug, *O. vicinus* on egg, nymphal instars 1, 2, 3, 4, and 5 of TPP and its preference for two prey species: TPP (nymphal instars 1 and 2) and western flower thrips, *Frankliniella occidentalis* (Pergande) (nymphal instars 1 and 2), were determined. The resulting data were well described by both Type I and II functional response models for prey eggs and first and second instar nymphs 1-2; and Type II for 3rd, 4th and 5th instar nymphs of TPP. While these results do not suggest that *O. vicinus* could regulate a TPP population under normal circumstances, the research suggests this species may reduce populations below economic threshold under circumstances of inundative release under cover in a glasshouse. The predator may have a greater biocontrol potential if release was timed to attack the eggs and smaller nymphal stages of TPP. The predator had a slight preference for thrips compared to the TPP at high densities of prey combinations, but despite that *O. vicinus* still responded strongly to TPP.

The prediction of the first emergence and peak abundance can help researchers and growers assess insect population development more effectively for the application of

chemical or cultural control measures or make other management decisions. Yellow sticky traps were used to determine the population development and phenology of the TPP over 5 site-years with respect to potato crops and in relation to ambient weather conditions. The relationship between field flight data and accumulated degree days was well described by both the Weibull and bimodal models. However, the bimodal model described the distribution of psyllid flight better than Weibull model. The occurrence of the first peak flight for the 5 site-years was between 722 to 749 degree days (DD) (above 7.1°C lower threshold) from a biofix on 1st November and the second peak occurred from 1189 to 1264 DD after the biofix. Although the bimodal model can provide precise predictions (within 6.6 days) for the first peak of adult psyllids in the field, it may not find practical application in potato crops in New Zealand due to low economic density threshold of this invasive insect species. Therefore, I anticipate improving the model by the incorporation of developmental parameters and events of immature stages of the psyllid based on long term data.

Results in this thesis have provided essential biological data of TPP, such as the developmental rates and life history parameters. These results, along with an evaluation of the functional response of *O. vicinus* and its potential for biological control and preliminary forecasting models, augment the limited existing knowledge of the biology of TPP so that further research and current management of this psyllid species can be better targeted.

Keywords: Tomato-potato psyllid (TPP), *Bactericera cockerelli*, temperature-dependent development, phenology, forecasting model, life table parameters, *Orius vicinus*, functional response, prey preference.

Table of Contents

Abstract.....	i
Table of Contents	iv
List of Tables	viii
List of Figures.....	x
List of Plates	xii
Chapter 1 Introduction.....	1
1.1 Species biology	3
1.2 Developmental studies	7
1.3 Life table analysis	7
1.4 Biological control.....	8
1.4.1 Predation functional responses	9
1.4.2 The role of alternative prey in improving biological control.....	10
1.5 Forecasting models	11
1.6 Summary of objectives.....	12
 Chapter 2 Estimating development rate and thermal requirements of tomato-potato psyllid <i>Bactericera cockerelli</i> (Sulc) (Hemiptera: Triozidae) reared on potato and tomato using linear and nonlinear models.....	 14
2.1 Abstract	15
2.2 Introduction.....	15
2.3 Material and methods.....	16
2.3.1. Plant and insect cultures.....	16
2.3.2 Experiments	17
2.3.3 Temperature - dependent models for egg, nymph, and total development	19

2.3.3.1 Linear modeling	19
2.3.3.2 Nonlinear modeling.....	20
2.3.3.3 Criteria for model selection.....	21
2.3.4 Statistical analysis	22
2.4 Results	22
2.5 Discussion	28

Chapter 3 Life table parameters of tomato-potato psyllid (*Bactericera cockerelli*)

(Hemiptera: Triozidae), feeding on potato under laboratory conditions32

3.1 Abstract	32
3.2 Introduction.....	32
3.3 Material and methods.....	34
3.3.1 Construction of life table	34
3.3.2 Life table parameters and data analysis	35
3.4 Results	36
3.5 Discussion	44

Chapter 4 Functional response of *Orius vicinus* (Heteroptera: Miridae), on tomato-potato psyllid, *Bactericera cockerelli* (Sulc) (Hemiptera: Triozidae) and prey preference between tomato-potato psyllid and western flower thrips, *Frankliniella occidentalis*

(Pergande) (Thysanoptera: Thripidae).....48

4.1 Abstract	48
4.2 Introduction.....	48
4.3 Material and methods.....	51
4.3.1 Insect cultures	51
4.3.2 Experiments	52
4.3.2.1 Functional response of <i>Orius vicinus</i> to TPP	52
4.3.2.2 Prey preference of <i>Orius</i>	52
4.3.3 Data analysis	53
4.3.3.1 Functional response of <i>Orius</i> to TPP	53
4.3.3.2 Prey preference.....	54

4.4 Results	54
4.4.1 Functional response	54
4.4.2 Prey preference	58
4.5 Discussion	60
 Chapter 5 Forecasting models for <i>Bactericera cockerelli</i> (Sulc) (Hemiptera: Triozidae)	
based on degree days in New Zealand.....	63
5.1 Abstract	63
5.2 Introduction.....	63
5.3 Material and methods.....	65
5.3.1 Trapping sites	65
5.3.2 Temperature data.....	66
5.3.3 Forecasting models	66
5.3.4 Parameter estimates.....	68
5.3.5 Validation of models.....	68
5.4 Results	70
5.4.1 Forecasting models	70
5.4.2 Model validation	74
5.5 Discussion	77
 Chapter 6 General discussion	80
6.1 Overview of the study.....	80
6.2 Temperature-dependent development.....	81
6.3 Life table parameters.....	82
6.4 Functional response and prey preference.....	85
6.5 Monitoring	87
6.6 Summary	90
6.7 Recommendations for future research	91
 References.....	93

Acknowledgements	113
-------------------------------	------------

Appendices.....	114
------------------------	------------

Appendix 1	114
------------------	-----

Appendix 2	115
------------------	-----

Appendix 3	117
------------------	-----

Appendix 4	118
------------------	-----

Appendix 5	119
------------------	-----

Appendix 6	120
------------------	-----

Appendix 7	121
------------------	-----

List of Tables

Table 2.1: Mean (\pm SD) development time (days) for egg, nymph and total development of <i>B. cockerelli</i> reared at different temperatures on potato and tomato	23
Table 2.2: Estimated parameters of development rate for describing development of <i>B. cockerelli</i> reared on potato and tomato using linear and nonlinear models.....	24
Table 2.3: Mortality rates (%) of <i>B. cockerelli</i> feeding on potato and tomato under laboratory conditions at different temperatures.....	28
Table 3.1: Pooled life table values for TPP fed on potato under laboratory conditions at $25\pm 1^{\circ}\text{C}$, 60% RH, and 16:8 (L: D) h.....	37
Table 3.2: Development time, adult longevity, pre-oviposition period, and oviposition period of TPP fed on potato under laboratory conditions at $25\pm 1^{\circ}\text{C}$, 60% RH, and 16:8 (L:D) h	40
Table 3.3: Life table parameters of TPP fed on potato under laboratory conditions ($25 \pm 1^{\circ}\text{C}$, RH 50 - 60%, and 16:8 h light: dark).....	41
Table 3.4: Life table (for female) and age-specific fecundity of TPP feeding on potato.....	41
Table 3.5: Summary of some studies related to life history of TPP	46
Table 4.1: Mean number \pm SD of different stages of <i>B. cockerelli</i> killed by adult of <i>O. vicinus</i> under laboratory condition ($25 \pm 1^{\circ}\text{C}$, RH 60%, and 16:8 h light: dark)	55
Table 4.2: Type I and II functional response parameters of <i>O. vicinus</i> predating egg and nymph 1-2 of <i>B. cockerelli</i>	55

Table 4.3: Maximum likelihood estimates (SE) for the logistic regression of proportion of prey eaten by the predator as a function of initial prey densities.....	57
Table 4.4: Coefficients for the attack rate, handling time, and maximum predation rate of <i>O. vicinus</i> feeding on <i>B. cockerelli</i> under laboratory condition ($25 \pm 1^{\circ}\text{C}$, RH 60%, and 16:8 h light: dark).....	57
Table 4.5: Mean \pm (SE) of western flower thrips and TPP consumed by <i>Orius vicinus</i> adults during 24-h experimental period as indicated by Manly's preference index (β) at various densities with an equal number of thrips and TPP.....	59
Table 5.1: Summary of data selected in various locations in New Zealand (from 2009-2012) used to develop and validate models that predict adult TPP trap captures in the field.....	66
Table 5.2: Parameter estimates resulting from Weibull and bimodal analysis of <i>B. cockerelli</i> adults caught in sticky traps at each site. The values in parentheses are standard error (SE) .	71
Table 5.3: Observed and predicted in DD at given adult TPP trap captures of <i>B. cockerelli</i> .	72
Table 5.4: Regression statistics for predicted versus observed adult trap captures for <i>B. cockerelli</i> in different locations.....	74
Table 5.5: Model validations using independent data set (leave-one out cross-validation) by degree day (DD) and day (d) (Early predictions produced positive values and late predictions produced negative values).....	75

List of Figures

Figure 1.1: Three types of functional response curves	10
Figure 2.1: The fit of linear and nonlinear models to development rate data of egg, total nymph (N1-N5) and total development (egg-adult) for <i>B. cockerelli</i> reared on potato leaves as a function of temperature.....	26
Figure 2.2: The fit of linear and nonlinear models to development rate data of egg, total nymph (N1-N5) and total development (egg-adult) for <i>B. cockerelli</i> reared on tomato leaves as a function of temperature.....	27
Figure 3.1: Age specific survivorship (l_x) of TPP fed on potato under laboratory conditions at $25 \pm 1^\circ\text{C}$, 60% RH, and 16:8 (L: D) h.....	38
Figure 3.2: Age specific fecundity (m_x) of TPP fed on potato under laboratory conditions at $25 \pm 1^\circ\text{C}$, 60% RH, and 16:8h (L: D)	39
Figure 4.1: Type I and II functional response of adult <i>O. vicinus</i> feeding on egg and nymph 1-2 of <i>B. cockerelli</i> under laboratory condition ($25 \pm 1^\circ\text{C}$, RH 60%, and 16:8 h light: dark) ..	56
Figure 4.2: Type II functional response of adult <i>O. vicinus</i> feeding on nymph 3-4 and nymph 5 of <i>B. cockerelli</i> under laboratory condition ($25 \pm 1^\circ\text{C}$, RH 60%, and 16:8 h light: dark)	58
Figure 4.3: Manly's preference values for <i>O. vicinus</i> when offered thrips (nymph 1-2) and psyllid (nymph 1-2) simultaneously with various densities but in a prey ratio 1:1	59
Figure 5.1: Number of TPP per trap per week in different locations from 2009-2012	70
Figure 5.2: Observed and predicted cumulated adult trap capture pattern of <i>B. cockerelli</i> using Weibull and bimodal models.....	73

Figure 5.3: Difference between running average temperature and rainfall for each season compared with the average over the three seasons at Pukekohe.....76

Figure 6.1: Degree days available and number of generations of TPP on potato crops at different sites in New Zealand. Degree days are calculated from July 1st89

Figure 6.2: Estimated dates on which each generation (egg to adult) completes for Pukekohe based on accumulated degree days90

Lists of Plates

Plate 1.1: Eggs of TPP on the edge and under side of a leaf (Photo: Whitney Cranshaw, Colorado State University, Bugwood.org).....	4
Plate 1.2: Different colours between nymphal instars of TPP (Photo: Whitney Cranshaw, Colorado State University, Bugwood.org).....	5
Plate 1.3: Clear-winged and cicada in shape (Photo Source: Simon Hinkley & Ken Walker Museum Victoria)	5
Plate 1.4: Psyllid sugar (Photo: Whitney Cranshaw, Colorado State University, Bugwood.org)	6
Plate 2.1: Adult female TPP (Photo: Pest and Diseases Image Library, Bugwood.org)	18
Plate 2.2: Adult male TPP (Photo: Pest and Diseases Image Library, Bugwood.org).....	19

Chapter 1 General Introduction

Biological invasions are not a recent phenomenon. They have occurred over geological and historical time periods where species have shifted their ranges naturally in response to moving land masses, volcanic activity and changing environmental conditions (White *et al.* 2008). However, because of anthropogenic-assisted mobility, the number of invasions and their associated impacts are increasing as species extend their ranges. As well, environmental changes not only allow many species to extend their range but also to exert greater impact through herbivory, predation and competition pressure (White *et al.* 2008). There are many (more than 4300) introduced species (including 90 species of vertebrates, perhaps 2200 species of invertebrates, and more than 2000 species of vascular plants) which have become established in the wild in New Zealand (Beggs 2001). The impacts of these alien invasive species can be particularly severe. For example, according to a New Zealand of Institute of Economic Research study, the damage caused by a recent insect invader, clover root weevil, could cost the economy between \$0.2 billion and \$1 billion annually if it were to spread nationwide (<http://www.biosecurity.govt.nz/media/16-02-06/clover-root-weevil>). Alien invasive species not only threaten the economy due to the impacts on agriculture but also threaten the country's indigenous ecosystems and biodiversity.

Alien invasive species cause three main categories of economic impacts to agriculture and human and animal health. First is the loss in potential economic output, for example, losses in crop production and reductions in domesticated animal and fisheries survival, fitness, and production (Mack *et al.* 2000). Second is the direct cost of combating invasions, including all forms of quarantine, control, and eradication (Mack *et al.* 2000). Third is the cost of combating invasive species that are threats to human health, either as direct agents of disease or as vectors or carriers of disease-causing parasites (Mack *et al.* 2000).

The threat of invasive species to native ecosystems is from predation on native fauna, damage to native plants by herbivores, competition for resources, habitat changes, vectors of disease and pathogens, hybridization, and ultimately extinctions (Mack *et al.* 2000). A New Zealand example of the detrimental impact of invasive species on biodiversity is the effect of two European wasp species that were introduced in 1945 (*Vespula germanica*) and 1970s (*Vespula vulgaris*) (Beggs 2001). These abundant invaders can reduce the standing crop of

honeydew in beech forests by more than 90% and so compete with native birds and invertebrates that also consume the honeydew. New invaders that are highly adaptable can evolve in response to their interactions with native species, as well as in response to the new abiotic environment (Mooney and Cleland 2001). For example, Huey *et al.* (2000) showed that the introduction of a new fruit fly into the west coast of North America resulted in the evolution of an apparently adaptive cline related to wing size. The developmental basis for the cline of wing size was different in the European native populations from the invader in North America.

Bactericera cockerelli (Sulc) (Hemiptera: Triozidae) is a recent invasive species in New Zealand establishing early in 2006 and has now spread through most of the country (Gill 2006, Teulon *et al.* 2009). *Bactericera cockerelli* was originally described as *Trioza cockerelli* by Sulc (1909). In 1910, Crawford established a new psyllid genus *Paratrioza*, and in 1911 *Trioza cockerelli* was assigned to *Paratrioza*. In 1997, Burckhardt and Lauterer changed the genus *Paratrioza* to the genus *Bactericera* as defined by combinations of adult, nymphal and egg characters, and changed the family name from Psyllidae to Triozidae. According to ESA (2012), *Bactericera cockerelli* has two common names: the tomato psyllid and the potato psyllid (Abdullah 2008). In New Zealand, this invasive insect is commonly referred to as tomato-potato psyllid (TPP) (Teulon *et al.* 2009) and this name will be adopted throughout this thesis.

Liu and Trumble (2006) showed that TPP could feed on species in 20 plant families. However, until recently, this homopteran insect was reported as a pest primarily in potato and tomato. TPP is a serious pest of solanaceous crops (Liu and Trumble 2004) and has been reported as a key pest of potato and tomato in many of the growing areas of Western North America (Cranshaw 1993). Both psyllid yellows and zebra chip are associated with TPP (Sengoda 2010). Scientists speculate that psyllid yellows is caused by a toxin injected into the plant by TPP while feeding (Sengoda 2010). However, to date, the nature of the toxin has not been identified (Abernathy 1991, Sengoda 2010). The symptoms of psyllid yellows include retarded growth, erectness of new growth, chlorosis, purpling of leaves, distortion of foliage, and stimulated flower bloom (Liu and Trumble 2006). TPP is also implicated as the primary vector of a recently identified bacterium, new to science. The *Liberibacter* bacterium, '*Candidatus Liberibacter solanacearum*', also known as '*Ca. Liberibacter*

psyllaorous', is reported as the casual agent of zebra chip in potato (Liefting *et al.* 2008, 2009, Hansen *et al.* 2008, Crosslin and Bester 2009, Abad *et al.* 2009). The TPP - Liberibacter complex affects the potato, tomato, capsicum, and tamarillo industries in New Zealand (Thomas *et al.* 2011). It causes significant yield losses, plant mortality, decreased quality of tubers and fruit, and increased control-related costs (Teulon *et al.* 2009). The tomato-potato psyllid and Liberibacter have been responsible for substantial economic losses across a wide geographic range including North America and New Zealand.

The recent arrival and the economic importance of TPP and Liberibacter in New Zealand and interest in the biology and management of these organisms make TPP a very suitable target for fundamental research leading to applied outcomes. Understanding how the lifecycle of pest insect is regulated is essential to studying its population ecology, and for forecasting population development and subsequent management.

1.1 SPECIES BIOLOGY

TPP was first described in 1909 from specimens collected from capsicum growing in a home garden in Colorado (Sulc 1909). Life stages include eggs, five nymphal instars, and adults (Pletsch 1947). In the United States, three to five generations have been recorded on potato crops per year (List 1939a, Pletsch 1947). However, in a favorable year there may be from 8 to 10 generations (Cranshaw 1993). In a very early laboratory study (temperature not specified), the life cycle (egg to adult) of TPP was found to take between 15 and 30 days (Knowlton and Janes 1931). The development and survival of TPP were reported to occur from between 15.5°C and 32.2°C with optimal development occurring at 26.6°C (Mohammad 1999). Temperatures above 30°C markedly reduce larval and adult survival (List 1939b). TPP adults mate more than once and the first mating usually occurs about three days after emergence (Pletsch 1947). Eggs are laid over a period of about 21 days and females can lay up to 500 or so eggs over their lifetime (Pletsch 1947). Eggs are oval in shape and bright yellow to orange in color. The eggs are attached to plant leaves by a stalk and are deposited usually on the edge or underside of the leaves on the upper part of the plants (Plate 1.1). The incubation period varies considerably with temperature but averages about 7 days (Wallis 1955).



Plate 1.1: Eggs of TPP on the edge and under side of a leaf (Photo: Whitney Cranshaw, Colorado State University, Bugwood.org).

The nymph goes through five scale-like stages and Knowlton and James (1931) reported that the psyllid remains a nymph for between 12-21 days but they did not cite any temperature. The nymph is orange to yellow when newly hatched and becomes pale green when mature (Wallis 1955) (see Plate 1.2). The nymph grows to 2mm in length and feeds on the underside of the leaf. Wing buds appear in the third instar and become obvious in the fourth and fifth instars (Pletsch 1947).



Plate 1.2: Different colours between nymphal instars of TPP (Photo: Whitney Cranshaw, Colorado State University, Bugwood.org).



Plate 1.3: Clear wings of TPP adult (Photo Source: Simon Hinkley & Ken Walker Museum Victoria).

The adult psyllid is about 2.1 to 2.5 mm long to the tip of the wings. It is a clear-winged insect resembling a miniature cicada in shape (Plate 1.3). On emerging the adults are light green in colour. After about three days they change to black with white markings which give them a grey appearance. These white markings are distinguishing characteristics of TPP, particularly the broad, transverse white band on the first abdominal segment and the inverted V-shaped white mark on the last abdominal segment (Wallis 1955). When at rest the wings are held in a roof-like position over the abdomen, typical of hemipteran insects (Wallis 1955) (see Plate 1.3). Psyllid feed like aphids and other hemipterans by inserting their stylets into the plant. They suck the sap and excrete the excess water and sugar as honey dew or as a solid waste (psyllid sugar). Psyllid sugar is the visual sign that is most likely observed on the plants (Plate 1.4).



Plate 1.4: Psyllid sugar (Photo: Whitney Cranshaw, Colorado State University, Bugwood.org).

1.2 DEVELOPMENTAL STUDIES

Temperature plays a major regulatory role in growth and development of insects and its influence on the life history of a pest species needs to be quantified to understand the pest's population dynamics (Nahrung *et al.* 2004). Temperature influences the development, survival, reproduction, movement, and dynamics of insects (Huffaker *et al.* 1999, Roy *et al.* 2002). Temperature can act to limit the geographic distribution of a species (Krebs 1994). Species-specific traits, including optimal temperature and lower and upper temperature thresholds are the most important components for biological activities (Golizadeh and Zalucki 2012). Thus, the relationship between temperature and developmental rate is an essential component of population dynamics and its accurate description is important for building phenological models to predict stage specific emergence times or outbreaks, and subsequently to develop sound control strategies (Bentz *et al.* 1991, Liu *et al.* 1995, Lactin *et al.* 1995, Zilahi-balogh *et al.* 2003).

There have been some previous studies (List 1939b, Marin-Jarillo *et al.* 1995, Abdullah 2008, Yang and Liu 2009, Yang *et al.* 2010) on the development of TPP but most of them did not cover the developmental relationship in response to the full range of temperatures. Therefore, developed a more precise description of the thermal characteristics of a population of TPP over a large temperature range (8 - 31°C), as an initial prerequisite to develop a comprehensive integrated pest management for this invasive insect species (Chapter 2).

1.3 LIFE TABLE ANALYSIS

A life table is used to calculate vital statistics (Carey 1993, Southwood 1995, Harari *et al.* 1997, Medeiros *et al.* 2000). It is a useful tool that is often used in biology to, 1) understand patterns and causes of mortality, 2) derive certain measures that help predict the likelihood of future growth or decline of a population, and, 3) provide useful information for managing a population. A life table study of a pest insect allows the analysis of population structure and stability so as to assess the likelihood of outbreak or slow population growth. As well, the information is extremely useful for constructing more detailed population

dynamic models to further understand population growth and decline in relation to environmental changes. Such models can be used to forecast possible population trajectories and to ask ‘what-if’ questions.

Development of a life table for an insect requires knowledge of the rate of development of the insect, age-specific mortality, survival of the original population with time, and age-specific fecundity. To better manage TPP, it is crucial to understand its occurrence and population dynamics under a range of temperatures. Because of time and resources, a life table of TPP at a variety of different temperatures could not be constructed. Instead, the life table parameters of TPP were investigated on potatoes at a temperature close to optimum so that maximal values for key population parameters could be determined. Therefore, Chapter 3 aims to provide the age-specific life table and the life history of TPP on potato plants under optimal laboratory conditions.

1.4 BIOLOGICAL CONTROL

The use of insecticides to control TPP may decimate natural enemy populations which can lead to more severe outbreaks. Furthermore, chemical suppression of TPP populations requires frequent applications of insecticides (Goolsby *et al.* 2007a) with highly variable results (Gharalari *et al.* 2009, Berry *et al.* 2009). In addition, TPP shows increasing resistance to insecticides (Liu and Trumble 2007). Therefore, we cannot rely only on insecticides to manage TPP populations. An integrated management program is an effective and environmentally sensitive as well as sustainable approach to pest management. According to Pedigo and Rice (2006), one of the first assessments that should be made in an integrated pest management program is the potential role of natural enemies in controlling pests. In pest management, natural enemies are clearly of interest because they can limit pest damage. However, little is known about potential biological control agents available for TPP except pathogenic fungi (Sanchez-Pena *et al.* 2007, Lacey *et al.* 2009, 2011). Investigations of potential biological control agents for TPP are very important. There are some generalist predators including lady beetles, *Hippodamia convergens*, and green lacewing that have been identified for control of TPP but none has provided useful levels of suppression of this insect pest in the field (Mohammad 1999, Liu and Trumble 2007). While considerable effort is

currently being put into the importation the parasitoid *Tamarixia triozae* (Burks) (Hymenoptera: Eulophidae) as a biological control for TPP in New Zealand (Workman and Whiteman 2009, Workman and Walker 2009), here I investigated *O. vicinus*, a potential natural enemy, to determine its potential to reduce TPP populations of glasshouse crops primarily through predation and prey preference.

The predatory mirid bug, *O. vicinus* (Ribaut) (Heteroptera: Miridae) was selected to test in this thesis because of the following reasons:

1. This predator has a wide range of prey (Wearing and Colhoun 1999) and is a general predator with prey species reported that include bark lice, psyllids, thrips, aphids, and leafhoppers (Lewis and Lattin 2010).

2. *O. vicinus* was sourced easily and kindly supplied by John Thompson - Bioforce Ltd Drury, New Zealand.

1.4.1 Predation functional responses

Some predators are quite specialized and feed on only one or a few closely related prey species, but most predators are more generalized and feed on a variety of similar organisms (Flint and Dreistadt 1998). Predators of economic importance in the control of insect pests include beetles (Coleoptera), bugs (Hemiptera), flies (Diptera), lacewings (Neuroptera), and wasps (Hymenoptera) (Flint and Dreistadt 1998). An important characteristic to assess the efficiency of a predator is its consumption response to changes in prey density. A predator consumption response to changes in prey density is described as the predator's functional response (Holling 1959, 1966) defined by the quantitative relationship between the number of prey consumed per predator and the prey density. The functional response of a predator to changes in prey density is a key factor in the population dynamics of predator-prey systems and in natural control of pest populations (Berryman 1992). The functional response can determine if a predator is able to regulate the density of its prey (Schenk and Bacher 2002). It has been used to infer the basic mechanisms underlying the interactions of predator-prey behaviour, to enhance practical predictive power for biological control, and even to clarify co-evolutionary relationships (Fan and Pettitt 1994). The predator consumption-prey density relationship includes three types of functional response: Type I, a

linear rise to a plateau; Type II, a curvilinear rise to a plateau; and Type III, a sigmoid curve rising to a plateau (Fig. 1.1).

Arthropod predators typically display one of these three typical functional responses, but the response may vary with crop phenology, habitat heterogeneity, age of predator, and other biotic and abiotic factors (Parajulee *et al.* 2006). In a Type I functional response, the number of prey killed increases linearly at a constant rate (proportion) up to a maximum and remains constant as prey density further increases (Parajulee *et al.* 2006); the satiation threshold (Fig. 1.1). In a Type II functional response, the number of prey killed approaches an asymptote hyperbolically as prey density increases (declining proportion of prey killed or inverse density dependence) (Fig. 1.1). A Type III functional response (Parajulee *et al.* 2006) occurs when the number of prey killed at low prey densities approaches a sigmoid function (increase in proportion of prey killed up to inflection point and then a decrease in proportion to an upper asymptote). The first part of the curve represents the density-dependent response (Fig. 1.1). The second (or upper) part of the curve after the inflection point is the same as a Type II response. Type III response is thought to be the only response where it is possible for the predator to regulate a prey population (Fernandez- Arhex and Corley 2003). In other words the predators need to remove an increasing proportion of the prey in order to check the prey population growth.

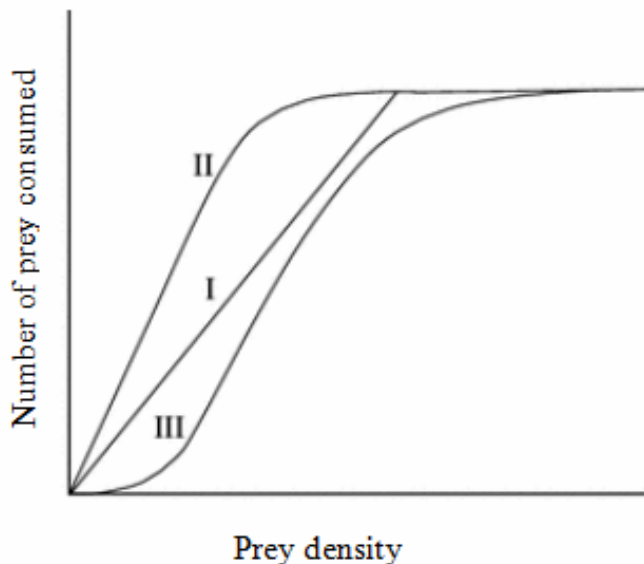


Figure 1.1: Three types of functional response curves.

1.4.2 The role of alternative prey in improving biological control

Most predators not only feed on a single prey species but exploit diverse prey species and are therefore involved in a complex web of interactions (Strauss 1991). The capture and consumption of alternative prey reduce the amount of time spent encountering the focal prey (Chesson 1989). If the predator has no preference for either the focal or alternative species, indirect effects occur between the two prey species depending on their local abundance. An increased abundance of prey A may relax predation on prey B; conversely, a decrease in prey A density may result in intensified predation on prey B (and *vice versa*) (Tschanz *et al.* 2007). However, any preference for a particular prey displayed by a predator directly affects the control efficiency of its various different prey species (Xu and Enkegaard 2009).

Therefore, Chapter 4 examines the functional response of *O. vicinus* feeding on TPP and prey preference of *O. vicinus* between TPP (focal prey) and western flower thrips (alternative prey).

Unfortunately it is more difficult to control invasive species by natural enemies because the enemy-release hypothesis states that invasive species are more successful in the new region of invasion than in their native region due to the absence of co-evolved natural enemies (Corlay *et al.* 2007). The aim of Chapter 4 was to investigate the effectiveness of *O. vicinus* as a predator so that its potential to limit the TPP population can be assessed to design sustainable controls of this serious invasive species.

1.5 FORECASTING MODELS

If an integrated pest management approach to controlling TPP is to be successful then precise timing of spray applications against TPP is crucial as many recommended insecticides are only efficient at certain stages of an insect's development. More precise timing reduces costs and the potential for resistance development as well as supports sustainable or integrated pest management practices. As monitoring and observing population development is time consuming, a robust timing model would assist growers to better time both monitoring and control measures. For example, knowing when the pest is likely to first appear and the time of its peak abundance could help growers to be more

prepared and to more precisely assess insect population development for the application of chemical or cultural control measures. It is for this reason that, forecasting models have been developed for many insects (Collier and Finch 2001). Many of these models are based on accumulated degree days (e.g. Eckenrode and Chapman 1972, Butts and McEwen 1981, Wold and Hutchison 2003, Schaub *et al.* 2005, Skinner *et al.* 2006, Damos and Savopoulou-Soultani 2010). Degree day models in particular can play an important role in integrated pest management by providing a simple means of predicting insect development, and therefore providing more precise timing for implementation of control activities. Modeling invader dynamics and management options also facilitates the search for the best management strategy as models help summarize relevant known aspects of a pest's biology and ecology, highlight uncertainties, and assess and prioritize potential control strategies through 'computer experiments' for field testing (Shea *et al.* 2006). Models also allow us to ask questions that are hard or even impossible to answer in the field (Shea *et al.* 2006). Thus it is clear that modeling approaches, if used correctly, can save valuable time and resources and therefore this is the focus of Chapter 5.

1.6 SUMMARY OF OBJECTIVES

In summary, this PhD aims to:

- 1) Determine important developmental parameters that describe population growth of *B. cockerelli* in relation to temperature.
- 2) Determine important life history parameters of *B. cockerelli* feeding on potatoes under laboratory conditions.
- 3) Determine the efficacy of a selected natural enemy, *O. vicinus*, for regulation of *B. cockerelli* population by laboratory experiments. With respect to predation in particular, one hypothesis was tested: that alternative prey reduces the functional response of predators to target prey.
- 4) Develop and compare forecasting models based on the relationship between the psyllid and climate to predict population phenology, seasonal timing and potential abundance.

The psyllid colonies used in all experiments throughout this thesis were considered to be free of *Candidatus Liberibacter* (Drayton pers. comm. Plant & Food Research, New Zealand).

Chapter 2 Estimating development rate and thermal requirements of tomato-potato psyllid *Bactericera cockerelli* (Sulc) (Hemiptera: Triozidae) reared on potato and tomato using linear and nonlinear models

The contents of this Chapter were published in a journal article; Tran, L.T., S.P. Worner, R.J. Hale, and D.A.J. Teulon. 2012. Estimating development rate and thermal requirements of *Bactericera cockerelli* (Hemiptera: Triozidae) reared on potato and tomato by using linear and nonlinear models. Environ. Entomol. 41(5): 1190-1198.

2.1 ABSTRACT

The temperature-dependent development of tomato-potato psyllid (TPP), *Bactericera cockerelli*, was studied in the laboratory at seven constant temperatures (8, 10, 15, 20, 23, 27, 31°C) with relative humidity of 50-60% and a photoperiod of 16L: 8D h on leaves of whole potato and tomato plants. Developmental time in days for immature stages and total development (egg to adult) on both host species were inversely proportional to temperature between 8 and 27 °C but increased at 31 °C. One linear and two nonlinear models were fitted to the data. The lower developmental thresholds, calculated using the linear model for egg, total nymph, and total development (from oviposition to adult emergence) were 7.9, 4.2, and 7.1 °C (reared on potato) and 7.2, 5.3, and 7.5 °C (reared on tomato), respectively. The thermal constant (K) for total development was 358 (reared on potato), and 368 (reared on tomato) degree days (DD). Two nonlinear models, Briere and Lactin fit the data well as measured by goodness-of-fit criteria, the residual sum of square (RSS) and Akaike information criterion (AIC). Temperature threshold parameters for these nonlinear models (T_0 , T_{opt} , and T_{max}) were estimated for eggs, total nymphal stages, and total developmental time (egg to adult). The Briere model is recommended for predicting optimum and upper temperature thresholds, while the linear model provided the most sensible prediction of the lower temperature threshold. Results from this study will provide basic information on the biology of TPP and have potential for the development of predictive models of the seasonal progress of this invasive pest.

2.2 INTRODUCTION

The tomato-potato psyllid (TPP) (*Bactericera cockerelli*) is a key insect pest of potato and tomato in many of the growing areas of western North America. This insect is also a recent invasive species in New Zealand, having established in early 2006. It has now spread through most of the country (Teulon *et al.* 2009). Even though this psyllid has been reported to feed on species from 20 plant families (Liu and Trumble 2006), it is best known as a pest of potato and tomato. In North America it is commonly known as the potato or tomato psyllid (Abdullah 2008) whereas in New Zealand it is known as the tomato-potato psyllid (TPP) (Teulon *et al.* 2009).

The recent arrival and the economic importance of TPP in New Zealand, its importance as a pest in North America, and current interest in the biology and management of the newly identified *Liberibacter* bacterium that it vectors, make this insect a very suitable target for fundamental research to support applied outcomes. Understanding how the lifecycle of this pest insect progresses, in relation to environmental factors such as temperature, is essential for understanding its population ecology, and forecasting population events on which to base subsequent management decisions (Nylin 2001). It is well known that temperature plays a major regulatory role in growth and development of insects and its influence on the life history of a pest species needs to be quantified so that models can be used to provide more precise predictions of the timing of population dynamics (Nahrung *et al.* 2004). Modeling both the pest dynamics as well as possible management options can facilitate the search for the best management strategy (Godfray & Waage 1991, Rees & Paynter 1997, Shea & Kelly 1998, Shea *et al.* 1998, Buckley *et al.* 2005, Shea *et al.* 2005, Shea *et al.* 2006). A number of previous studies have been carried out to characterize the development of TPP. A study by List (1939) on TPP development indicated that a temperature of 26.6°C was most favorable for psyllid development and survival but that larval and adult survival is low above 30°C. Another study by Marin-Jarillo *et al.* (1995) concluded that the lower developmental threshold of TPP is 7.0°C. In addition, Mohammad (1999) indicated that development and survival were low below 15.5°C. Apart from these disparate studies, little further work has been attempted to determine the full developmental relationship of TPP in response to temperature on different hosts. Because this species has

begun to invade regions of the world and appears to threaten others, there is a clear need for a more detailed study of TPP development on different varieties and crops to assist greater preparedness.

The objective of this Chapter was to determine the effect of selected constant temperatures on the development rate of the eggs, nymphs, and total development (egg to adult) of TPP on potato and tomato plants to determine the full development rate-temperature relationship. The development rate-temperature relationship can then be used to estimate the important developmental parameters, the lower and upper developmental thresholds, optimum temperature for development, and a thermal constant (degree days) for each stage. Determination of the developmental parameters of the psyllid will allow the use of a model or models for prediction of the occurrence of important life stages such that more timely and effective management actions can be carried out.

2.3 MATERIAL AND METHODS

2.3.1 Plant and insect cultures

Tomato (Yates 'Moneymaker') and potato plants ('Agria'- a common potato variety grown in New Zealand) were used in this study. The tomato seeds were germinated in trays and after about 2 weeks the seedlings transplanted into plastic pots used for growing the plants. Potatoes were grown from seed tubers. Tomato and potato plants were used individually (one plant per pot) in all experiments. All potted plants were watered three times a week.

Colonies of TPP used for this study came from Plant & Food Research, Lincoln-Canterbury, New Zealand. All TPP were reared on potted tomato seedlings in cages (50W x 45L x 60H cm) in a controlled temperature (CT) room ($25 \pm 1^\circ\text{C}$, RH 50- 60%, and 16:8 h light: dark). Five tomato plants were placed in each clean rearing cage and colonies were initiated by placing psyllids on to the plants using a fine-tipped paintbrush. The colonies, eventually comprising up to 300-500 insects, were illuminated by overhead lights (TL-D LIFEMAX 30W/865 Cool Daylight).

The psyllid colonies used in experiments were considered to be free of *Candidatus Liberibacter* (Drayton pers. comm. Plant & Food Research, New Zealand). All adult psyllids used in all experiments and developmental bioassays were standardized by selection of insects with teneral coloration (light or pale green) indicating that they had emerged within the previous 2-3 days (Knowlton and James 1931).

2.3.2 Experiments

Egg, nymph and adult development times were determined at constant temperatures of 8°C, 10°C, 15°C, 20°C, 23°C, 27°C, and 31°C (± 1). A humidity of approximately 50-60% and constant photoperiod of 16:8 L: D were maintained at each temperature. Approximately equal numbers of males and females (100-200 in total) were selected and placed on 10 tomato or potato plants in separate cages. Males and females were distinguished by the shape of the apex of the abdomens (Abdullah 2008). The mature female abdomen, which terminates with a short ovipositor, is well rounded and more robust than the male abdomen (Plate 2.1 and 2.2). After 24 hours, plants with more than 20 eggs were selected for the experiments. On each plant the number of eggs was reduced to 20. Three plants for each plant species, each with 20 eggs, were placed in each of two constant temperature cabinets at the same temperature, comprising two replicates of 60 psyllid eggs for each temperature investigated.

Eggs and nymphs were checked daily and the position of each nymph was recorded to follow individual development. Frequent transfer to fresh plant material was required as host plant quality declined rapidly at the low and high part of the temperature range. Because of the high mortality caused by the frequent transfer of very small insects onto fresh plant material, only those insects able to complete development to adult were included in the analysis. Developmental times and rates for all psyllids that completed development to adult were recorded and averaged for each replicate constant temperature cabinet at each temperature.

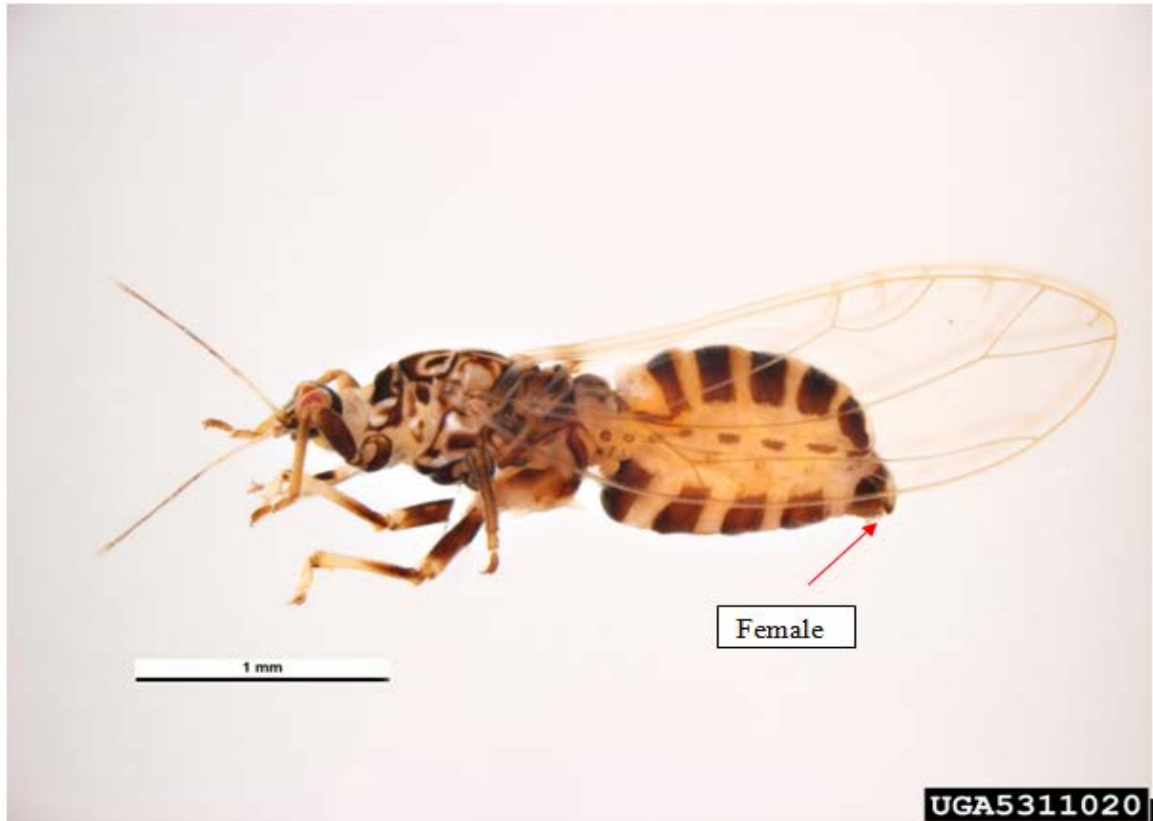


Plate 2.1: Female TPP adult (Photo: Pest and Diseases Image Library, Bugwood.org).

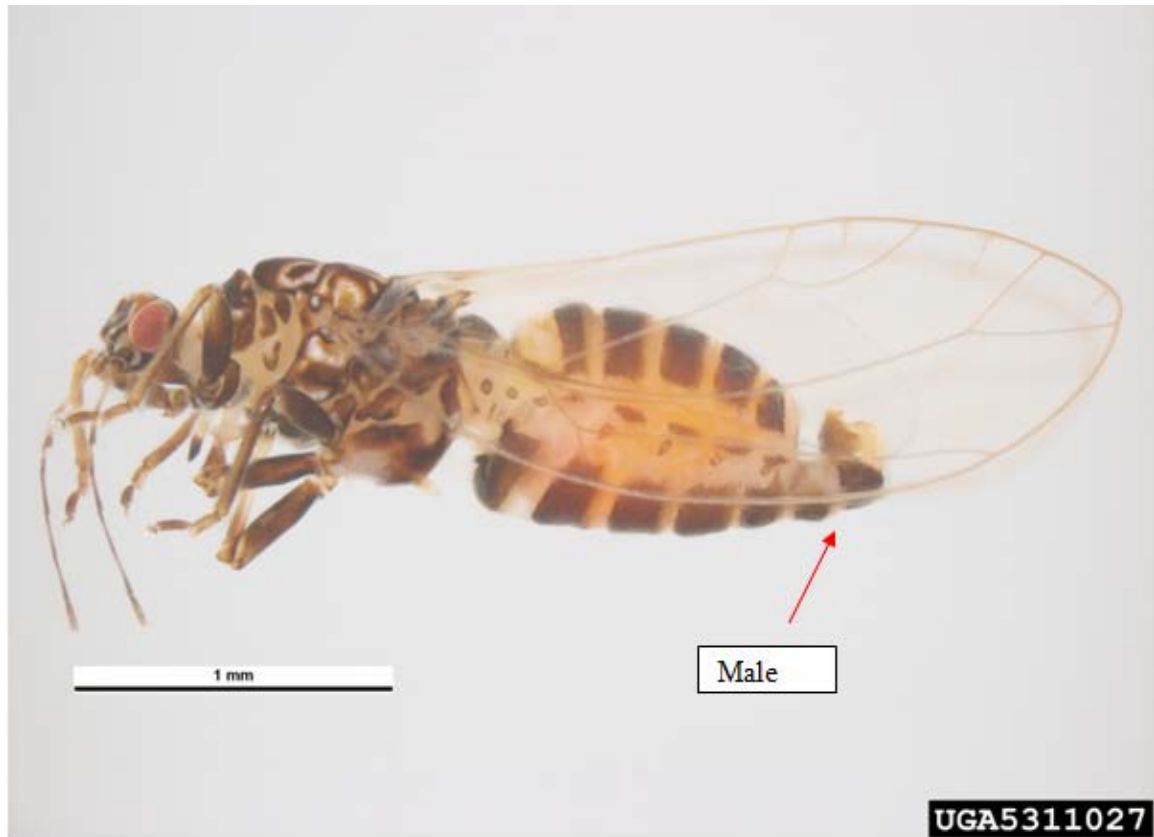


Plate 2.2: Male TPP adult (Photo: Pest and Diseases Image Library, Bugwood.org).

2.3.3 Temperature-dependent models for egg, nymph, and total development

The development rate curves for all stages of psyllid development were clearly nonlinear (Figs. 2.1 and 2.2). Two types of models, linear and nonlinear, were used to estimate important developmental parameters.

2.3.3.1 Linear modeling

First, a linear model was fitted to the data that fell within the linear portion of the development rate curve (Figs. 2.1 and 2.2), to estimate a lower threshold for development (T_0) and thermal constant in degree days (DD). I chose a linear model because both T_0 and the thermal constant derived from the linear development rate model are widely used for insect phenology prediction (Worner 1992). Other considerations for using the linear model as a parsimonious approach to modeling species phenology for practical application were, 1)

both linear and non-linear development rate models can be sensitive to the temperature variability and profile of a particular site and neither approach has been adequately shown to outperform the other under all conditions, especially in oceanic climates (Worner 1988), 2) nonlinear model performance under fluctuating conditions can be variable (Worner 1992), and 3) there is no evidence that a single nonlinear model is better than any other under all circumstances, especially under field conditions.

Estimation of the lower threshold for development and thermal constant was based on linear regressions for egg, nymph, and total development over the linear range of psyllid development versus temperature. The developmental rate (1/development time in days) vs temperature relationship can be described by a linear equation $y = a + bx$, where y is development rate (1/days), x is temperature, a is the intercept and b is the slope. The lower temperature threshold for development (T_0) was estimated by solving the equation for development rate (y) = 0 (in other word $T_0 = -a/b$). The number of degree-days (DD) required for complete development (the thermal constant K) was estimated by $1/b$ (Campbell *et al.* 1974, Worner 1988, Nahrung *et al.* 2008).

To fit the linear model, observed developmental rates at low and high temperatures were constrained because of the sensitivity of the slope parameter to nonlinearity. Fitting a straight line to unconstrained data or non-linear portion of the curve could result in unrealistic estimates (Lamb 1992, Bergant and Trdan 2006, Walgama and Zalucki 2006). Even slight nonlinearity around the optimum temperature will result in a slope that can give an inaccurate lower threshold and thermal constant. In this study, nonlinearity resulted in an unrealistic low or negative lower threshold and thermal constant for each life stage. Data were constrained to the linear portion of the curve by constraining data at low and high temperatures to maximize the coefficient of determination R^2 that is a measure of the variability accounted for by a straight line. The coefficient of determination is also a measure of the quality of fit of the linear regression to the data (Zar 1999).

2.3.3.2 Nonlinear modeling

Along with the lower threshold for development, the optimal and maximal temperatures for development make up the three cardinal temperatures for the species

(Régnière and Logan 2003). Because the optimal and maximal temperatures are useful for modeling both insect phenology and population dynamics, two nonlinear models were fitted to the unconstrained data to estimate these parameters. A number of nonlinear models of developmental rate as a function of temperature have been proposed over the decades (Stinner *et al.* 1974, Logan *et al.* 1976, Sharpe and DeMichele. 1977, Lamb 1992, Lactin *et al.* 1995, Briere *et al.* 1999). These models involve mathematical expressions of varying complexity but several different models have been reported in recent studies as being useful descriptors of insect development. However preliminary testing revealed that only two nonlinear models, the Lactin *et al.* (1995) and the Briere *et al.* (1999) were fitted with development for all stages of TPP. Therefore, these two models were selected to estimate the upper temperature threshold and the optimum temperature for development of TPP.

The formulae of two models are as follows:

$$y = e^{px} - e^{[pT_m - (T_m - x)/\Delta T]} + \lambda$$

Lactin (1995)

Where x is rearing temperature ($^{\circ}\text{C}$), p , T_m , ΔT , and λ are fitted parameters. The optimum temperature for development is determined by the formula: $T_{\text{opt}} = [\Delta T * \log_e(\Delta T * p) / (1 - \Delta T * p)] + T_m$ (Ramalho *et al.* 2009)

$$y = ax(x - T_0)(T_{\text{max}} - x)^{1/2}$$

Briere (1999)

Where x is the rearing temperature ($^{\circ}\text{C}$), a is an empirical constant, T_0 is the lower development threshold; T_{max} is the lethal temperature threshold. The optimum temperature is calculated by the formula: $T_{\text{opt}} = [4 T_{\text{max}} + 3 T_0 + (16 T_{\text{max}}^2 + 9 T_0^2 - 16 T_0 T_{\text{max}})^{1/2}] / 10$ (Briere *et al.* 1999, Grout and Stoltz 2007).

2.3.3.3 Criteria for model selection

The following criteria were used to assess the performance of each model. First, the model should describe the data accurately. Therefore, the residual sum of squares (RSS), coefficient of determination (R^2) and the Akaike information criterion (AIC) were used to evaluate the goodness of fit (Haghani *et al.* 2009). A good model must explicitly include higher values of R^2 and smaller values of RSS (Roy *et al.* 2002, Kontodimas *et al.* 2004) and

AIC. While the coefficient of determination R^2 was used to assess goodness of fit and determine maximum linearity in linear regression, it was not used to discriminate between models with different numbers of parameters simply because models with more parameters will always provide a better fit (Haghani *et al.* 2009). Instead, the AIC, an independent parameter (Vucetich *et al.* 2002), was used; defined as:

$$AIC = n \ln (SSE/n) + 2P$$

Where n is the number of observations and P is the number of model parameters including the intercept, and SSE is the sum of squares for the model error term. Second, the model should allow estimation of parameters with biological significance (Briere *et al.* 1999, Roy *et al.* 2002, 2003, Haghani *et al.* 2009). The models investigated here allowed the estimation of key biological parameters of development which are the lower temperature threshold, the optimal temperature, and the high temperature threshold (Roy *et al.* 2002).

2.3.4 Statistical analysis

The effect of temperature on development time on different hosts was analyzed using the Tukey multiple comparison procedure (Zar 1999). Model fitting and parameter estimation were conducted using linear and nonlinear regression functions in R (R Version 2.9.2). The optimal temperature, the lower temperature threshold, and the high temperature threshold were numerically evaluated from the parameter estimates in those models where no analytical values were available (Smits *et al.* 2003).

2.4 RESULTS

Mean developmental time of all surviving eggs, nymphs (all instars combined), and total development (from oviposition to adult emergence) at constant temperatures on two different host plants (tomato and potato) are shown in Table 2.1. On both plant species, the developmental durations of all immature stages and total development decreased in relation to temperature as it increased from 8°C to around 27°C. Thereafter the developmental times started to increase for all stages. There were few significant differences ($p < 0.05$) between the developmental duration of the different life stages of TPP when reared on potato and

tomato at each temperature (Table 2.1). The developmental times for TPP reared on tomato were in general longer than on potato for total development and the immature stages. For example, at 8°C the total development of TPP reared on potato required 90.3 days while it took 97.8 days on tomato.

Table 2.1: Mean (\pm SD) development time (days) for egg, nymph and total development of *B. cockerelli* reared at different temperatures on potato and tomato.

Temp	Duration time in days					
	Egg		Nymph		Total (egg-adult)	
	Potato	Tomato	Potato	Tomato	Potato	Tomato
8°C	32.15 \pm 2.91Aa	33.89 \pm 2.52Aa	58.15 \pm 1.07Aa	63.56 \pm 1.13Ab	90.31 \pm 2.78Aa	97.78 \pm 2.59Ab
10°C	29.04 \pm 1.52Ba	29.22 \pm 3.07Ba	38.09 \pm 4.68Ba	45.33 \pm 4.23Bb	67.13 \pm 5.07Ba	74.56 \pm 3.04Bb
15°C	17.96 \pm 1.22Ca	19.3 \pm 1.91Cb	29.04 \pm 2.36Ca	32.15 \pm 1.96Cb	47.00 \pm 3.12Ca	51.45 \pm 3.22Cb
20°C	7.34 \pm 1.33DFa	7.26 \pm 1.80Da	19.17 \pm 1.77Da	20.14 \pm 2.54Da	26.51 \pm 2.66Da	27.40 \pm 3.86Da
23°C	6.28 \pm 1.95EDa	7.02 \pm 1.22Db	16.85 \pm 3.03EGa	17.71 \pm 1.57Ea	23.21 \pm 2.92Ea	24.69 \pm 2.43Eb
27°C	5.91 \pm 1.44Ea	6.7 \pm 1.59Db	15.23 \pm 2.30EFa	15.41 \pm 1.55Fa	21.11 \pm 2.25Fa	22.08 \pm 2.54Fa
31°C	6.38 \pm 0.96EFa	6.78 \pm 1.26Da	19.13 \pm 1.26DGa	19.33 \pm 1.19DEa	25.5 \pm 1.67DEa	26.11 \pm 1.7DEa

Means within the same temperature and the same insect stage followed by the same small letter are not significantly different. Means followed by the same capital letter on the same plant in the same column are not significantly different ($P < 0.05$, TukeyHSD).

Table 2.2: Estimated parameters of development rate for describing development of *B. cockerelli* reared on potato and tomato using linear and nonlinear models.

		<i>B. cockerelli</i> reared on potato			<i>B. cockerelli</i> reared on tomato		
	Parameter	Total	Egg	Nymph	Total	Egg	Nymph
Linear	a	-0.019927 (0.004883)	-0.085194 (0.03274)	-0.0134082 (0.0143392)	-0.0204283 (0.0063)	-0.06769 (0.021632)	-0.0169813 (0.0072)
	b	0.002792 (0.00025)	0.010791 (0.001849)	0.0032194 (0.00073)	0.0027174 (0.00032)	0.009373 (0.001222)	0.0032313 (0.00037)
	T ₀	7.1	7.9	4.2	7.5	7.2	5.3
	K	358	98.1	310	368	107	309
	R ²	0.97	0.85	0.83	0.95	0.90	0.95
	AIC	-53.9	-32.06	-40.98	-50.9	-38.69	-49.24
	RSS	0.000016	0.004	0.00014	0.0000267	0.00176	0.000035
Briere	a	0.0000225 (0.0000023)	0.00011 (0.000025)	0.000025 (0.000006)	0.0000216 (0.0000024)	0.000084 (0.0000155)	0.000027 (0.0000035)
	T ₀	-2.04 (1.91)	4.1 (3.001)	-8.4 (5.9)	-1.54 (1.992)	1.74 (2.67)	-4.59 (2.71)
	T _{max}	33.91 (0.44)	33.9 (1.177)	34.0 (0.89)	34.13 (0.515)	34.6 (1.06)	34.13 (0.5578)
	T _{opt}	26.9	27.5	26.4	27.1	27.8	26.9
	R ²	0.98	0.89	0.92	0.98	0.94	0.97
	AIC	-126.94	-59.9	-100.22	-126.3	-74.7	-115.34
	RSS	0.000053	0.0064	0.00036	0.000056	0.00223	0.0001224

(Continued on next page)

Table 2.2 (*continued*)

		<i>B. cockerelli</i> reared on potato			<i>B. cockerelli</i> reared on tomato		
	Parameter	Total	Egg	Nymph	Total	Egg	Nymph
Lactin	p	0.00214 (0.000159)	0.008136 (0.001541)	0.00266 (0.00036)	0.002059 (0.000177)	0.007811 (0.002055)	0.0026 (0.000147)
	T _m	40.16 (3.5476)	37.87 (7.92)	38.51 (5.47)	40.688 (4.479)	43.56 (10.76)	36.54 (3.1597)
	ΔT	2.351 (0.9677)	2.45 (3.05)	2.0974 (1.615)	2.4233 (1.193)	4.463 (4.576)	1.4892 (0.8752)
	λ	-1.00752 (0.0023)	-1.048783 (0.02435)	-1.00318 (0.0055)	-1.007745 (0.002546)	-1.044 (0.0219)	-1.00562 (0.002398)
	T ₀	3.5	5.9	1.2	3.7	5.6	2.2
	T _{opt}	27.6	28.0	27.6	27.8	28.0	28.2
	T _{max}	33.6	33.9	33.2	33.8	36.4	32.7
	R ²	0.98	0.88	0.92	0.97	0.93	0.97
	AIC	-125.74	-58.46	-100.25	-123.37	-70.73	-121.42
	RSS	0.00005	0.0062	0.000312	0.0000598	0.00257	0.0000687

The value in parentheses is the standard error (SE) for each parameter.

One linear and two nonlinear models were used to determine the relationship between developmental rate and temperature. These models fitted the data of the current study well, as evidenced by high values of R² and small values of RSS and AIC (Table 2.2). The linear model (Figures 2.1 (a) and 2.2 (a)) was used to estimate a lower temperature threshold and thermal constant. Table 2.2 shows the lower threshold temperatures of egg, nymph, and total development that are 7.9, 4.2, and 7.1°C, respectively (reared on potato) and 7.2, 5.3, and 7.5°C, respectively (reared on tomato). The two nonlinear models, Briere (1999) and Lactin (1995), were used to estimate optimum temperatures (T_{opt}) and upper temperature threshold (T_{max}) for development of total and immature stages of TPP on the two host plants (Table 2.2). The optimal temperature and upper temperature threshold estimated by the two nonlinear models were nearly identical (Table 2.2). However, differences were found at the estimations of lower threshold for the three models. The Briere (1999) estimates for the

lower threshold were much lower than estimates from the linear and Lactin (1995) models except for the egg stage when reared on potato (Table 2.2).

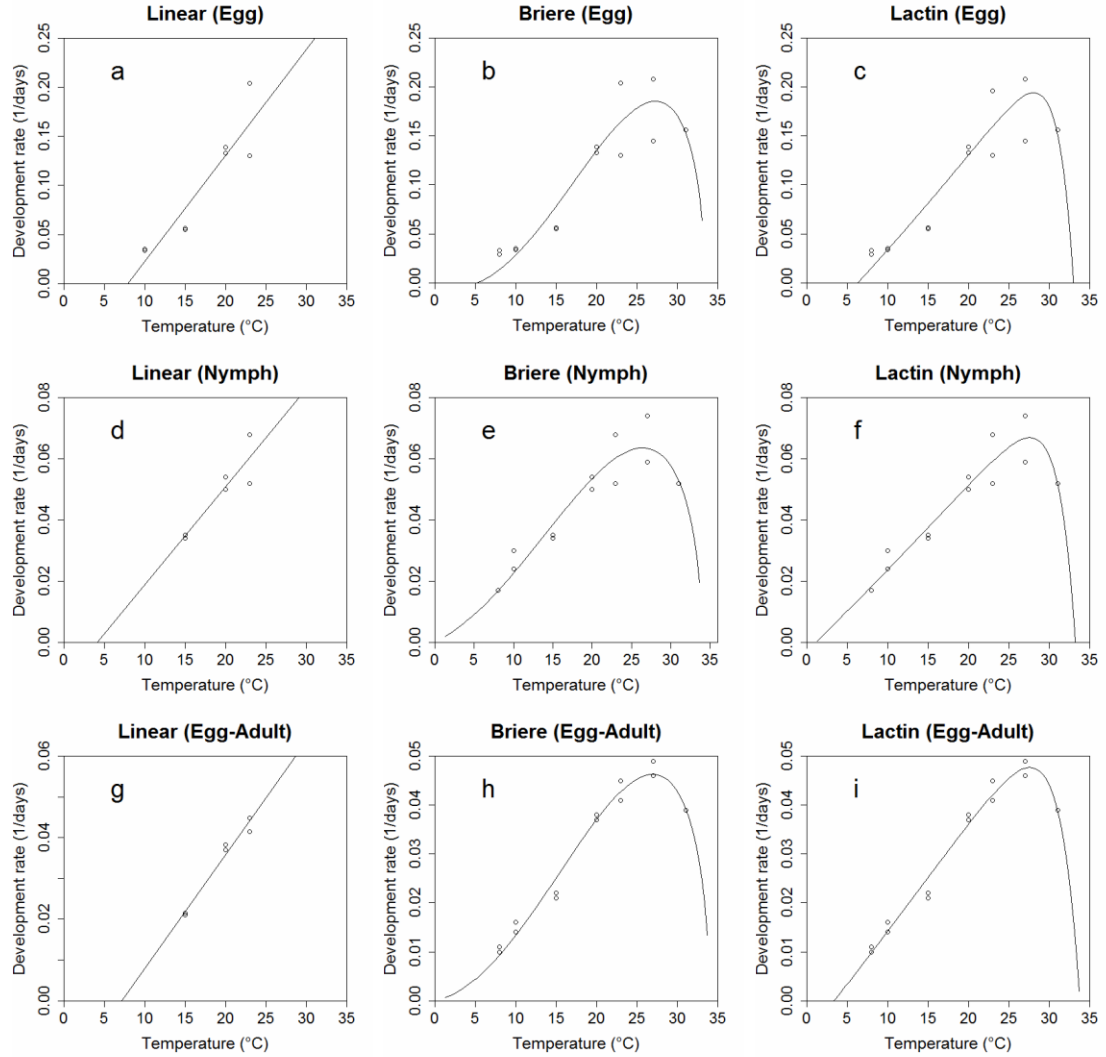


Figure 2.1: The fit of linear and nonlinear models to development rate data of egg, total nymph (N1-N5) and total development (egg-adult) for *B. cockerelli* reared on potato leaves as a function of temperature.

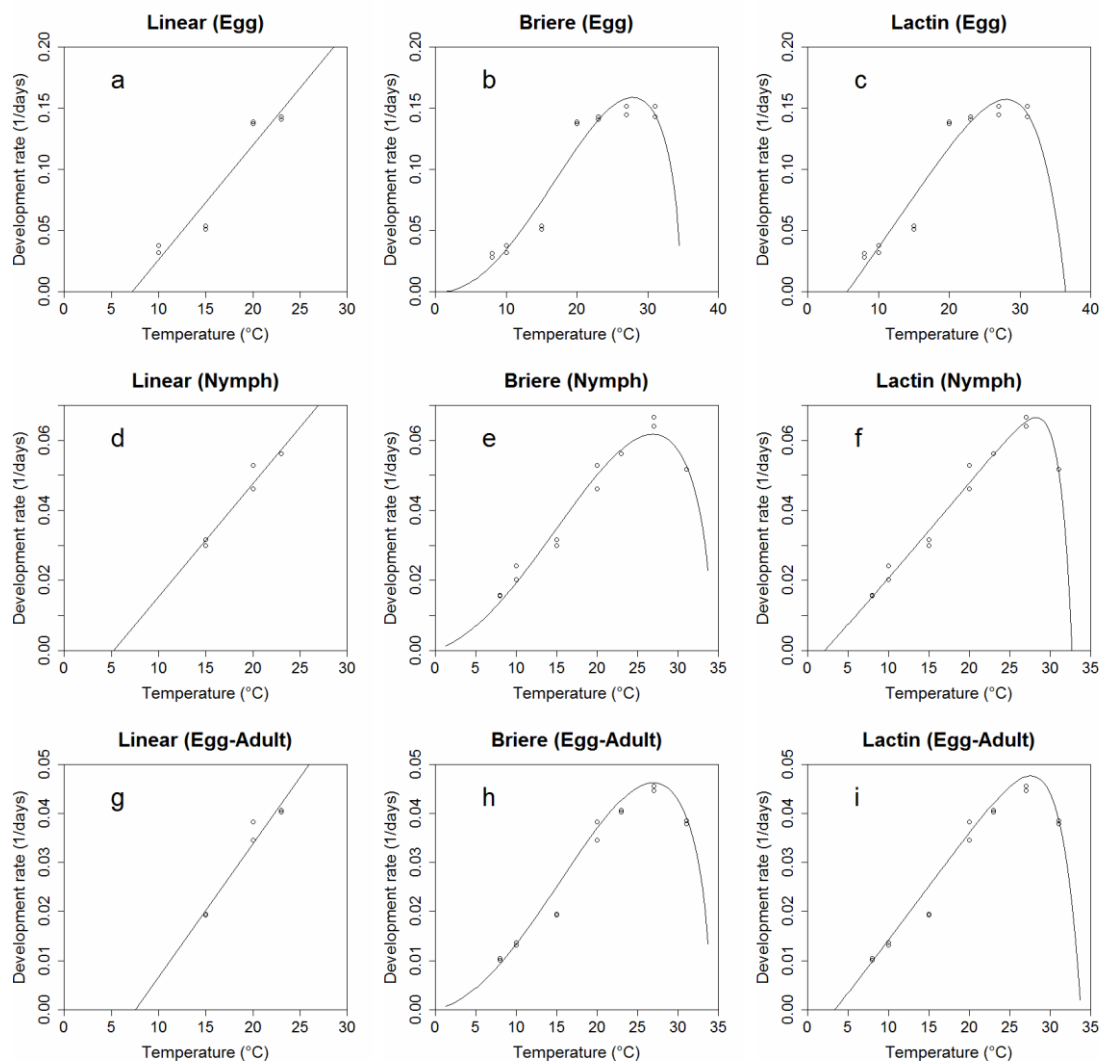


Figure 2.2: The fit of linear and nonlinear models to development rate data of egg, total nymph (N1-N5) and total development (egg-adult) for *B. cockerelli* reared on tomato leaves as a function of temperature.

There were very high mortality rates of TPP found at 8°C and 31°C on both host plant species (Table 2.3). At 8°C, *B. cockerelli* could complete their life cycle but had extremely high mortality rates; 93% when feeding on tomato and 89% when feeding on potato.

Table 2.3: Mortality rates (%) of *B. cockerelli* feeding on potato and tomato under laboratory conditions at different temperatures.

Temperatures	Mortality rates (%) (Sample size n =120)						
	8°C	10°C	15°C	20°C	23°C	27°C	31°C
Potato	89	81	81	71	67	63	87
Tomato	93	78	67	64	59	58	85

2.5 DISCUSSION

The aim of this Chapter was to estimate important developmental parameters to be used to forecast TPP population phenology in the field. High mortality was caused by the repeated transfer of the very small psyllids to fresh plant material necessitated by the rapid decline in plant quality at the low and high part of the temperature range. Every attempt was made to keep mortality of TPP to a minimum. The juvenile stages are somewhat flattened and scale-like and difficult to remove from a leaf. However, studies of development of TPP at the optimum temperature range report mortalities very similar to what was found in this study. For example, Yang and Liu (2009) reported 50% mortality from egg to adult for TPP reared on eggplant at 27°C and 66% reared on bell pepper. Abdullah (2008) reported 60% mortality for TPP reared on tomato at 26-27° C. Also, Yang *et al.* (2010) reported 47% mortality on potato at 26.7° C. To my knowledge no study reports TPP mortality at temperatures lower than 16°C. Because of the high mortality, average developmental rates of TPP able to complete development to adult for each constant temperature were used to fit both linear and nonlinear developmental rate curves. There was considerable variability as well as nonlinearity in developmental rates at low (8 and 10°C) and at high temperatures (27 and 31°C) as shown in Fig. 2.1 (b, c, e, f, h, i) and 2.2 (b, c, e, f, h, i). The lower threshold for development and the thermal constant or degree days for complete development of the target stage are both highly sensitive to the accuracy of developmental rate measured near the optimal temperature. In addition to this variability, high mortality at the low and high ends of the temperature range gave clear justification to constrain the developmental data and use only the linear part of the developmental relationship to estimate the linear parameters (Lamb

1992, Bergant and Trdan 2006, Walgama and Zalucki 2006). Many authors suggest that any evaluation of the accuracy of the lower developmental threshold should be based on its comparison with experimental results (Jalali *et al.* 2010, Walgama and Zalucki 2006, Kontodimas *et al.* 2004). Table 2.3 shows very high mortality of TPP (89% reared on potato and 93% reared on tomato) at 8°C in this study. While high mortality occurred partly at low and also high temperature for the reasons discussed, both laboratory and field observation suggested that a lower threshold of approximately 7°C is close to where development no longer occurs. There is only one other study (Marin-Jarillo *et al.* 1995) that investigated lower temperature development for TPP. This study estimated the lower temperature threshold to be about 7°C for the complete life cycle (egg to adult) which is confirmed in this study, although it is not clear what developmental rate model they used to estimate the lower temperature threshold. The most favorable temperature for development and survival of TPP reported by List (1939) is 26.6°C. The List (1939) estimate is only slightly lower than that estimated by two nonlinear models in this study, which was 26.9°C and 27.1°C by the Briere and 27.6°C and 27.8°C by the Lactin when reared on potato and tomato, respectively.

Some studies also use the Briere and Lactin models to estimate the lower developmental threshold (Roy *et al.* 2002, Aghdam *et al.* 2009, Jalali *et al.* 2010, Sandhu *et al.* 2010, Arbab and McNeill 2011) in the hope that accounting for nonlinearity will give greater accuracy. Accounting for nonlinearity at lower temperatures is particularly valid, especially if it is a true reflection of underlying physiological processes (Sharpe & deMichele 1977). However, a number of researchers suggest that nonlinearity in development rates may be caused by factors other than temperature such as a genetic effect (Lamb 1992), or differential mortality at low temperatures and/or low temperature affecting food quality (Campbell *et al.* 1974, Lamb 1992). No matter whether applying a nonlinear or linear model to estimate a lower developmental threshold, extrapolation from the observed development rates at low temperatures tends to occur. Lamb (1992) suggested that even if any or all of the exogenous effects discussed above are true, extrapolation of the linear curve is still likely to give a good approximation of the average lower threshold for the population. Lamb (1992) also suggested that it is useful for practical purposes (as opposed to theoretical purposes) to have a single value or lower threshold point close to where development no longer occurs. In several studies, nonlinear models have been fitted to developmental data to confirm the lower

temperature threshold derived from a linear regression (Roy *et al.* 2002, Aghdam *et al.* 2009, Jalali *et al.* 2010). In this study, the two nonlinear models, especially the Briere model, failed to correctly estimate the lower temperature threshold for any developmental stages of TPP giving unrealistically low and often negative values. Despite this, based on a comparison with experimental data for evaluating the accuracy of estimating critical temperatures suggested by Kontodimas *et al.* (2004), these nonlinear models were successfully used to estimate the optimal and upper threshold temperatures. For both host plant species, the values for T_{opt} generated by the Lactin model were slightly higher than those estimated by the Briere model in most cases (Table 2.2). However, the T_{max} values from the Briere model tended to be a little higher than those generated by the Lactin model except for egg stage reared on tomato (T_{max} estimated by Lactin and Briere models were 36.4 and 34.6 respectively). Overall, the Briere model fitted the data slightly better with more negative AIC values (Anderson 2008, p.60), lower RSS for most life stages of TPP, and a higher or equal R^2 compared with the Lactin model (Table 2.2). In conclusion, I suggest that the best approach is to use the linear model to estimate the lower temperature thresholds and the Briere model to estimate optimal and upper development parameters for the development of TPP.

While it is possible to use a daily nonlinear developmental rate relationship to predict TPP phenology, a more complex nonlinear model needs hourly temperatures for accurate developmental rate accumulation. Hourly temperatures will not often be available to model TPP phenology and it is difficult to judge whether an hourly nonlinear model would give any advantage over a simple linear or degree day model when used for forecasting. Any error associated with parameter estimates of a nonlinear model and/or the climate data used will quickly accumulate (Worner 1988).

The mathematical description of the developmental rate of *B. cockerelli* reared on potato and tomato in this thesis can underpin further research on population dynamics of this pest species, but more importantly, the parameters can be used to estimate and predict the progression of TPP populations in the field in relation to site-specific temperature profiles such that more precise timing predictions can be made for pest management. For example, such predictions could help optimize control decisions by identifying when TPP might be expected to exceed an economic threshold at a particular location or when the maximal

population of TPP is likely to be present. Indeed, as field data are collected, those data will be used to validate and refine the models developed in this Chapter.

Chapter 3: Life table parameters of tomato-potato psyllid (*Bactericera cockerelli*) (Hemiptera: Triozidae), feeding on potato under laboratory conditions

3.1 ABSTRACT

The lifecycle of the tomato-potato psyllid (TPP), *Bactericera cockerelli*, was evaluated on potato plants in the laboratory at $25\pm1^{\circ}\text{C}$, 50-60% RH, and at a photoperiod of 16:8(L: D) h at the Lincoln University, New Zealand, during June-September, 2010. The mean pre-oviposition period was 7.87 ± 1.35 days, and the mean oviposition period was 43.6 ± 14.97 days. The mean developmental period for the egg stage was 6.08 ± 1.21 days, and for the nymph period was 16.94 ± 1.35 days. The mean of total developmental period was 23.02 ± 1.67 days. The survival of eggs, nymphal stage and total development (all stages) was 71, 51, and 48%, respectively. Female mean fecundity was 388.07 ± 78.9 eggs per female. Adult longevity for male and female was 34.13 ± 11.31 and 51.47 ± 15.36 days, respectively. The sex ratio was 0.52M: 0.48F. Gross reproduction ($\sum m_x = 186.272$), intrinsic rate of increase ($r_m = 0.098$), net reproductive rate ($R_o = 73.202$), mean generation time ($T = 43.821$ days), doubling time ($DT = 7.075$ days), and finite rate of increase ($\lambda = 1.103$) were estimated from the laboratory data. These data together with environmental data can be used as basis for simulation models to explore potential control methods in the field.

3.2 INTRODUCTION

The tomato-potato psyllid (TPP), *Bactericera cockerelli*, is a polyphagous, phloem-feeding insect pest that is a pest of economically detrimental to cultivated solanaceous crops in the United States, Mexico, and New Zealand (Yang and Liu 2009, Teulon *et al.* 2009). This insect pest is an economically important crop pest that not only causes damage through its feeding but also transmits the bacterium, *Candidatus Liberibacter solanacearum*, which causes zebra chip disease in potato (Punya *et al.* 2012). The potato, *Solanum tuberosum* L. (Solanaceae), is one of the most important crops for human nutrition worldwide and is a healthy source of carbohydrates, high-quality protein, essential vitamins, minerals, and trace

elements (Golizadeh and Razmjou 2010) and therefore pest damage to potato crops is considered to be a serious problem.

A thorough understanding of the population dynamics of any pest insect requires the construction of life tables (Harcourt 1969). To construct a life table, the mortality during and between the different ages (stages) is determined, which then permits the derivation of survivorship curves (Norris *et al.* 2003). Therefore, the life table of an insect pest can be used to predict possible rates of population change, and can aid in identification of key mortality factors operating at different ages (stages) in the life cycle.

A life table is a record of survival and reproductive rates in a population, broken down by age, size, or developmental stage. Life tables provide comprehensive descriptions of age-specific survival rate and fecundity of insect populations (Zied *et al.* 2003). As such, a life table is a useful tool to understand patterns and causes of mortality, predicting the future growth or decline of populations, and managing populations of pest insects such as TPP. This tool can provide very important demographic parameters (Maia *et al.* 2000) such as for every interval of age (x), the number of deaths (d_x), the survivors remaining (l_x), the rate of mortality (q_x), and the expectation of further life (e_x). The applications of demographic studies allow analysis of population stability and structure and can help predict outbreak in pest species and examine the dynamics of colonizing or invading species (Vargas *et al.* 1997). Such knowledge is important for the design of effective integrated pest management programs. In addition, Carey (1993) suggested that demographic information is useful for constructing population models to understand the dynamics of biological invasions and the spread of parasites, viruses, and diseases.

There have been some previous studies to establish life table parameters of TPP. For example, the life history of TPP has been studied in the laboratory and in the field for tomato (Abdullah 2008, Mandriz *et al.* 2011), eggplant and bell peppers (Yang and Liu 2009) and potatoes (Yang *et al.* 2010). However, the biology and life history of this insect pest on different varieties of plant species and at different temperatures is poorly documented. Because of this, and as part of a series of studies of TPP, the aim of this Chapter was to measure life table parameters of TPP feeding on Agria potatoes under laboratory conditions at a temperature close to the optimum temperature. Conducting the trial at close to optimum temperature ensures that measured population parameters should give values close to their

maximum, thus allowing for consideration of worst case scenarios with respect to pest management. Because of technical constraints, an exact optimum temperature had not been derived from developmental data described in Chapter 2. A temperature of $25 \pm 1^\circ\text{C}$ was chosen as close to optimum temperature based on initial assessment of the developmental data in Chapter 2. Note that there has been no change to the original estimate of an optimum temperature of 26.7°C determined by List (1939) despite using tomato as a host and only for nymphal development.

3.3 MATERIAL AND METHODS

3.3.1 Construction of life table

Potato (*Agria*) plants used in this study were grown from seed tubers. These plants, 1-2 months old and 20-30 cm in height, were used individually (one plant per pot) in all experiments. These potato plants were infested with psyllids by introducing adults to caged (50W x 45L x 60H cm) plants in a controlled temperature (CT) room ($25 \pm 1^\circ\text{C}$, RH 50- 60%, and 16:8 h light: dark) at Lincoln University, New Zealand, during June - September, 2010. After oviposition for 24 hours, plants with more than 25 TPP eggs were selected for the experiment. On each plant the number of eggs was reduced to 25. Four plants with 25 eggs were placed in another cage in a constant temperature room. Therefore there were a total of one hundred newly laid eggs (< 24h old) and these were used to determine the duration and survival of different life stages. The survival of eggs, nymphs, and adults were recorded daily. Nymphal stages were distinguished as described in Chapter 2.

Cup cages (made from 1.0-liter clear, plastic cups with ventilation and a 10 x 40 mm access hole) were used to determine TPP fecundity following the method of Yang (2009). Newly emerged psyllids (< 2h old) were collected and sexed as described by Knowlton and Janes (1931). One individual pair (male and female) was introduced into a cup cage with a fresh potato leaf. The leaf was kept fresh by using wet cotton wool tied to the petiole by plastic wrap. Leaves were removed and replaced daily and the eggs on each removed leaf were counted under a microscope. A total of 15 male-female pairs were monitored daily until

all psyllids died. Life tables and fecundity schedules were constructed, from which population growth parameters were calculated.

3.3.2 Life table parameters and data analysis

Data analysis was carried out following the method by Birch (1948) and Southwood (1978). Life tables were constructed using the following parameters:

x : the pivotal age for the age class in units of time (days)

l_x : the number of surviving individuals at the beginning of age class x .

L_x : the number of individuals living between ages x and $x+1$

d_x : the number of individuals dying during the age interval x ; $d_x = l_x - l_{x+1}$

$100q_x$: percent apparent mortality; $q_x = d_x / l_x$

S_x : survival rate during a stage; $S_x = (l_{x+1}) / (l_x)$

T_x : total number of age x units beyond the age x ; This is the sum of numbers in the $L(x)$ column from age x to the last row in the table.

e_x : life expectancy for individuals of age x

m_x : age-specific fertility, the number of living females born per female in each interval class

R_o : net reproductive rate (in days). This is equal to the sum of the $l_x m_x$ products, or $R_o = \sum l_x m_x$

T : Cohort generation time (in days), approximated by $T \approx \sum x l_x m_x / \sum l_x m_x$ (time between the birth of the parents to that of their progeny)

r_m : The intrinsic rate of natural increase, calculated by, $r_m \approx \ln(R_o) / T$

DT : Doubling time (in days), the number of days required by a population to double, calculated by,

$$DT = \ln(2) / r_m$$

λ : The finite capacity of increase, calculated by, $\lambda = e^{r_m}$

After r_m was computed for the original data (r_{all}), the jackknife method (Meyer *et al.* 1986) was applied to estimate the variance for r_m and other population parameters. The jackknife method removes one observation from the original data set and recalculates the statistic of interest from the truncated data set. These new estimates, or pseudo-values, form a set of numbers from which mean values and variances can be calculated and compared statistically (Maia *et al.* 2000). The steps for the application of the method are the following:

$$r_{m(j)} = n * r_{all} - (n-1) * r_{m(i)}$$

$$r_{m(\text{mean})} = \frac{\sum_{j=1}^n r_{m(j)}}{n}$$

$$\text{VAR}r_{m(\text{mean})} = \frac{\sum_{j=1}^n (r_{m(j)} - r_{all})^2}{n-1}$$

$$\text{SEMr}_{m(\text{mean})} = \sqrt{\frac{\text{VAR}(r_{m(\text{mean})})}{n}}$$

Where n is the number of replications (n=15), and $r_{m(i)}$ is the intrinsic rate of n-1 females. Algorithms for jackknife estimation of the means and variances were described only for r_m . Similar procedures were used for the other parameters (R_o , λ , T and DT). All calculations were carried out using Microsoft Office Excel 2003 and R software (R version 2.9.2).

3.4 RESULTS

From the 100 eggs at the beginning of the life table study, 71 eggs hatched successfully. TPP has 5 nymphal instars before becoming an adult. Forty-eight individuals from the original 71 survived to become adults (Table 3.1, Fig. 3.1). The life table showed that relatively high mortality occurred during the egg and the first instar stages when compared to other instars. This level of survivorship, 59 out of 100 (Table 3.1), is typical of insect species (Begon and Mortimer 1981, Win *et al.* 2011) where there is high mortality in the early stages. The age specific survival (l_x) and age specific fecundity (m_x) of TPP are presented in Fig. 3.1 and Fig. 3.2.

Table 3.1: Pooled life table values for TPP fed on potato under laboratory conditions at 25±1°C, 60% RH, and 16:8 (L: D) h.

Stage x	l_x	L_x	d_x	$100q_x$	S_x	T_x	e_x
Egg	100	85.5	29	29	71	391	3.91
Instar 1	71	65	12	16.9	83.1	305.5	4.30
Instar 2	59	58	2	3.4	96.6	240.5	4.08
Instar 3	57	55.5	3	5.3	94.7	182.5	3.20
Instar 4	54	53	2	3.7	96.3	127	2.35
Instar 5	52	50	4	7.7	92.3	74	1.42
Adult	48	24					

*x: developmental stage; l_x : number of entering stage; L_x : number alive between age x and x+1; d_x : number dying in stage x; $100q_x$: percent apparent mortality, S_x : survival rate within stage, T_x : total number of age x units beyond the age x, e_x : life expectancy.

The means for developmental periods for each developmental stage, the longevities for male and female adults, the pre-oviposition period, oviposition period, and female fecundity of TPP are given in Table 3.2. The pre-oviposition period was 7.87 days with a range of 6-11 days. The oviposition period was 43.60 ranging from 19-80 days. The total developmental period for the pre-adult stages was 23.02 days, whereas adults lived as long as 51.47 days, and 34.13 days for female and male respectively.

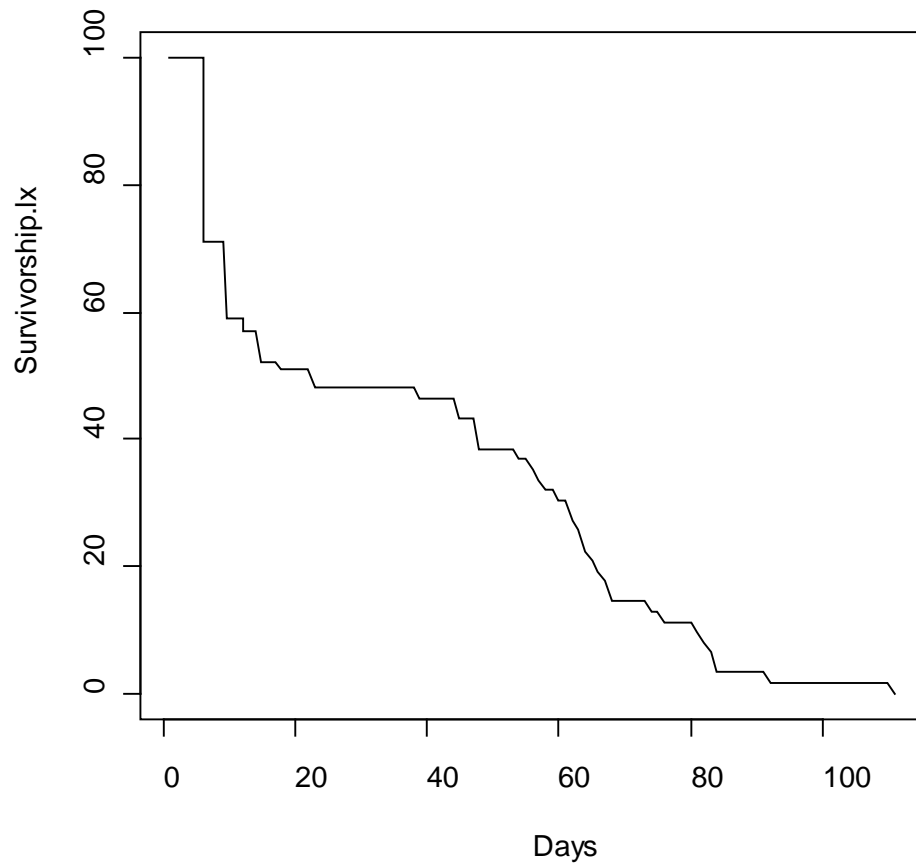


Figure 3.1: Age specific survivorship (l_x) of TPP fed on potato under laboratory conditions at 25 ± 1 °C, 60% RH, and 16:8 (L: D) h.

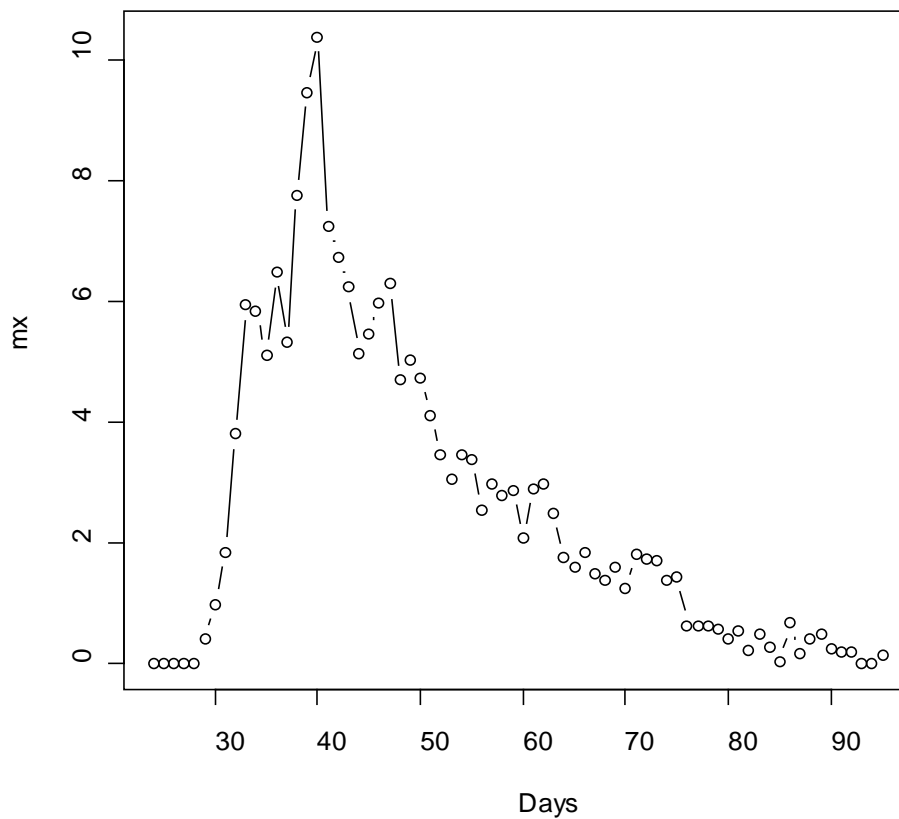


Figure 3.2: Age specific fecundity (m_x) of TPP fed on potato under laboratory conditions at $25\pm 1^\circ\text{C}$, 60% RH, and 16:8 h (L: D).

The population growth parameters of TPP are given in Table 3.3. The intrinsic rate of increase (r_m) of TPP was 0.098, the net reproductive rate (R_0) was 73.202 offspring, the finite rate of increase (λ) was 1.103, the generation time (T) was 43.821 days, the doubling time (DT) was 7.075 days, and the gross reproductive rate (Σm_x) was 186.272 offspring. The sex ratio of the psyllids that made it to adulthood ($n=48$) was 0.48F:0.52M. A mean maximal daily fecundity of 21.7 eggs was observed for one female (Table 3.4). For the total life span, a maximal fecundity of 576 eggs was recorded for a single female. The mean female fecundity of TPP was 388.07 eggs per female.

Table 3.2: Developmental time, adult longevity, pre-oviposition period, and oviposition period in days of TPP fed on potato under laboratory conditions at 25±1 °C, 60% RH, and 16:8 (L:D) h (Sex ratio: 48%F: 52%M).

Parameter	Stage	n	Mean	SE
Developmental time (days)	Egg	71	6.08	1.21
	First instar	59	3.44	0.50
	Second instar	57	2.68	0.46
	Third instar	54	2.76	0.43
	Fourth instar	52	2.77	0.42
	Fifth instar	51	5.27	0.45
	Total development	48	23.02	1.67
Adult longevity (days)	Male	25	34.13	11.31
	Female	23	51.47	15.36
Pre-oviposition period (days)	Female	23	7.87	1.35
Oviposition period (days)	Female	23	43.60	14.97
Fecundity (eggs/female)	Female	23	388.07	78.9

Table 3.3: Life table parameters of TPP fed on potato under laboratory conditions (25 \pm 1°C, RH 50 - 60%, and 16:8 h light: dark).

Parameters	Unit	True calculation	Jackknife estimate
Gross reproduction ($\sum m_x$)		186.272	
Intrinsic rate of increase (r_m)	1/day	0.098	0.098 \pm 0.0012
Net reproductive rate (R_o)	Females/Generation	73.202	73.207 \pm 4.5539
Mean generation time (T)	days	43.821	43.839 \pm 0.4442
Doubling time (DT)	days	7.075	7.074 \pm 0.0874
Finite rate of increase (λ)	1/day	1.103	1.104 \pm 0.0013

Table 3.4: Life table (for females) and age-specific fecundity of TPP feeding on potato.

x (days)	l_x	Egg per female	m_x	$l_x m_x$	$x l_x m_x$
1-27	0.48				
28	0.48	0.866667	0.416	0.19968	5.59104
29	0.48	2.066667	0.992	0.47616	13.80864
30	0.48	3.866667	1.856	0.89088	26.7264
31	0.48	7.933333	3.808	1.82784	56.66304
32	0.48	12.4	5.952	2.85696	91.42272
33	0.48	12.2	5.856	2.81088	92.75904

(Continued on next page)

Table 3.4 (*continued*)

x (days)	l_x	Egg per female	m_x	$l_x m_x$	$x l_x m_x$
34	0.48	10.66667	5.12	2.4576	83.5584
35	0.48	13.53333	6.496	3.11808	109.1328
36	0.48	11.13333	5.344	2.56512	92.34432
37	0.48	16.2	7.776	3.73248	138.1018
38	0.48	19.73333	9.472	4.54656	172.7693
39	0.464	21.66667	10.4	4.8256	188.1984
40	0.464	15.13333	7.264	3.370496	134.8198
41	0.464	14.06667	6.752	3.132928	128.45
42	0.464	13	6.24	2.89536	121.6051
43	0.464	10.73333	5.152	2.390528	102.7927
44	0.464	11.4	5.472	2.539008	111.7164
45	0.432	12.46667	5.984	2.585088	116.329
46	0.432	13.13333	6.304	2.723328	125.2731
47	0.432	9.8	4.704	2.032128	95.51002
48	0.384	10.46667	5.024	1.929216	92.60237
49	0.384	9.866667	4.736	1.818624	89.11258
50	0.384	8.6	4.128	1.585152	79.2576
51	0.384	7.2	3.456	1.327104	67.6823
52	0.384	6.4	3.072	1.179648	61.3417
53	0.384	7.2	3.456	1.327104	70.33651
54	0.368	7.066667	3.392	1.248256	67.40582
55	0.368	5.333333	2.56	0.94208	51.8144
56	0.352	6.2	2.976	1.047552	58.66291
57	0.336	5.8	2.784	0.935424	53.31917
58	0.32	6	2.88	0.9216	53.4528

(Continued on next page)

Table 3.4 (continued)

x (days)	l_x	Egg per female	m_x	$l_x m_x$	$x l_x m_x$
59	0.32	4.333333	2.08	0.6656	39.2704
60	0.304	6.066667	2.912	0.885248	53.11488
61	0.304	6.2	2.976	0.904704	55.18694
62	0.272	5.2	2.496	0.678912	42.09254
63	0.256	3.666667	1.76	0.45056	28.38528
64	0.224	3.333333	1.6	0.3584	22.9376
65	0.208	3.866667	1.856	0.386048	25.09312
66	0.192	3.133333	1.504	0.288768	19.05869
67	0.176	2.866667	1.376	0.242176	16.22579
68	0.144	3.333333	1.6	0.2304	15.6672
69	0.144	2.6	1.248	0.179712	12.40013
70	0.144	3.8	1.824	0.262656	18.38592
71	0.144	3.6	1.728	0.248832	17.66707
72	0.144	3.533333	1.696	0.244224	17.58413
73	0.144	2.866667	1.376	0.198144	14.46451
74	0.128	3	1.44	0.18432	13.63968
75	0.128	1.333333	0.64	0.08192	6.144
76	0.112	1.333333	0.64	0.07168	5.44768
77	0.112	1.333333	0.64	0.07168	5.51936
78	0.112	1.2	0.576	0.064512	5.031936
79	0.112	0.866667	0.416	0.046592	3.680768
80	0.112	1.133333	0.544	0.060928	4.87424
81	0.096	0.466667	0.224	0.021504	1.741824
82	0.08	1	0.48	0.0384	3.1488

(Continued on next page)

Table 3.4 (*continued*)

x (days)	l_x	Egg per female	m_x	$l_x m_x$	$xl_x m_x$
83	0.064	0.6	0.288	0.018432	1.529856
84	0.032	0.066667	0.032	0.001024	0.086016
85	0.032	1.4	0.672	0.021504	1.82784
86	0.032	0.333333	0.16	0.00512	0.44032
87	0.032	0.866667	0.416	0.013312	1.158144
88	0.032	1	0.48	0.01536	1.35168
89	0.032	0.533333	0.256	0.008192	0.729088
90	0.032	0.4	0.192	0.006144	0.55296
91	0.032	0.4	0.192	0.006144	0.559104
92	0.016	0	0	0	0
93	0.016	0	0	0	0
94	0.016	0.266667	0.128	0.002048	0.192512
Total			186.272	73.20166	3207.75

3.5 DISCUSSION

Life table parameters, including survival rates, development, and reproductive rates are clearly different for different temperatures and for different host plants. In previous studies, life tables for TPP have been conducted on potato at 26.7°C (Yang *et al.* 2010); on tomato at 26-27°C by Abdullah (2008) and in a greenhouse by Mandriz *et al.* (2011); and on eggplant and bell pepper at 26.7°C (Yang and Liu 2009). Except for the study by Mandriz *et al.* (2011), all studies of the life history of TPP were conducted under what is considered to be the optimum temperature (26.7°C) determined by List (1939) and confirmed in Chapter 2.

The life table in my study was conducted on potato at 25°C that was lower than optimum temperature by nearly 2°C.

In this chapter experiment, the total developmental time of TPP (23.02 days reared on potato at 25°C) was 3.4 days longer compared with (19.6 days reared on potato at 26.7°C) the results of Yang *et al.* (2010), and 1.91 days longer compared with (21.11 days reared on potato at 27°C) the results of Tran *et al.* (2012). Conversely, the adult longevity (male 34.13 days, female 51.47 days) in here was shorter than that (male 35.3 days, female 62.1 days) reported by Yang *et al.* (2010). Consequently, TPP had a lower intrinsic rate of increase (0.098) in my study compared with (0.1966) found by Yang *et al.* (2010). The higher intrinsic rate of increase reported by Yang *et al.* (2010) was probably due to the faster development of immature stages (shorter generation time), higher survivorship and higher fecundity rate at the higher experimental temperature (Table 3.5). This suggested that 25°C is not the optimal temperature for TPP. In contrast, the pre-oviposition period, and oviposition period in my study were similar when compared with that reported by Yang *et al.* (2010) (Table 3.5).

The reported total development time (egg-adult) for TPP on potato of 19.6 days (Yang *et al.* 2010) is 4.5, 6.6, and 8.8 days shorter than that on bell pepper, eggplant (Yang and Liu 2009), and tomato (Abdullad 2008), respectively, indicating that potato is a better host plant for TPP than bell pepper, eggplant, and tomato with respect to developmental time (Table 3.5). My study also showed that the fecundity of TPP (Table 3.5) on potato was higher than that on eggplant (Yang and Liu 2009), and tomato (Abdullad 2008) but lower than that on bell pepper (Yang and Liu 2009). The intrinsic rate of increase (r_m) and net reproductive rate (R_0) on my study were slightly higher than that on bell pepper (Yang and Liu 2009), and tomato (Madriz *et al.* 2011) but lower than that on eggplant (Yang and Liu 2009). In addition, my study had a mean generation time of TPP higher than that on eggplant but lower on bell pepper and tomato. These indicated that along with a greater intrinsic rate of increase (r_m) is a shorter generation time and *vice versa*. These results agree with to those reported on the life table of TPP by Madriz *et al.* (2011).

Table 3.5: Summary of some studies related to life history of TPP.

	Abdullad 2008 (at 26-27°C) Tomato	Yang and Liu 2009 (at 26.7°C)		Yang <i>et al.</i> 2010 (at 26.7°C) Potato	My study (at 25°C) Potato	Tran <i>et al.</i> 2012 (at 27°C)	
		Eggplant	Bell pepper			Potato	Tomato
Total development time (days)	28.4	24.1	26.2	19.6	23.02	21.11	22.08
Fecundity (eggs/female)	231.8	338	403	399.7	388.1		
Pre-oviposition period (days)	6.9	8.8	8.0	8.4	7.9		
Oviposition period (days)		53	47	43.9	43.6		
Intrinsic rate of increase (r_m)		0.1099	0.088	0.1966	0.098		
Net reproductive rate (R_o)		84.51	59	102.86	73.2		
Mortality (%)	37.7 (egg)	15.4 (egg)	15.1 (egg)	46.8	29 (egg)		
	52.7	39.9 (1 st)	57.2 (1 st)	(total)	41 (1 st)		
	(nymphs)	42.2 (2 nd)	61.1 (2 nd)		43 (2 nd)		
	59.4	43.8 (3 rd)	63.4 (3 rd)		46 (3 rd)		
	(total)	44.7 (4 th)	65.2 (4 th)		48 (4 th)		
		45.7 (5 th)	65.2 (5 th)		49 (5 th)		
		49.8 (total)	65.4		52 (total)		
			(total)				

In this study higher mortality of TPP occurred during the egg stage and nymphal stage 1 than other stages (Table 3.1 and Fig. 3.1). There were relatively few deaths during the adult stage. These data were similar to the trends described in previous studies (Davis 1937, Liu *et al.* 2006; Yang and Liu 2009; Madriz *et al.* 2011) who reported most nymphal mortality of TPP occurred during the egg stage and early nymphal stages. The mean net reproductive rate (R_o) of TPP was 73.2. However, I cannot compare this parameter with other studies as the comparison of two or more populations by their net reproductive rate

(R_0) can be misleading unless the mean lengths of the generation time are the same (Birch 1948). The same net reproductive rate (R_0) may occur in two or more populations, but their intrinsic rates of increase may be quite different because of different generation times (Satpute *et al.* 2005).

The differences in the estimated life table parameters of TPP observed in this study compared with others discussed above are clearly due to differences in temperatures and host plants. It is well known that temperature is the most important factor which influences the development and reproduction of insects resulting in variable fecundity, development period, survival rates, and life expectancy (Schowalter 2006, Siswanto *et al.* 2008). Host plant is also an important factor that influences the development, survival, reproduction and life table parameters of insects (Varley and Gradwell 1970, Greenberg *et al.* 2001, Hansen *et al.* 2004, Liu *et al.* 2004). For example, Greenberg *et al.* (2011) reported that performance of *Spodoptera exigua* (Lepidoptera: Noctuidae) was best on pigweed, worst on cabbage, and intermediate on cotton, pepper, and sunflower. In addition, descriptions of clutch size and number of clutches (lifetime fecundity) vary widely among studies, caused in part by diet quality, varying temperatures and photoperiods, or differences among experimental populations (Drankin *et al.* 1995, Lemos *et al.* 2003).

Understanding the variations of TPP population response to different host plants and different temperatures could have useful implications for its management. In addition, determination of life table parameters and their variation allows us to estimate maximal responses to estimate their biotic potential under specific conditions. These data together with environmental data can be used as basis for simulation models to explore potential control methods in the field. In addition, a simulation model developed in such a manner could be coupled with predator population dynamics models to develop TPP management strategies involving biological control programs in crops.

Chapter 4 Functional response of *Orius vicinus* (Heteroptera: Miridae), on tomato-potato psyllid, *Bactericera cockerelli* (Sulc.) (Hemiptera: Triozidae) and prey preference between tomato-potato psyllid and western flower thrips, *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae)

4.1 ABSTRACT

Orius vicinus (Ribaut) has been reported to feed on red spider mite, leafhopper, and thrips and is now being investigated for biological control programs for some pests in New Zealand. The functional responses of the adult stage of the predatory bug, *O. vicinus* feeding on egg, nymphal instars 1, 2, 3, 4, and 5 of the tomato-potato psyllid (TPP), *Bactericera cockerelli* (Sulc.) were determined. Experiments were also conducted to determine the prey preferences of this predatory bug between two prey species: TPP (nymphal instars 1 and 2) and western flower thrips (*Frankliniella occidentalis* (Pergande)) (nymphal instars 1 and 2). Predation experiments were conducted under laboratory conditions of $25\pm 1^{\circ}\text{C}$, 60% RH and 16:8 h (L: D). Prey densities of 2, 4, 8, 16, and 32 individuals were offered to the predator comprising ten replicates at each density. The functional response was determined using logistic regression. The parameters of the functional response, searching efficiency (a) and handling time (T_h) were estimated by non-linear regression. The resulting data were well described by both Type I and II functional response models for prey eggs and first and second instar nymphs, and Type II for 3rd, 4th and 5th instar nymphs of TPP. *O. vicinus* had a slight preference for thrips compared to the psyllid at high densities of prey combinations.

4.2 INTRODUCTION

The tomato-potato psyllid (TPP), *Bactericera cockerelli* (Sulc) (Hemiptera: Triozidae), is a polyphagous, phloem-feeding insect pest that is causing considerable economic impact to cultivated solanaceous crops in the United States, Mexico, and, more recently, in New Zealand (Liu and Trumble 2006, Munyaneza *et al.* 2007a,b, Teulon *et al.*

2009, Yang and Liu 2009). This pest is a newly invasive pest species of vegetable and fruit crops especially potato, tomato, capsicum and tamarillos (*Solanum betaceum*) in New Zealand (Teulon *et al.* 2009). The tomato-potato psyllid is thought to have originated in North America, where it is found in the United States west of the Mississippi, and southern areas of the Canadian provinces of British Columbia, Alberta, and Saskatchewan (Wallis 1951), and also in glasshouses in Ontario (Ferguson and Shipp 2002) and Mexico. In recent years, *B. cockerelli* has directly or indirectly caused serious yield losses in potato, tomato, and pepper production in western North America (Liu and Trumble 2006, Munyaneza *et al.* 2007a,b, Gao *et al.* 2009). In addition, Zebra chip, a new and serious disease of potatoes vectored by TPP, has caused millions of dollars in losses to the potato industry in the United States, Mexico, Central America, and New Zealand (Munyaneza 2012). Management of this pest is difficult because there is an increasing trend for TPP to become resistant to insecticides at least in parts of North America (Liu and Trumble 2007) and there is concern that the same will happen in New Zealand (Walker *et al.* 2012). Therefore, biological control is a potential option for control of TPP to be integrated with other management practices including insecticides.

Orius vicinus occurs widely in Europe. It has been recorded from eastern Turkey and Tadzhikistan, and may also be found in northern Africa. It is not known how the species became established in New Zealand (Lariviere and Wearing 1994). *O. vicinus* is a general predator with prey species reported including bark lice, psyllids, thrips, aphids, and leafhoppers (Lewis and Lattin 2010). Because psyllids are one of the prey of *O. vicinus* (Lariviere and Wearing 1994), the functional response of this predator feeding on various nymphal stages of TPP under laboratory condition, were determined.

Ecologists have focused extensively on functional and numerical responses of predators as a means of assessing the impact of a natural enemy on a prey population (Sabaghi *et al.* 2012). The functional response relates to the change in the predation rate with changing prey density whereas numerical responses of the predator can be expressed in terms of a progressive change in the number of the predator progeny in relation to increasing prey density (Solomon 1949). A predator's functional response to prey density plays a fundamental role in successful biological control programs (Holling 1966; Hassell 1978; Fathi and Ganbalani 2009). Determination of the relationship between the average number of

prey consumed by each predator and the density of prey in a certain area is essential to judge the efficiency of the biocontrol agent. Therefore, determining the effects of predation on a prey population is most commonly done through the analysis of a predator's functional response (Huffaker and Messenger 1976, Jalalizand *et al.* 2011). The functional response can be categorized into three types according to the shape of the predator consumption vs prey density curve (Holling 1959, 1966). Most invertebrate predators demonstrate a Type II response, whereas the Type III is exhibited by both vertebrate and invertebrate predators (Riechert and Lockley 1984). The Type III response is supposed to be the only one that is capable of potentially regulating a prey population (Fernandez- Arhex and Corley 2003). However, that depends on the numerical response of the predator such that certain predators with a Type II response have been shown to successfully regulate a prey population. An example of a Type II response that results in a successful biological control is the functional response of *Trioxys complanatus* feeding on *Therioaphis trifolii* (Hughes *et al.* 1992, Fernandez- Arhex and Corley 2003). Scientists often make an initial determination of the potential of a natural enemy by using functional response studies on individual predators feeding on a single patch of prey species (Flinn *et al.* 1985, De Clercq *et al.* 1998, Wells and McPherson 1999, Lester *et al.* 2000, Lester and Harmsen 2002, Stewart *et al.* 2002, Nachappa *et al.* 2006).

A number of the species in the prey range of *O. vicinus* are likely to coexist in crops such as aphids and thrips. Thus, the ability of *O. vicinus* to prey on other pests (aphids or thrips) may reduce the predation pressure on the target pest (TPP) intended to be controlled. Prey preference of a predator is defined as a disproportionate attack rate on one prey species, when more than one prey species is available (Cock 1978, Sherratt and Harvey 1993). The prey preference of one predator is assessed by providing predators a choice of prey over a relatively short time interval (Toft 1995, Meyling *et al.* 2003, Legaspi *et al.* 2006). This prey preference implies an ability to distinguish between different types of prey and to choose to take one rather than the other. Knowledge of the prey preference may help to improve the understanding of the foraging behaviour of insect predators, which is considered to be central to insect ecological studies (Fellowes *et al.* 2005). As the prey preference of a predator directly affects the control efficiency of its various prey (Xu and Enkegaard 2009), and western flower thrips are often found in glasshouse and are pests on the same crops as TPP

(capsicum and tomato), the preference of *O. vicinus* for psyllid and western flower thrips at various densities, was examined.

The specific objectives of this Chapter were to, 1) determine the functional response, handling time, and attack coefficient of *O. vicinus* predation on *B. cockerelli* when prey items were offered alone (single-prey) at different densities, and, 2) determine the feeding preference of *O. vicinus* on psyllid and thrips.

4.3 MATERIAL AND METHODS

4.3.1 Insect cultures

All TPP were reared on potted tomato (Yates ‘Moneymaker’) or potato seedlings (‘Agria’) in cages in a controlled temperature (CT) room ($25 \pm 1^\circ\text{C}$, RH 60%, and 16:8 h light: dark). The rearing cages (50W x 45L x 60H cm) had a door-like front panel that provided a single access point to water plants and to get access to the insects. The panel comprised a fine mesh polyester netting to provide ventilation.

O. vicinus were supplied by BioForce (Drury), a New Zealand company that rears biological control agents (bioforce.net.nz). These predators were maintained in cages in a controlled temperature (CT) room ($25 \pm 1^\circ\text{C}$, RH 60%, and 16:8 h light: dark). The predators were fed with various stages of TPP reared on potato plants. To reduce the behavioural adaptation of this predator to TPP, predators were used as soon as possible (3-5 days) after receiving them from the supplier. All *O. vicinus* using in this study were adults of both sexes.

Western flower thrips (*Frankliniella occidentalis* (Pergande)) (nymphal instars 1 and 2) were supplied by Plant & Food Research, Lincoln, New Zealand. These thrips were originally collected from capsicum in commercial greenhouses in Auckland. Thrips were maintained on potted flowering chrysanthemums, *Dendranthema grandiflora* at Lincoln, Canterbury. The plants used for the colony are held in two temperature-controlled perspex boxes (six plants per box) with a temperature maintained at $25 \pm 1^\circ\text{C}$ under a 16:8 h light: dark cycle. A fresh uninfected plant was placed in each box every 3 days and the oldest plant was removed at the same time.

4.3.2 Experiments

4.3.2.1 Functional response of *O. vicinus* to TPP

The experiments were performed in the same laboratory conditions used for rearing the predator and the TPP culture. Five densities (2, 4, 8, 16, and 32) of TPP eggs, nymphal instars 1 and 2, nymphal instars 3 and 4, and nymphal instar 5 were randomly selected and tested. Each adult *O. vicinus* (5-10 days old) was tested once only, and then discarded. For each density, TPP were arranged evenly on the upper surface of a potato leaf then placed in an experimental arena comprising ten 9 cm diameter Petri dishes fitted with mesh lids. The *Orius* predators were starved for 24h and added singly to each Petri dish with different prey densities and different prey stages. After 24h each predator was withdrawn from the Petri dish and the unconsumed preys were counted. Each treatment density had 10 replicates (*i.e.* 10 individual *O. vicinus* tested at each density) and five controls without predators.

4.3.2.2 Prey preference of *O. vicinus*

The experiments were performed in the same laboratory conditions used for experiments of functional response. Four density combinations of TPP (nymphal stages 1-2, and thrips (nymphal stages 1-2) at density ratios of 4:4, 8:8, 16:16, and 32:32 were prepared. Each adult *O. vicinus* (5-10 days old) was used once and then discarded. TPP and thrips were arranged on a potato leaf in a plastic cylinder (8 cm diameter, 9 cm high). The lower surface of the cylinder was sealed with fine mesh (for ventilation) and the upper surface of the cylinder was covered by parafilm. The predators were starved for 24h and added singly to a cylinder with a different prey density combination. After 24h, predators were withdrawn from each cylinder and any unconsumed prey was counted. Each density combination had 15 replicates and four controls without predators.

4.3.3 Data analysis

4.3.3.1 Functional response of *O. vicinus* to TPP

Parameters for the Type I functional response were estimated using linear regression (Holling 1959). As mentioned by some authors (Trexler *et al.* 1988, Casas and Hulliger 1994, Pervez and Omkar 2005), Type II and Type III functional responses are usually difficult to discriminate. A logistic regression model (1) was used to determine the shape of each predator-prey functional response curve by considering the proportion of prey attacked (N_a/N_o) as a function of the density of prey offered (N_o) (Juliano 2001). The data were fitted to a polynomial function that describes the relationship between N_a/N_o and N_o :

$$\frac{N_a}{N_o} = \frac{\exp(L_o + L_1 N_o + L_2 N_o^2 + L_3 N_o^3)}{1 + \exp(L_o + L_1 N_o + L_2 N_o^2 + L_3 N_o^3)}, \quad (1)$$

Where L_o, L_1, L_2 , and L_3 represent the intercept, linear, quadratic, and cubic coefficients, respectively, as estimated using maximum likelihood tests (R version 2.9.2). If $L_1 > 0$ and $L_2 < 0$, then the proportion of prey consumed is assumed to be positively density dependent, thus describing a Type III functional response. Conversely, if $L_1 < 0$, the proportion of prey consumed declines linearly with the initial number of prey offered, thus describing a Type II functional response (Juliano 2001).

The Holling ‘disc equation’ (2) (Holling 1959) for Type II response and the Hassell equation (3) (Hassell 1978) for Type III response were also used to estimate handling time T_h (the time spent pursuing, subduing, and consuming each prey item) and attack coefficients a (the rate at which the predator encounters prey items per unit of prey density)

$$N_a = (a T N_o P) / (1 + a T_h N_o), \quad (2)$$

$$N_a = N_o \{1 - \exp[(d + b N_o)(T_h N_e - T) / (1 + c N_o)]\}, \quad (3)$$

Where T is the total experimental time (here $T=24$ h) and P is the predator density (here $P=1$), and b, c , and d are constants of the function that relates a and N_o in a Type III functional responses: $a = (d + b N_o) / (1 + c N_o)$. Parameters were obtained by fitting the models to observed data using nonlinear least square regression in R (R Version 2.9.2).

4.3.3.2 Prey preference

Predator preference was calculated using Manly's preference index (Manly 1974). The sum of Manly's β for all prey species is 1 and prey species with large values of Manly's β indicates preference for that species.

$$\beta = \frac{\log(\frac{e_1}{A_1})}{\log(\frac{e_1}{A_1}) + \log(\frac{e_2}{A_2})}$$

Where β is the preference to prey Type I (here thrips), e_1 and e_2 are the number of prey of Type I and II (here TPP) remaining after the experiment, and A_1 and A_2 are the number of prey Type I and II presented to the predator. If the preference index is close to 1, the predator prefers Type I prey, if close to 0, it prefers Type II prey. An index value close to 0.5 indicates no preference. In addition, the significant difference of the prey consumed by the predator between thrips and TPP was compared using the Tukey comparison procedure in R (R Version 2.9.2).

4.4 RESULTS

4.4.1 Functional response

Predation data for various stages of *B. cockerelli* consumed by adults of *O. vicinus* are presented in Table 4.1. The number of prey at different stages consumed by the predator decreased significantly as prey increased size from egg to nymph 5 at high prey densities offered (16 and 32). The number of prey consumed by the predator was negatively correlated with the prey densities offered.

Table 4.1: Mean number \pm SD of different stages of *B. cockerelli* consumed by adult *O. vicinus* under laboratory conditions ($25 \pm 1^\circ\text{C}$, RH 60%, and 16:8 h light: dark).

Prey offered	Mean number of the prey (at different stages) consumed by the predator			
	Egg	Nymph 1-2	Nymph 3-4	Nymph 5
2	1.9 \pm 0.316a	1.8 \pm 0.422a	1.9 \pm 0.316a	1.5 \pm 0.707b
4	3.7 \pm 0.675a	3.7 \pm 0.675a	3.7 \pm 0.675a	3.0 \pm 0.943b
8	7.3 \pm 1.059a	7.2 \pm 1.135ab	6.9 \pm 1.449bc	3.4 \pm 0.699d
16	14.8 \pm 1.686a	14.5 \pm 1.509ab	8.4 \pm 1.897b	3.8 \pm 1.033c
32	23.1 \pm 2.558a	21.5 \pm 3.974b	9.5 \pm 2.369c	4.1 \pm 1.100d

Means within the same prey offered followed by the same letter are not significantly different ($P < 0.05$, TukeyHSD).

The functional responses of *O. vicinus* to the egg and nymph 1-2 stages of TPP fitted both Type I and II functional response (Table 4.2, Fig. 4.1).

Table 4.2: Type I and II functional response parameters of *O. vicinus* predating egg and nymph 1-2 of *B. cockerelli* (a is attack rate and T_h is handling time).

Model	Egg			Nymph 1-2		
	Intercept (\pm SE)	Slope (\pm SE)	R^2	Intercept (\pm SE)	Slope (\pm SE)	R^2
Type I	1.35 (0.98)	0.71 (0.06)	0.98	1.57 (1.14)	0.66 (0.07)	0.97
Type II	a (\pm SE)	T_h (\pm SE)	R^2	a (\pm SE)	T_h (\pm SE)	R^2
	0.046 (0.003)	0.345 (0.06)	0.99	0.047 (0.004)	0.434 (0.08)	0.99

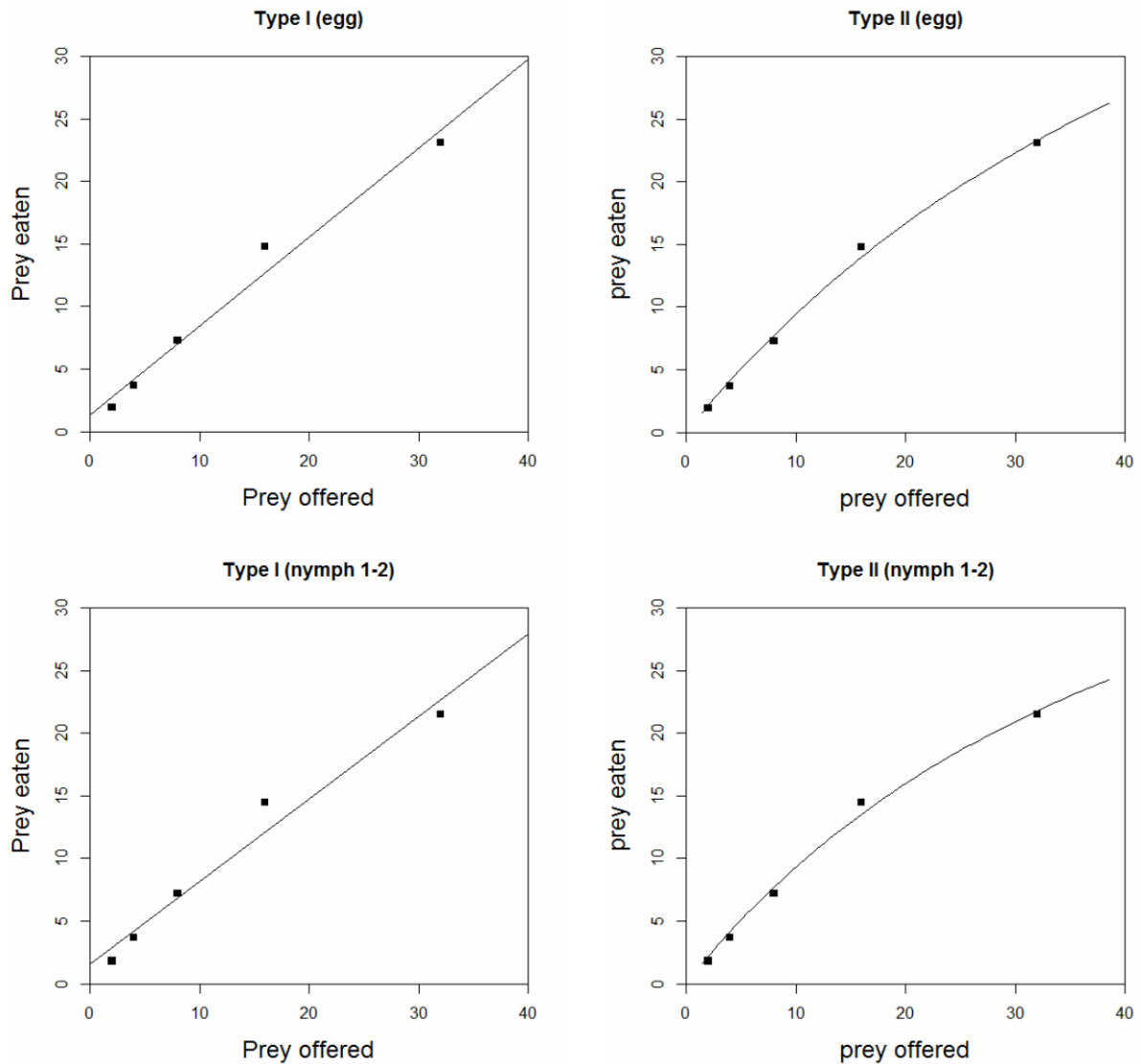


Figure 4.1: Type I and II functional response of adult *O. vicinus* feeding on egg and nymphal stages 1-2 of *B. cockerelli* under laboratory condition ($25 \pm 1^\circ\text{C}$, RH 60%, and 16:8 h light: dark).

Table 4.2 shows parameters of Type I and Type II functional response of adult *O. vicinus* feeding on egg and nymph 1-2 of *B. cockerelli*. The Type II provided slightly better fit based on higher R^2 (Table 4.2). The slopes of the linear regression, the attack rates, and the handling times between egg and nymph 1-2 are very similar.

The logistic regression for the predatory bug *O. vicinus* had a significant linear parameter $L_1 < 0$ (Table 4.3) for nymphal stages 3-4 and nymphal stage 5 indicating the proportion (but not number) of prey eaten by the predator declined with increasing prey density. A declining proportion of prey eaten compared with a constant proportion (Type I, linear response), or an increasing proportion (Type III response) shows that the data are appropriately described by a Type II functional response (Table 4.4, Fig. 4.2). Therefore Holling's disc equation (equation 2) was used to estimate the functional response parameters.

Table 4.3: Maximum likelihood estimates (SE) for the logistic regression of proportion of prey eaten by the predator as a function of initial prey densities.

Parameter	Stages of the prey	
	Nymph 3-4	Nymph 5
Intercept (L_0)	2.985(0.158)	2.9427(0.902)
Linear (L_1)	-0.063(0.036)	-0.6134(0.2163)
Quadratic (L_2)	-0.013(0.0024)	0.0301(0.0144)
Cubic (L_3)	0.00035(0.00004)	-0.0005(0.0003)

Handling time (T_h) and attack rates (a) of *O. vicinus* feeding on nymph 3-4 and nymph 5 of *B. cockerelli* are summarized in Table 4.4.

Table 4.4: Coefficients for the attack rate, handling time, and maximum predation rate of *O. vicinus* feeding on *B. cockerelli* under laboratory condition ($25 \pm 1^\circ\text{C}$, RH 60%, and 16:8 h light: dark).

Parameters	Stages of the prey	
	Nymph 3-4	Nymph 5
Attack rate a (1/hour)	0.06419 (0.01127)	0.0657 (0.01456)
Handling time T_h (hour)	1.9548 (0.191)	5.2827 (0.38368)
Maximum predation rate ($1/T_h$)	12.28	4.54

The values in parentheses are the standard error (SE).

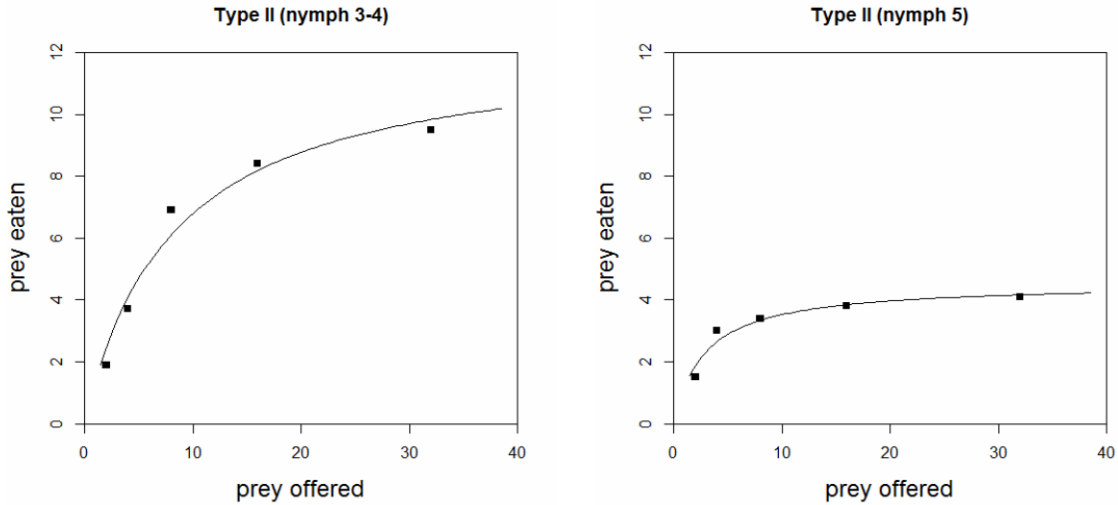


Figure 4.2: Type II functional response of adult *O. vicinus* feeding on nymph 3-4 and nymph 5 of *B. cockerelli* under laboratory condition ($25 \pm 1^\circ\text{C}$, RH 60%, and 16:8 h light: dark).

It is clear that the handling time (T_h) per prey was longest for the larger nymph 5 (5.2827 h) than for the egg (0.34547 h), nymph 1-2 (0.433602 h), and nymph 3-4 (1.9548 h) stages of the prey (Table 4.4). The highest theoretical maximum predation rate was estimated for the egg stage reaching 69.5 egg / 24 h followed by nymph 1-2, nymph 3-4, and nymph 5 with a maximum predation rates 55.35 / 24 h, 12.28 / 24 h, and 4.5 / 24 h, respectively

4.4.2 Prey preference

Manly's measure of preference was greater than 0.5 at all prey densities (Table 4.5, Fig. 4.3) although only at two combinations of high prey densities (16:16 and 32:32) were thrips significantly more preferred than psyllids ($p < 0.05$; Table 4.5).

Table 4.5: Mean \pm (SE) of western flower thrips and TPP consumed by *O. vicinus* adults during 24-h experimental period as indicated by Manly's preference index (β) at various densities with an equal number of thrips and TPP.

Prey densities (Ratio 1:1)	Number of prey consumed		Preference index (β)
	Thrips	TPP	
4:4	3.87	3.73	0.56
8:8	7.6	7.06	0.58
16:16	9.33	6.67	0.62*
32:32	13.13	8.4	0.64*

* β significantly different ($p < 0.05$, Tukey HSD)

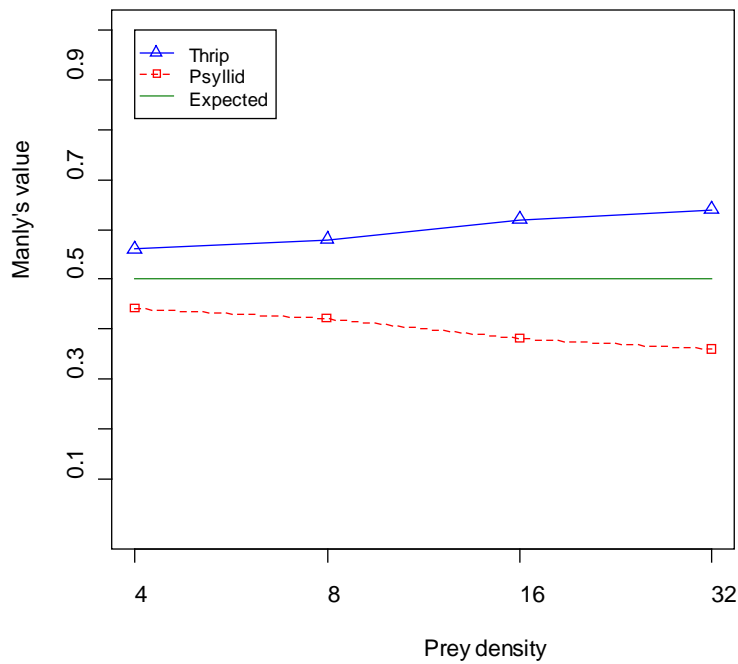


Figure 4.3: Manly's preference values for *O. vicinus* when offered thrips (nymph 1-2) and psyllid (nymph 1-2) simultaneously with various densities but in a prey ratio 1:1.

4.5 DISCUSSION

The functional response of *O. vicinus* suggests that *O. vicinus* is not only a consumer of eggs but also nymphs of all instars of *B. cockerelli*. The functional responses in this study showed that a number of eggs and nymphs in all instars of the prey eaten by the predator greatly increased as prey density increased but at a declining rate. Although the functional response of *O. vicinus* to the egg and nymphal instars 1-2 of TPP fits both Type I and II response, the Type II functional response fits the data slightly better than Type I based on the R^2 value (Table 4.2). Type I is a linear response, while Type II assumes that the predation rate increases at a decreasing rate, leveling off to a plateau. Both Type I and II functional responses were reported by Gitonga *et al.* (2002) for *Orius albidipennis* feeding on varying densities of *Megalurothrips sjostedti*. The Type II functional response is found to be the most frequent in insects and Fathi and Ganbalani (2010) reported Type II functional responses of *Orius niger* to second instar *Thrips tabaci*, *Orius minutus* to second instar *Thrips tabaci*, and *Orius minutus* to *Tetranychus urticae*. Examples of other studies of small insect predators are those by Dransfield (1979) who reported that *Aphidius uzbekistanicus* showed a Type II functional response to *Metopolophium dirhodum*, Zamani *et al.* (2006) reported Type II for *A. matricariae* and *A. colemani* to *Aphis gossypii*, Fathpour *et al.* (2004) reported Type II for *D. rapae* to *B. brassicae*, and Type II functional response has also been reported by Tahriri *et al.* (2007) for *A. matricariae* to *A. fabae*.

O. vicinus is mirid bug able to prey on eggs and all nymphal stages of TPP but its efficiency declines as density increases (Table 4.3). The handling time is a good indicator of consumption rate and predator efficacy because it reflects the cumulative effect of time taken during capturing, killing, subduing, and digesting the prey (Veerave and Baskaran 1997, Kasap and Atlihan 2010). The handling times for the different stages of TPP were different and in general, they increased as prey size increased. This result agrees with a study by Flinn *et al.* (1985) that reported handling time of the predator *Reduviolus americanoferus* feeding on leafhopper and pea aphid is proportional to the size of the prey, the larger the prey longer the time taken to eat it. Not surprisingly, longer handling times generally occur with larger prey because predators feed longer on one prey thereby reducing the predation rate such that a smaller proportion of the prey are eaten. Additional observations of the feeding patterns of *O.*

vicinus clearly showed that the predator is less capable of catching fifth instar nymphs of *B. cockerelli* than other stages of the prey. Variations in size of the prey appear to affect the handling time. Propp (1982) observed that the 5th instar of *Nabis americanoferus* took longer to consume larger prey than smaller prey. Therefore, a higher handling time of the predator feeding on instar 5 of TPP of this study is not unexpected, because instar 5 of TPP is more than 5 times larger in body width (1.1 mm) than instar 1 (0.2 mm). With larger prey items, *O. vicinus* needs to spend more time handling, subduing, killing and digesting its prey. Clearly, the efficiency of utilization of prey food by the predator may be most effective when *O. vicinus* preys on young (egg, first, and second instar of *B. cockerelli*). In addition, the Type II functional response curves showed that the proportions of TPP consumption by *O. vicinus* were higher at lower densities in all stages of *B. cockerelli*. The decline in consumption rate at higher densities might be due to the attainment of satiation (Mills 1982) although that effect would be presumably be manifested in handling time when digestive pause is taken into account. There was no shortage of prey at high densities. The higher proportion of prey consumption at lower densities suggested that the prey would be more effective at controlling TPP population at lower densities. A predator-prey model could confirm this capability but unfortunately detailed information about *O. vicinus* population dynamics is required. A detailed population model was beyond the scope of this thesis.

O. vicinus preferred western flower thrips (nymph 1-2) to psyllid (nymph 1-2) when the two prey were provided at the same densities. The preference indices (β) increased with increase of prey densities, implying that this predator exhibited density-dependent predation on thrips and inverse density-dependent response to the psyllid. No strong switching response was observed, where at high prey densities one prey species is not consumed due to a predator's preference for another prey species. Significant preferences were observed at higher densities of both prey (16:16 and 32: 32) (Table 4.5) and this reduced the functional response of the predator to the target prey (TPP in this case). While the predator appeared to preferentially consume thrips, it also responded to TPP. Observations show that one *O. vicinus* may consume an average of 13.1 thrips (nymph 1-2), but only 8.4 TPP (nymph 1-2) per day. When only TPP is present in a laboratory setting, the predator clearly showed that it can reduce the number of TPP present. However, in the field it is highly likely that predators will encounter more than one prey species in the same habitat.

In conclusion, from evidence of Type II functional responses and their consumption capacity (Table 4.1), I can suggest that *O. vicinus* may have a greater biocontrol potential at lower densities of *B. cockerelli*. The alternate prey used in this study did not cause the predator to switch completely and the size of the preference observed in this study may be of little predictive value determining the effectiveness of the predator in biological control program in the conditions of a glasshouse. This study is an initial laboratory study undertaken to determine the functional response of *O. vicinus* feeding on TPP and the preference of this predator to both thrips and TPP. It forms the basis for future research and provides some parameters for more detailed predator prey model. However, some factors such as plant architecture or plant traits (Krips *et al.* 1999, Pratt *et al.* 2002, Xu and Enkegaard 2010) may affect the searching and foraging behaviour of the predator. Thus, further studies for functional and numerical response and prey preference of *O. vicinus* to thrips and psyllid will be needed for an evaluation in long-term and realistic large-scale conditions at least in a plant.

Chapter 5 Forecasting models for *Bactericera cockerelli* (Sulc) (Hemiptera: Triozidae) based on degree days in New Zealand

5.1 ABSTRACT

The seasonal flight activity of the tomato-potato psyllid (TPP) *Bactericera cockerelli* (Sulc) was studied in field potato crops using sticky traps in four locations during 3 years in both the North and South Islands in New Zealand from November 2009 to March 2012. Temporal distribution models describing TPP adult flight activity in the field were constructed based on degree days (DD). The relationship between field flight data and the models based on accumulated degree days was well described by both the Weibull and bimodal models. However, the adult summer population development and subsequent flights of TPP in the field showed a bimodal abundance pattern in which the first peak abundance occurred between 722 to 749 degree days (above 7.1°C lower threshold) from a biofix on 1st November. The second peak occurred from 1189 to 1264 DD after the biofix. Detailed comparison and validation of each model with respect to the prediction of the timing of the peak population suggest that the bimodal model has better practical potential than the Weibull model for predicting the distribution of TPP in the field.

5.2 INTRODUCTION

The tomato-potato psyllid (TPP), *Bactericera cockerelli* (Sulc) (Hemiptera: Triozidae), is a key economic pest of potato and tomato. This insect has recently been identified as a vector of *Candidatus Liberibacter solanacearum*, the putative causal agent of zebra chip potato disease. Zebra chip presently causes millions of dollars in losses to the potato industry in the United States, Mexico, Central America, and New Zealand (Munyaneza *et al.* 2009). In New Zealand, both the psyllid and ‘*Candidatus Liberibacter*’ are now reported from potato crops in Auckland and Canterbury (Cameron *et al.* 2011).

Precise timing of spray applications or the introduction of biological control agents (in crops under cover) against TPP is crucial because recommended insecticides or predators or parasitoids are only effective at certain stages. More precise timing reduces costs and the

potential for resistance development as well as supports sustainable or integrated pest management practices. However, monitoring and observing the population development of any insect are time consuming, therefore a robust phenological model would assist growers to better time such measures (Schaub *et al.* 2005) and should be key to any successful pest management program. Phenological models can identify important events in an insect life cycle for researchers and growers to time their control practices. The identification of first emergence and peak abundance can help researchers or growers more effectively assess insect population development for the application of chemical or cultural control measures as well as provide growers with information on the best time to collect biological control agents for redistribution, or to make other management decisions (Skinner *et al.* 2006). For example, Wold and Hutchison (2003) successfully used a phenology model to detect emergence and predict a peak of adults *Lygus lineolaris* in the field. Baek *et al.* (2008) successfully used a degree day based model to predict the time of peak occurrence of *Helicoverpa assulta* in hot pepper fields. Additionally, Kumral *et al.* (2008) successfully used a phenology model to predict larval emergence patterns of the olive psyllid, *Euphyllura phillyreae* that could be used as a forecasting method for improved timing of insecticide applications.

An appropriate biofix, defined as the date to begin accumulation of degree days (Flint and Gouveia 2001) and temperature development thresholds which comprise a lower and upper thresholds (Flint and Gouveia 2001, Blanco and Hernandez 2006, Diaz *et al.* 2007, Akotsen-Mensah *et al.* 2011) are required to develop basic phenology models. The lower and upper temperature thresholds for TPP on potato have been estimated as 7.1 and 33.9°C, respectively (Tran *et al.* 2012, Chapter 2). The accuracy of degree-day models can be significantly enhanced by use of relevant biofixes that correspond to predictable biological events (Welch *et al.* 1981, Nowatzki *et al.* 2002). Often, first trap catch is chosen as a biofix. First trap catch can provide a good basis to calibrate the start of degree day accumulation in the absence of more detailed biological data, or events such as host plant phenology (Worner *et al.* 1995). The aim of this study was to predict the timing of population development and the identification of peak abundance based on air temperature degree day accumulations beginning from a biofix defined as the average date the first TPP is trapped in the field.

All phenology models should be calibrated or validated against observed field data. Because adult TPP are highly efficient vectors of *Candidatus Liberibacter solanacearum* compared with nymphs (Buchman *et al.* 2011), monitoring adults has become a key to the application of efficacious control practices wherever TPP causes problems in crops. Several sampling tools have been used for monitoring TPP such as sweep nets, vacuum sampling, yellow sticky traps, plant symptoms and plant sampling methods (Cranshaw and Hein 2004, Goolsby *et al.* 2007a,b). Using the knowledge gained from monitoring and sampling of the phenology and population dynamics, particularly of adult TPP, is important to refine current control practices.

5.3 MATERIAL AND METHODS

5.3.1 Trapping sites

Data from yellow sticky trap surveys at four locations (Pukekohe, Manawatu, Waikato and Lincoln) in New Zealand over a variable number of years were used to develop the phenology models, and to validate them by identifying the distribution and peak periods of adult TPP within potato crops throughout the growing season over the years 2009 to 2012.

Double-sided yellow sticky traps (each side measuring 100 × 250 mm; Bug-Scan®, Biobest Biological Systems) were placed in potato crops. Four to five traps were placed at canopy height of potato plants in each site. Each trap was secured at the top and bottom to a stake and replaced weekly. Traps were stored in A4 file copy pockets to allow identification of TPP through the clear plastic.

Trap capture data used in this study were collected in various locations throughout New Zealand (Table 5.1) by the author as well as staff of Plant & Food Research. Data used in this study were selected from pesticide-free potato crops. The seven data sets from a variable number of seasons at each site comprising weekly trap catches were used to develop and validate the models (Table 5.1). Only 5 of the 7 data sets could be used to develop models because they covered the full flight period such that the distribution of captures over time allowed predictions of 5, 50, 95% TPP cumulative trap captures in the field. Two data sets (Lincoln 2009-2010 and 2010-2011) did not cover the full flight period and were not

used to develop models. Trap count data within each week were pooled to obtain weekly trap captures.

Table 5.1: Summary of sample sites for TPP trapping in potato crops in various locations in New Zealand (from 2009-2012) used to develop and validate models that predict adult TPP trap captures in the field.

Years	Locations	Weather station
2009-2010	Pukekohe ^a	On site
	Manawatu ^a	Levin Aws
	Waikato ^a	Matamata, Hinuera Ews
	Lincoln ^b	Lincoln, Broadfield Ews
2010-2011	Pukekohe ^a	On site
	Lincoln ^b	Lincoln, Broadfield Ews
2011-2012	Pukekohe ^a	On site

^a used to develop and validate models, ^b used for validation only.

5.3.2 Temperature data

Air temperature data were obtained from weather station summaries published by National Institute of Water and Atmospheric Research of New Zealand (Table 5.1). Daily minimum and maximum temperatures for each site were interpolated from weather stations nearest each field. Air temperature degree-days (Celsius) accumulated from the biofix (November 1st) were calculated according to method of Arnold (1960) where:

$$\text{Degree days} = \frac{(T_{\max} + T_{\min})}{2} - (T_{\text{base}}) \times 1 \text{ day}$$

T_{\max} is the daily maximum temperature (°C), T_{\min} is the daily minimum temperature, and T_{base} is base temperature for insect development. In this study T_{base} is 7.1°C (Tran *et al* 2012, Chapter 2).

5.3.3 Forecasting models

The relationship between the cumulative percentage of TPP caught in the traps and degree days was modeled using a Weibull function and a bimodal equation. The two-parameter Weibull function has often been used to describe the distribution of insects completing a developmental stage in response to time or temperature (Pinder III *et al.* 1978, Wagner *et al.* 1984, McBrien and Judd 1998, Wold and Hutchison 2003, Kim and Lee 2008). The Weibull function equation is:

$$f(x) = 100(1 - \exp(-(x/a)^b)) \quad [1]$$

Where $f(x)$ is the cumulative percentage of insects captured, x is degree-days, and a and b are model parameters.

According to Kim *et al.* (2000), the Weibull function (Equation 1) can describe insect population patterns that have a single peak. However, this function may not be adequate for describing *B. cockerelli* population development because *B. cockerelli* populations appear to have two strong peaks during the main growing season (*e.g.* Fig. 5.1). Therefore, a nonlinear bimodal model was also fitted to the observed data using the matched-asymptotic method (Vollset *et al.* 1991). This bimodal model has been successfully used to describe spring emergence pattern of *Carposina sasakii* by Kim *et al.* (2000), and flight activity of adult *Helicoverpa assulta* by Baek *et al.* (2008). For this model, the equations of two sigmoid functions are combined. The two functions, with matched asymptote define the final model. The first function, that describes the first peak, is represented by a sigmoid equation (Equation 2).

$$f_1(x) = \frac{a}{1 + \exp(-\frac{x-b}{c})} \quad [2]$$

Where x is time in degree days, a is transition height which is the height of the first peak, b = transition center which is time in degree days at 50% trap captures of the first peak, and c is a parameter controlling the steepness of the first peak curve.

The second function is a logistic equation (Equation 3) and describes the second peak.

$$f_2(x) = \frac{d}{1 + (x/g)^f} \quad [3]$$

Where d is transition height, in other words is the height of the second peak ($= 100 - a$), g is the transition center which is the time in degree days at 50% trap captures of the second peak, and f is a parameter controlling the steepness of the second peak curve.

A combination of these two functions (Equation 4) is

$$f_3(x) = a \left\{ \frac{1}{1 + \exp\left(-\frac{x-b}{c}\right)} + \left(\frac{d}{a}\right) / \left[1 + \left(\frac{x}{b+e}\right)^f\right] \right\} \quad [4]$$

The parameters are defined as follows: a is the height of the first peak, d is the height of the second peak (= 100- a), b is time in degree-days of the first peak, c and f are parameters controlling the steepness of the first and second peak, respectively, and e is time in degree days between the first and second peaks.

5.3.4 Parameter estimates

The average first trap catch over all sites was chosen as a biofix (November 1st), in the absence of more detailed biological data or events such as host plant phenology.

Data from 5 sites: Pukekohe 2009-2010, Pukekohe 2010-2011, Pukekohe 2011-2012, Manawatu 2009-2010, and Waikato 2009-2010 (Table 5.1) were used to develop the models. Data from the field trap catches from 2009 to 2012 were converted to cumulative proportions. Models were parameterized on the weekly cumulative trap captures (dependent variable) and cumulative degree days (independent variable) calculated from the biofix (November 1st). Because of year to year variability in population numbers (Fig. 5.1, Appendix 1-7) the weekly trap capture data were normalized within each year by calculating the proportion of weekly trap capture of the total trap capture within the year. Parameters of models were estimated using nonlinear regression functions in R (R Version 2.9.2).

5.3.5 Validation of models

Each model was validated using leave-one-out cross-validation (Cawley and Talbot 2004, Lankin-Vega *et al.* 2008). Use of a separate data set for model validation allowed the generation of a data set that is independent of the data used to develop the DD models.

For leave-one-out validation 4 site-years were combined to develop a model then the remaining site-year was used for model validation. The result was five different data sets to use to develop five different models and five site-years for model validation as follows:

1) Combined 4 site-years (Pukekohe 2009-2010, Pukekohe 2010-2011, Pukekohe 2011-2012, and Waikato 2009-2010) to develop the model and used Manawatu 2009-2010 to validate the model (called Manawatu 09-10 model).

2) Combined 4 site-years (Pukekohe 2009-2010, Pukekohe 2010-2011, Pukekohe 2011-2012, Manawatu 2009-2010) to develop the model and used Waikato 2009-2010 to validate the model (called Waikato 09-10 model).

3) Combined 4 site-years (Pukekohe 2010-2011, Pukekohe 2011-2012, Manawatu 2009-2010, and Waikato 2009-2010) to develop the model and used Pukekohe 2009-2010 to validate the model (called Pukekohe 09-10 model).

4) Combined 4 site-years (Pukekohe 2009-2010, Pukekohe 2011-2012, Manawatu 2009-2010, and Waikato 2009-2010) to develop the model and used Pukekohe 2010-2011 to validate the model (called Pukekohe 10-11 model).

5) Combined 4 site-years (Pukekohe 2009-2010, Pukekohe 2010-2011, Manawatu 2009-2010, and Waikato 2009-2010) to develop the model and used Pukekohe 2011-2012 to validate the model (called Pukekohe 11-12 model).

The first peaks in Lincoln 09-10 and Lincoln 10-11 were not available because I started trapping after the time of first peak occurrence (see Appendix 1-7). However, because Lincoln 09-10 and Lincoln 10-11 were therefore independent data sets (that is, they were not used in constructing the models) they were useful for model validation. Both Lincoln data sets were used to validate each of the other five models separately.

The degree day accumulation for separate data sets and the parameters for each model were inserted into the Weibull and bimodal models to calculate the predicted rate of TPP trap captures. One way of comparing models between sites and years is to determine the relationship between predicted and observed trap captures using linear regression (Nowatzki *et al.* 2002, Borchert *et al.* 2004, Damos and Savopoulou-Soultani 2010). Models can be compared by comparing the slope and y-intercept values between observed and predicted trap catches. Linear regression also gives an idea of goodness of fit that is normally determined by calculating the coefficient of determination (R^2). Moreover, the fit of the Weibull and bimodal models can also be compared statistically based on Akaike's information criterion (AIC). A simple practical comparison between observed and predicted values in calendar dates was also used to further validate models.

5.4 RESULTS

5.4.1 Forecasting models

The Weibull function explained 98 - 99% of the variability between cumulative percentage trap captures and accumulated degree days for TPP. The bimodal function explained 99% of the variability between degree days accumulated and cumulative percentage trap captures for TPP (Table 5.2 and Fig. 5.2). Estimated parameters for the bimodal distribution for TPP in Table 5.2 showed that the parameter a , the height of cumulative first peak, was from 40.85 to 50.09%. Thus, about 49.91 to 59.15% of cumulative percentage trap captures occurred during second peak period. The first peak (b) and the second peak (parameters $b + e$) occurred between 722 to 749 DD and 1189 to 1264 DD post-biofix, respectively. The Weibull model did not adequately describe two apparent peaks of TPP trap captures in the field, and its prediction of 50% of total trap captures over the season ranged from 955 to 1050 DD a less precise prediction compared with the observed data than an estimate of 950 to 1105 DD when using bimodal model (Table 5.3).

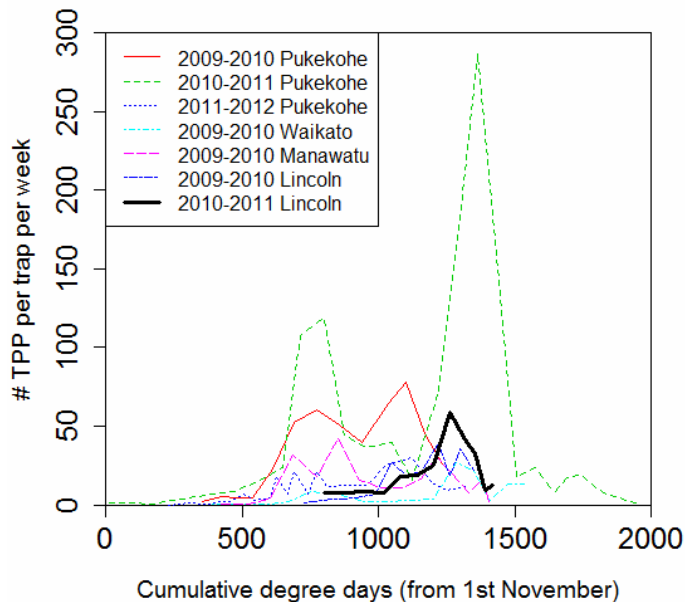


Figure 5.1: Number of TPP per trap per week in different locations from 2009 to 2012.

Table 5.2: Parameter estimates resulting from Weibull and bimodal analysis of *B. cockerelli* adults caught in sticky traps at 5 locations-years. The values in parentheses are standard error (SE).

Models	Parameters	Models				
		Manawatu	Waikato	Pukekohe	Pukekohe	Pukekohe
		09-10	09-10	09-10	10-11	11-12
Weibull	a	1128.14	1054.19	1154.49	1085.50	1154.39
		(9.39)	(8.00)	(12.26)	(7.12)	(10.63)
	b	3.69	3.79	3.71	3.79	3.89
		(0.15)	(0.15)	(0.2)	(0.13)	(0.19)
Bimodal	a	40.85	50.09	43.49	42.99	41.43
		(1.25)	(1.15)	(0.4)	(0.72)	(0.65)
	b	721.99	734.57	743.09	728.06	749.28
		(6.13)	(4.71)	(2.35)	(2.81)	(3.54)
	c	76.43	79.38	78.51	72.81	75.61
		(3.66)	(2.66)	(1.63)	(1.53)	(2.33)
	d	65.15	53.56	59.08	61.27	62.06
		(2.24)	(1.56)	(0.7)	(1.06)	(1.1)
	e	517.38	454.06	521.41	463.04	504.34
		(6.26)	(3.53)	(2.42)	(2.17)	(3.48)
	f	-11.12	-12.80	-15.6	-10.53	-14.12
		(0.62)	(0.6)	(0.37)	(0.27)	(0.46)
AIC	Weibull	150	144	164	137	158
	Bimodal	62	52	27	16	43
R ²	Weibull	0.980	0.992	0.981	0.992	0.980
	Bimodal	0.999	0.999	0.999	0.999	0.999

The two models estimated that 5, 25, 50, 75, and 95% cumulative trap captures over the sites and seasons should occur at between 480-540, 760-840, 955-1050, 1150-1260, and 1410-1550 DD post-biofix, respectively for Weibull model; and at 560-600, 735-780, 950-

1105, 1175-1275, and 1350-1430 DD postbiofix, respectively for bimodal model (Table 5.3). Although the Weibull distribution showed excellent fit to the data, its prediction accumulated degree days deviated more from observed than those of the bimodal distribution (Table 5.3).

Table 5.3: Observed and predicted in DD (minimal and maximal range for all sites) at given adult TPP trap captures of *B. cockerelli*.

Cumulative percent of TPP	Observed	Bimodal prediction	Weibull prediction
5%	570 - 605	560-600	480-540
25%	730-760	735-780	760-840
50%	950-1100	950-1105	955-1050
75%	1180-1275	1175-1275	1150-1260
95%	1350-1450	1350-1430	1410-1550

Linear regression statistics for observed versus predicted cumulative percentages of adult TPP trap captures are presented in Table 5.4. These statistics also show both bimodal and Weibull models fit the data well as shown by this method and as indicated by high values of the coefficient of determination R^2 ranged from 0.80 to 0.99 (Table 5.4).

On the whole, the bimodal function describes the observed data better than the Weibull function and has a smaller AIC and slightly higher R^2 than the Weibull model (Table 5.2). Of greater importance, however, is that the bimodal function describes and estimates two peaks of TPP flights as indicated by trap captures, with the first peak occurring from 722 to 749 DD, and the second peak from about 1189 to 1264 DD after biofix (Table 5.5).

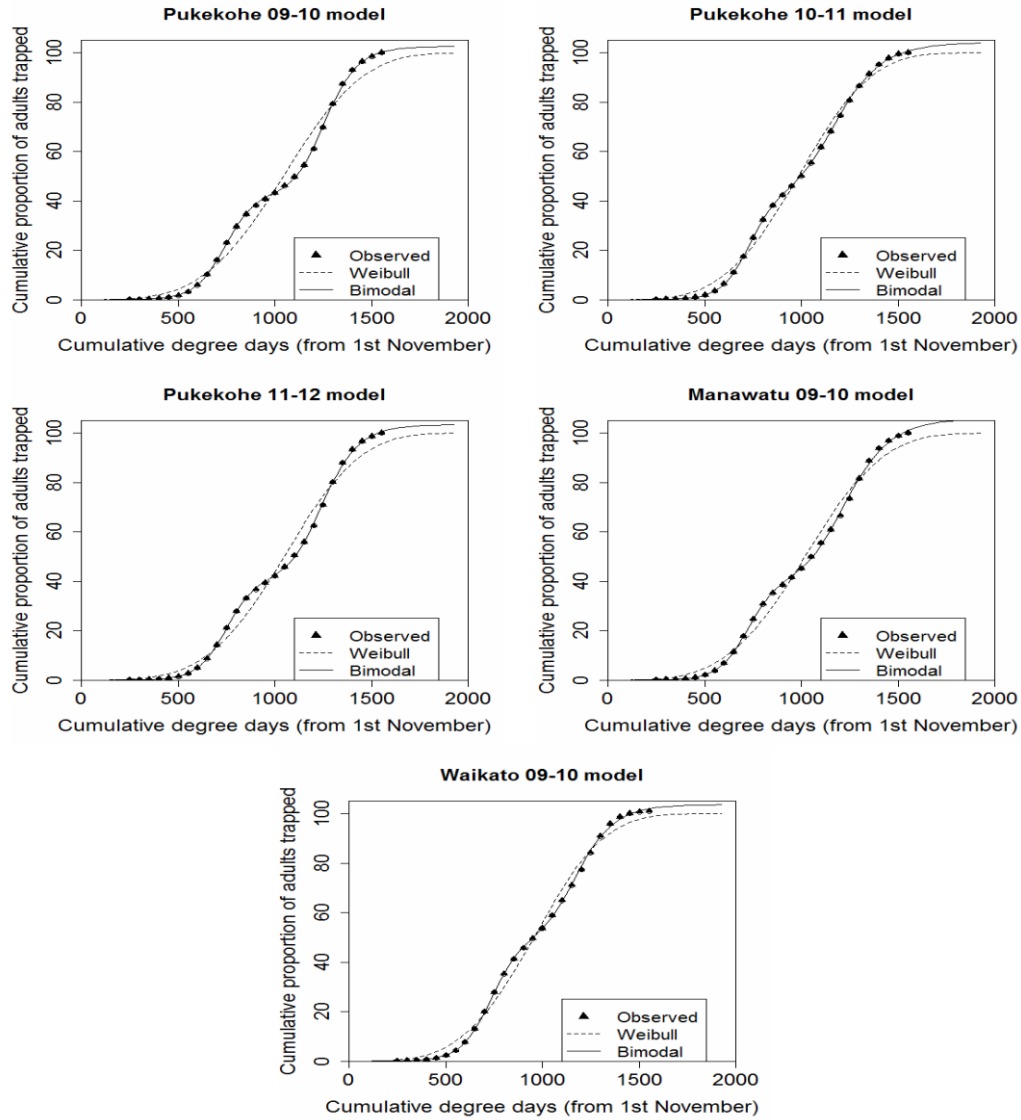


Figure 5.2: Observed and predicted cumulated adult trap capture pattern of *B. cockerelli* using Weibull and bimodal models.

Table 5.4: Regression statistics for predicted versus observed adult trap captures for *B. cockerelli* in different locations.

Models		Slope	Intercept	R ²	P-values
Manawatu	Bimodal	0.88 ± 0.019	1.57 ± 1.19	0.99	1.7E-16
09-10	Weibull	0.86 ± 0.029	2.7 ± 1.7	0.98	5.87E-14
Waikato	Bimodal	1.04 ± 0.124	18.52 ± 5.73	0.83	7.88E-07
09-10	Weibull	0.98 ± 0.129	20.21 ± 5.96	0.80	2.32E-06
Pukekohe	Bimodal	0.63 ± 0.028	1.74 ± 1.49	0.98	1.47E-10
09-10	Weibull	0.68 ± 0.016	1.13 ± 0.87	0.99	1.89E-13
Pukekohe	Bimodal	0.99 ± 0.064	7.92 ± 3.79	0.94	4.01E-11
10-11	Weibull	0.96 ± 0.07	9.57 ± 4.21	0.92	3.63E-10
Pukekohe	Bimodal	0.74 ± 0.028	-3.09 ± 1.40	0.97	1.96E-16
11-12	Weibull	0.74 ± 0.04	-2.91 ± 1.76	0.96	1.09E-14

5.4.2 Model validation

The leave-one-out cross-validation described in the methods created five independent data sets to validate five models (Table 5.5). Model validation shows that the Manawatu 09-10 models can predict very well the first and second peak of TPP trap captures with the error smaller than 3.8 days (Table 5.5). The least effective of the five models is Pukekohe 10-11 model that predicted the second peak of TPP trap captures with the maximum error of 15.9 days (Table 5.5). In Table 5.5, I used data collected in Lincoln, Canterbury for validation only.

Table 5.5: Model validation using independent data set (leave-one-out cross-validation) by degree day (DD) and day (d) (Early predictions produced positive values and late predictions produced negative values).

Models	Peak	Observed	Predicted	Observed-Predicted
Manawatu 09-10	1 st	686 DD	722 DD	-36 DD (-3.8 d)
	2 nd	1211 DD	1239 DD	-28 DD (-2.9 d)
Waikato 09-10	1 st	757 DD	735 DD	+22 DD (+2.2 d)
	2 nd	1283 DD	1189 DD	+94 DD (+9.4 d)
Pukekohe 09-10	1 st	775 DD	743 DD	+32 DD (+3 d)
	2 nd	1102 DD	1264 DD	-162 DD (-15 d)
Pukekohe 10-11	1 st	799 DD	728 DD	+71 DD (+6.6 d)
	2 nd	1363 DD	1191 DD	+172 DD (+15.9 d)
Pukekohe 11-12	1 st	775 DD	749 DD	+26 DD (+2.4 d)
	2 nd	1118 DD	1253 DD	-135 DD (-12.5 d)
*Lincoln 09-10	1 st	NA	NA	NA
	2 nd	1218 DD	1189-1264 DD	-46 to 29 DD (-5.6 to 3.6 d)
*Lincoln 10-11	1 st	NA	NA	NA
	2 nd	1260.5 DD	1189-1264 DD	-4.5 to 71 DD (-0.6 to 8.7 d)

* Lincoln 09-10 and Lincoln 10-11 are not models but were used for validation of all other five models. It is for this reason that a range of values are presented here, this range encompasses output from all five model validations.

NA is not available because traps placed after the first peak at Lincoln, Canterbury and these data were not used to develop models.

Days were converted from DD (average daily DD above 7.1 °C from 1st November to 31st March for three years in Lincoln, Manawatu, Pukekohe, and Waikato as 8.1; 9.5; 10.8; and 10.0 DD, respectively).

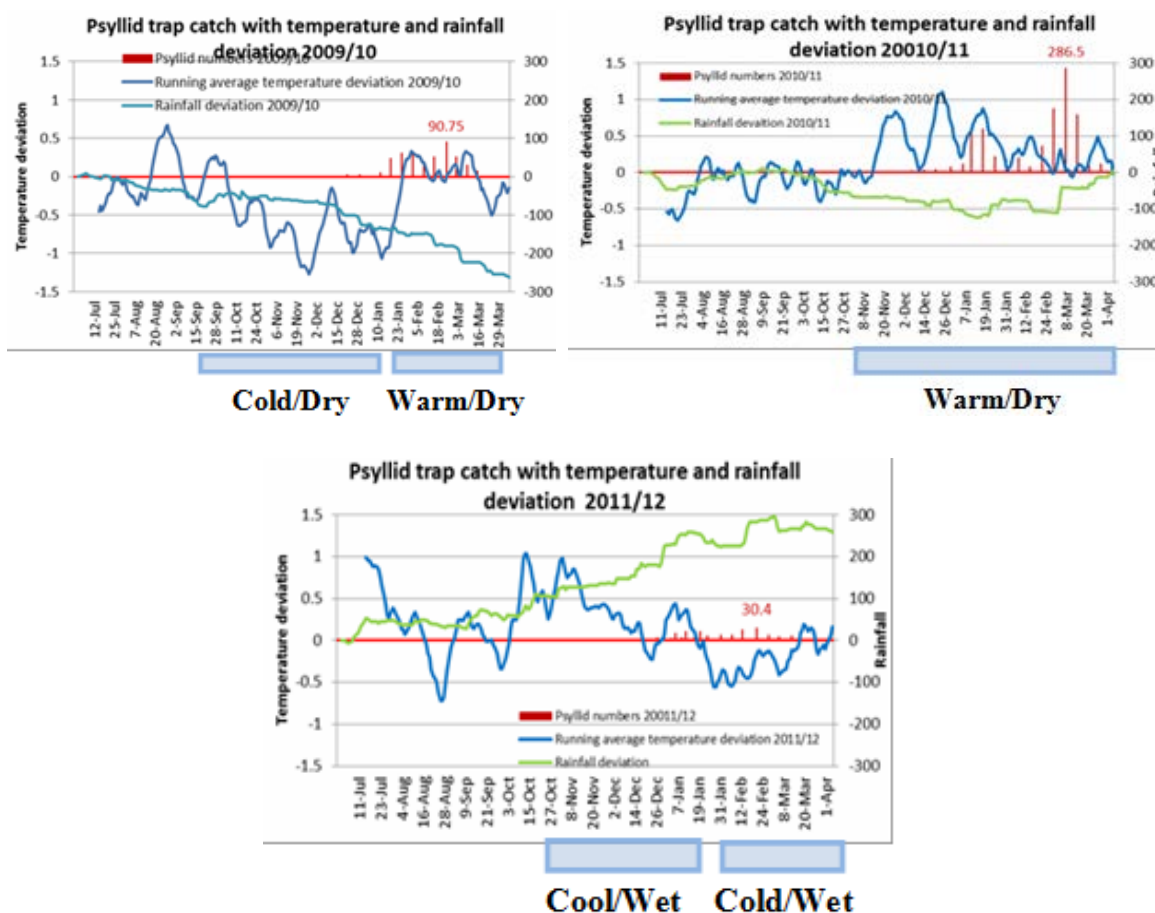


Figure 5.3: Difference between running average temperature and rainfall deviation for each season compared with the average over the three seasons at Pukekohe.

The differences between the annual running average temperatures and rainfall for each season at Pukekohe compared with the average over the three seasons are shown in Figure 5.3. The red horizontal line is the average temperature and rainfall over the three seasons. The red vertical bars are the weekly trap catches. The blue lines are the running average (averaged daily over the previous seven days to smooth the trace) temperature differences and the green line the running average rainfall deviations.

Clearly, timing of warm, cold, wet and dry periods influences population numbers. In Figure 5.3, the 2009-10 season was cooler overall, influencing degree day accumulation. The 2011-12 season had very warm temperatures in early winter as well as October November and December resulting in high DD accumulation compared with the 2009-10 season. However, for that season (2011-2012) population numbers were very low probably because it

was very wet with colder temperatures over late December, January and February (Fig. 5.3). Figure 5.3 also shows that mean weekly catch of psyllid adults in sticky traps is affected by precipitation and temperature. For example, the second peak trap captures of psyllids for the 2010-2011 warm-dry season was 287 psyllids per trap per week, in contrast, only 30 psyllids per trap per week for the 2011-2012 cold-wet season in Pukekohe (Fig. 5.1 and 5.3). However, no relationship between the timing of the first or second peaks of psyllid trap captures and precipitation was found. Although Pukekohe 2011-2012 had a much higher amount of rainfall, the first and second peak of psyllid trap captures occurred earlier than that of Pukekohe 2010-2011.

5.5 DISCUSSION

Degree day models can play important roles in integrated pest management by providing a means of predicting insect development, and therefore providing more precise timing for implementation of control activities (Broatch *et al.* 2006). The results of this study show that the trap capture pattern of psyllids during summer can be predicted using degree days. Depending on years and locations, the population of psyllid adults was first captured in traps in late October to early November, with two peaks in abundance over the growing season. The first peak occurs in late January to early February, the second peak in early to late March. Numbers gradually decline until the crops desiccated.

In general, there was a good fit between observed and predicted data for *B. cockerelli* trap captures in all sites, the parameters of the two models vary between years and locations. However, such variation is not unexpected, because errors such as temperature measurements, and sample estimates of population sizes varied among data collection in different sites and years. Regardless of the errors and other difficulties that caused the model predictions to deviate from observed values during the growing season, all slopes and intercepts of regressions were still very similar to each other for each site-year and still within reasonable limits (Borchert *et al.* 2004, Damos and Savopoulou-Soultani 2010). However, the comparison between predicted and observed trap catches (Table 5.3) showed that the Weibull was less accurate than the bimodal model. For example, at 5 percent of cumulative psyllid trap captures, observed values ranged from 570 – 605 DD, bimodal

predicted values ranged from 560 – 600 DD (within the range of observation), and Weibull predicted values ranged from 480 – 540 DD (outside the range of observation). Based on the overall performance of two models, the results showed that the bimodal distribution can predict better than the Weibull model with smaller AIC and higher values of R^2 in most cases (Table 5.2).

Many applied entomology models that attempt to predict the timing and abundance of insects are based on temperature only. Graphical representations such as those presented in Figure 5.3 based on normalized data, can help interpret population dynamics expressed as a time series in relation to other important environmental variables. Including other variables such as precipitation may help explain fluctuations in population abundance over sites and seasons to indicate interesting hypotheses and useful future research to refine initial models.

The first peak of psyllid trap captures could be predicted by the bimodal model with at most an error of 6.6 days. More variation was found for the second peak with the greatest error being 15.9 days (Table 5.5). This is probably due to the greater overlap of psyllid generations at that time making it more difficult to identify the true peak in psyllid abundance.

For the bimodal model to be useful for pest management it is likely that data of several years and a separate model for each region are required. Because of the need for more regional data and because the economic threshold for TPP is low due to rapid transmission of *Liberibacter* (Lacey *et al.* 2011), the bimodal model may have limited practical application. The most important event is to predict the beginning of the flight period in each region for control purposes before population build up. A more practical application for degree day accumulations is discussed in Chapter 6. The bimodal model however may be used to predict the first peak and second peak of adult psyllid in the fields in New Zealand.

In summary, for the data available for this study the bimodal distribution model appears to provide the better model than Weibull model of adult psyllid abundance as indicated by trap captures. In particular, the bimodal model can provide precise predictions for the first peak of adult psyllid compared with calendar days. For many insects, precise timing of population development and peak abundances are extremely important for growers to make decisions to enable them to synchronize scouting with other management activities related to insect developmental stages. While, the bimodal model developed in this study

may not find practical application in potato crops in New Zealand in its present form, In the future, the model could be improved by the addition of developmental parameters and events of immature stages of the psyllid based on long term data on a wide range of potato crops in different sites and years. I anticipate that further data observations can help to refine the models predict more precisely the first occurrence of TPP on the crop to assist improved management of TPP in the field.

Chapter 6 General discussion

6.1 OVERVIEW OF THE STUDY

Bactericera cockerelli (Sulc) has been a major pest of solanaceous crops for decades (Butler and Trumble 2012). The historical distribution of this serious pest was America (Wallis 1951), namely Central America (Secor & Rivera-Varas 2004) and the southern United States (Munyaneza *et al.* 2007a). More recently, this insect invaded and became an important pest in New Zealand (Gill 2006, Teulon *et al.* 2009). Many studies have been conducted to determine the relationship of this pest to plant injury and to develop management strategies to alleviate the damage caused by this pest in a wide variety of solanaceous plants (Butler and Trumble 2012). Studies in the past decade have focused on the genetic variability in this invasive species, the interactions between this insect and the pathogen (*Candidatus Liberibacter solanacearum*) it carries, and the potential of the insect and the pathogen to cause economic damage to crop plants (Butler and Trumble 2012). The population dynamics of this insect has not been documented very well and is needed for more detailed study of development of this insect to assist greater preparedness for control. Because of this the objectives of this thesis were to: 1) determine important developmental parameters that describe population growth of TPP in relation to temperature; 2) determine important life history parameters of *B. cockerelli* feeding on potatoes under laboratory condition; 3) determine the efficacy of a selected natural enemy, *O. vicinus* for regulation of TPP population, potentially in glasshouses particularly in the presence of alternative prey, and, 4) develop and compare forecasting models based on the relationship between the psyllid and climate to predict population phenology, seasonal timing and potential abundance.

The research comprised both laboratory experiments and field studies. In Chapter 2, experiments were performed in controlled temperature cabinets to determine the temperature-dependent development of TPP. Life table parameters of this psyllid were determined and described in Chapter 3. The functional response and prey preference of predatory *O. vicinus* feeding on psyllid and thrips were outlined in Chapter 4. In Chapter 5, field monitoring data

of psyllid trap captures around New Zealand were combined with accumulated degree days to develop preliminary forecasting models of psyllid in the field.

6.2 TEMPERATURE-DEPENDENT DEVELOPMENT

One of the critical areas of knowledge for any pest species that is relevant for its management is to determine its developmental rate over a range of temperatures. Such information can then be used to relate development to temperature through physiological time (in this case degree days) that can often give a more accurate estimate of important life cycle events over different seasons and locations compared with calendar days or chronological time. Thermal summations or degree days have been used successfully over many years for forecasting insect development and phenology to form the basis of management decisions (Worner and Penman 1983, Kuhrt *et al.* 2006).

The developmental time and survival rate of *B. cockerelli* were assessed on potato and tomato plants over a range of temperatures in the laboratory. As expected the developmental duration of all psyllid stages was affected by temperature. Based on those development times, regression analysis was used to estimate the lower and upper temperature thresholds, the optimum temperature, and the degree day requirements for psyllid development. Regression models were fitted to the development rates versus temperature data for the psyllid egg stage, nymphal stage, and total development (egg-adult), respectively. All were well described by linear regression equations as indicated by high R^2 values (ranging from 0.83 to 0.97). The lower temperature threshold estimated for total development was 7.1°C reared on potato and 7.5°C reared on tomato. The number of degree days required for the psyllid to complete the egg-adult developmental period, based on estimates of development at constant temperatures, was 358 DD for psyllids reared on potato and 368 DD reared on tomato. The optimum and upper temperature threshold were estimated by nonlinear models. The Briere nonlinear model was found to provide a slightly better fit than the Lactin nonlinear model with optimum temperatures of 26.9°C for psyllids reared on potato and 27.1°C for psyllids reared on tomato. Upper temperature thresholds were estimated as 33.9°C for psyllids reared on potato and 34.1°C on tomato. The approach chosen to estimate the lower temperature threshold for *B. cockerelli* was the linear model while the Briere nonlinear

model was used to estimate the optimum temperature and upper temperature threshold for the development of TPP. These lower and upper temperature thresholds are key developmental parameters that, along with degree day requirements, are used to develop temperature-based phenology models. The phenology models have long been used as part of decision support systems to help growers predict spray timing or begin pest scouting (Welch *et al.* 1978, Worner and Penman 1983, also see <http://www.nappfast.org/>). Practical use of degree day models is described in more detail below.

There was very high mortality (90%) of TPP at 8°C reinforcing the idea for a lower threshold for development around 7.1° C. This suggests that *B. cockerelli* may not be very cold tolerant and needs to find a refugia to survive during cold periods. Mean temperatures over the winter season in New Zealand in sites where field data were collected in this study were 8.9, 10.1, 9.2, and 6.8°C for Waikato, Pukekohe, Manawatu, and Canterbury, respectively. This may explain why TPP is only found in small numbers on its secondary hosts in the field at this time in many parts of New Zealand.

As far as can be ascertained, there is only one other study (Marin-Jarillo *et al.* 1995) that estimated the lower temperature threshold (7.0°C) and thermal requirement (355 DD) of *B. cockerelli* on tomato. These estimates were confirmed by this research, however, Marin-Jarillo *et al.* (1995) did not specify the humidity and photoperiod in which their study was carried out. Also they used a smaller range of temperature (16-29°C) than this study (8-31°C). In addition, the Marin-Jarillo *et al.* (1995) study did not estimate an optimum temperature or upper temperature threshold. Overall, this study confirmed the lower temperature threshold and provided an estimate of an optimum temperature and the upper temperature threshold of TPP's development. Such information can be used in more detailed models of population projection and was originally used as a guide for carrying out life table studies at near optimum conditions.

6.3 LIFE TABLE PARAMETERS

The development of a laboratory rearing method for *B. cockerelli* enabled the basic demographic parameters of this species to be determined. These parameters can underpin useful applications: analyzing population stability and structure, estimating extinction

probabilities, predicting life history evolution, predicting outbreak in pest species, and examining the dynamics of colonizing or invading species (Vargas *et al.* 1997, Haghani *et al.* 2006). Demographic information may also be useful in constructing population models (Carey 1993) and understanding interactions with other insect pests and natural enemies (Omer *et al.* 1996). Life table parameters such as reproduction, fecundity, oviposition, and lifespan for *B. cockerelli* were determined on potato at a constant temperature of 25°C (Chapter 3). While there have been some studies to determine the life history parameters of TPP at different temperatures and on different plant species (eg. Yang and Liu 2009, Yang *et al.* 2010), the data in my study are among the most extensive established for TPP. While temperature is the most important factor in determining the rate of development, the host plant species is also important to life history. Different host plant species often vary in suitability for specific insects in terms of their effects on survival, development, and reproductive rate (Yang and Liu 2009). For example, development time was shorter and survival greater when *B. cockerelli* were fed on eggplant compared with bell pepper (Yang and Liu 2009). Under laboratory conditions in this current study it was determined that potato is a better host plant for *B. cockerelli* immatures than tomato, based on shorter developmental times (Chapter 2, Tran *et al.* 2012). Along with the studies of Yang *et al.* (2010) and Yang and Liu (2009), I further confirmed that potato is a better host plant for *B. cockerelli* immatures than eggplant and bell pepper.

With respect to TPP survivorship and mortality on potato in laboratory studies, the highest mortality occurred during the egg stage (29%) followed by the first instar (17%) in my study, as is known for many insects (Begon and Mortimer 1981, Win *et al.* 2011). Over 94% of the 5th instar TPP successfully became adults. The pre-oviposition period was 7.9 days (141 DD) with a range from 6-11 days (107-197 DD). Interestingly, the oviposition period, 43.6 days (780 DD), with a range from 19-80 days (340-1432 DD) in my study is similar to that of Yang *et al.* (2010) who reported that the oviposition period of TPP reared on potato was 43.9 days. Such a long oviposition period may partly explain why there are always overlapping generations of psyllids in the field over a single growing season. Collett (2000) reported that growth and development of other psyllid nymphs occur throughout most of the year. The total developmental period for pre-adult stages was 23.02 days at 25°C, whereas adults lived as long as 51.47 days, and 34.13 days for female and male respectively

at this temperature. Such adult longevity may help explain why, along with other cardiaspine psyllid species (brown lace lerp) studied by Collett (2000), TPP is likely to have overlapping generations in the field in favorable environments.

A mean maximum oviposition rate of 21.7 eggs per day was observed for one female of *B. cockerelli* (Table 3.4). The mean total oviposition of one female was 388 eggs (Chapter 3). The levels of fecundity of TPP observed in this study is very close to that determined by Yang *et al.* (2010) who reported a total individual fecundity (of TPP reared on potato at $26.7 \pm 2^\circ\text{C}$) of 400 eggs. Data presented here falls within the range of cardiaspine psyllid species reported as ranging from 45 to 700 eggs per female by Collett (2000). The net reproductive rate or the average number of offspring a female would have during her lifetime is an important indicator of population dynamics (Varley and Gradwell 1970, Kumral *et al.* 2007). It is a key statistic that summarizes the physiological capability of an animal relative to its reproductive capacity (Kumral *et al.* 2007). Comparison of net reproductive rate often provides considerable insight beyond that available from the independent analysis of individual life history parameters (Liu *et al.* 2004). For example, the net reproductive rate may reflect the potential of a certain host plant to increase TPP fitness and therefore population size. The net reproductive rate (R_0) of *B. cockerelli* on potato was found to be 73.2 ± 4.5 , indicating that *B. cockerelli* is capable of increasing its population numbers hugely within a generation despite a high mortality rate (46%) in the egg and first instar stage. The net reproductive rate observed in this study was higher than that reported by Yang and Liu (2009) on bell pepper ($R_0 = 59$), and on tomato ($R_0 = 7 - 12.40$) reported by Madriz *et al.* (2011) but lower than that reported by Yang and Liu (2009) for TPP reared on eggplant ($R_0 = 84.51$). With respect to its potato host, the net reproductive rate ($R_0 = 73.2$) observed in this study was much lower than the $R_0 = 102.9$ observed in the study by Yang *et al.* (2010) of TPP on potato. The difference may be due to the difference between the temperatures used in two studies. The current study was carried out at 25°C while the study by Yang *et al.* (2010) was carried out at 26.7°C . The cohort life table in this study was constructed based on an unlimited food supply in the environment free from natural enemies. Therefore, predators or parasitoids are not included as mortality factors on TPP development. Further studies are needed to elucidate more specifically the importance of mortality factors as a result of natural

enemy populations and their ability to provide biological control for TPP on crops under field and glasshouse conditions.

6.4 FUNCTIONAL RESPONSE AND PREY PREFERENCE

Predators play an important role in biological control and thus can be economically important within production systems (Siddique 1985). *Orius vicinus* is a generalist predator of several phytophagous pest species including bark lice, psyllids, thrips, aphids, and leafhoppers (Lewis and Lattin 2010). This predator was suggested to be an effective biological control agent against pests in apple and stonefruit orchards in New Zealand, and in greenhouses if mass-reared and released (Lariviere and Wearing 1994).

I evaluated the potential of the predatory bug *O. vicinus* as a potential biological control of *B. cockerelli* and especially in glasshouses. Two aspects were studied: 1) the functional response of *O. vicinus* to varying densities of *B. cockerelli*; 2) the prey preference of *O. vicinus* between psyllid and western flower thrips at various densities. Functional response analyses are often used to compare two or more candidate biological control agents. The most effective biological control agent is expected to be one that exhibits Type III functional response (Murdoch and Oaten 1975). In this study, *O. vicinus* exhibited Type II functional response (Chapter 4), which means that the predation rate or the proportion of population predated decreases with an increase in *B. cockerelli* density. A Type II functional response indicates an inverse density-dependent relationship between the predator and the host populations, and thus such predators are thought not able to regulate a prey population. An effective predator must remove an increasing proportion of the prey population as it grows to be able to regulate it thereby producing stable population dynamics. Based on this theoretical prediction, it seems *O. vicinus* would not be expected to be an effective biological control agent of TPP. One might expect that the Type II response of *O. vicinus* will mean that there are likely to be frequent outbreaks and crashes in the host and predator populations predicted by inversely density-dependent population dynamics. However, this functional response study was conducted in closed Petri dishes. According to Van Lenteren and Bakker (1977), many studies on functional response in laboratory may suffer from the artificiality of laboratory experimentation.

In addition, if the TPP population greatly exceeds the relatively low level at which the predatory bugs are satiated, then the predators are unlikely to be effective against the psyllid. The functional responses of predators tend to level off due to satiation, causing the maximum predation rate to settle at much lower values than expected from the predator's time budget for handling and searching (Sabelis 1992, Isikber 2005). Therefore, this could limit the success of TPP control by *O. vicinus*.

The functional response of the predator to the target prey is dependent on species of alternative prey (Musthapa 2010), where the presence of the alternative prey can affect the number of target prey eaten by predators. One obvious effect is that the pursuit, capture and consumption of alternative prey reduce the encounter time available for predators towards the target prey (Chesson 1989). For example, consumption of corn earworm eggs (target prey) by big-eyed bugs (predator) dropped over fivefold when pea aphids (alternative prey) were present, from an average of 11.18 to 2.00 (Eubanks and Denno 2000). In the case of abundant alternative prey species, predators may develop a search pattern resulting in a preference for the more common species (Murdoch and Oaten 1975, Tschanz *et al.* 2007). In population dynamics studies, prey switching is usually modeled as a sigmoid functional response and it may play an important role in elevating the persistence of predator-prey systems (Van Baalen *et al.* 2001). Switching occurs when predators change to alternative prey when the density of their preferred prey is low (Murdoch 1969). In the current study, the predator *O. vicinus* preferentially consumed the western flower thrips over the target prey TPP. While the predator appeared to preferentially consume the thrips, *O. vicinus* also responded to TPP. In the more straight forward functional response experiments with only TPP, the predator clearly showed that it may have potential to reduce a TPP population especially the juvenile stages under circumstances of inundative release in a glasshouse. However, to fully determine that potential, would require further research to determine the numerical response of the predator to predation. Knowledge of the numerical response would allow the impact of predator consumption on prey populations using the combination of functional and numerical response, to be assessed. It is possible that the combination of functional and numerical responses of the predator will result in a direct density dependent response where an increasing proportion of prey are predated (up to some level) as the prey population increases and thus the population is regulated.

In this study, the functional response and the effects of alternative prey of *O. vicinus* alone may only give an indicative predictive value in determining effectiveness of the predator in a biological control program of TPP. However, the responses do indicate that this predator will consume both TPP and thrips. This means that the predators can remain in the crop and maintain themselves on thrips (or similar non-target prey) if the TPP population is at low density. While laboratory experiments with single- prey and two-prey systems, may not give completely confident predictions about the effectiveness of *O. vicinus* for augmentative biological control of TPP in a greenhouse or field, nevertheless, the functional responses of *O. vicinus* feeding on TPP and prey preference of this predator on thrips and TPP serve as a useful guideline for estimating the potential impact of this predator on both thrips and TPP populations and for the design of further studies.

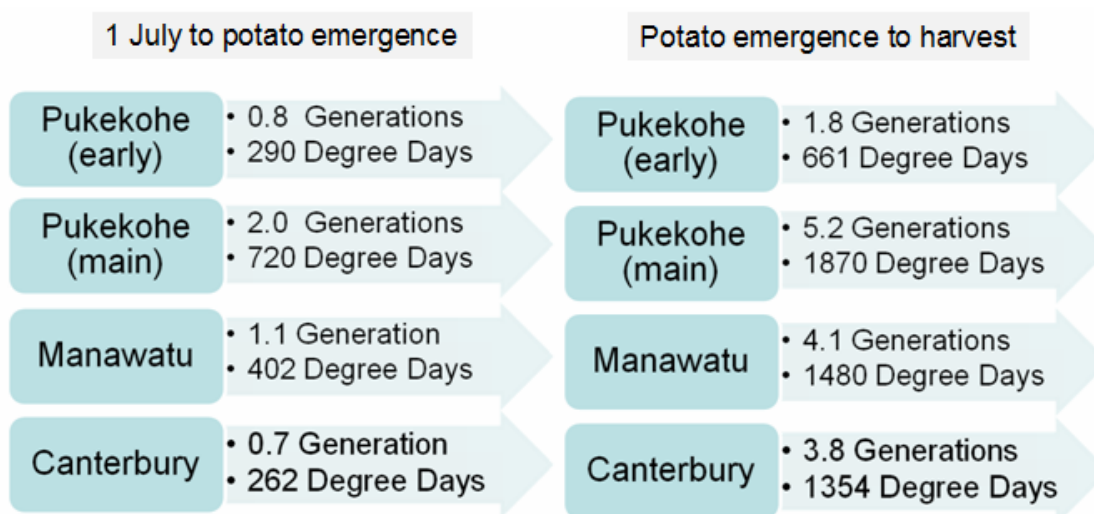
6.5 MONITORING

Phenological models are useful for predicting the timing of events in an insect's life-cycle for pesticide or natural enemy applications or monitoring assessments. The main purpose of the models described in Chapter 5 is to allow growers or entomologists to predict the time of peak flight activity of adult TPP in the field in order to attempt to better target spray applications. This may lead to a reduced number of applications. Because adult psyllids are highly efficient vectors of *Candidatus Liberibacter solanacearum* compared with TPP nymphs (Buchman *et al.* 2011), the particular focus in the TPP forecasting models and monitoring data used in this study was to estimate the timing of adult TPP peak flight activity in a number of critical sites around New Zealand.

Monitoring TPP was carried out at weekly intervals during growing seasons for three years (2009-2010, 2010-2011, and 2011-2012) using yellow sticky traps in unsprayed potato crops in various locations in New Zealand. The phenological pattern of TPP indicates that adult TPP have two peaks in abundance during a potato growing season in the field. The time of the first peak has important implications for timing of control measures as the peak egg infestation of TPP is reported to be related to the trend of adult trap captures (Walker *et al.* 2011). The pre-oviposition period of TPP is 7.87 ± 1.35 days under laboratory condition at 25°C (Chapter 3) suggesting that under optimum conditions the first peak of TPP eggs might

be one week after the first peak in adult abundance. Because the average temperature at the first adult TPP peak from late January to early February (Chapter 5) is around 20 °C and egg incubation needs about 7 to 8 days (Chapter 2, Tran *et al.* 2012), we can use this information to estimate the time of maximal abundance of 1st instars of TPP in the field. For example, the first adult TPP peak on 5th February under environmental conditions of around 20°C, provides an estimate of the time of maximal abundance of 1st instars based on the total time of pre-oviposition period and incubation period of $7.87 + 7.34 = 15.21$ days after 5th February (Assuming the pre-oviposition period at 20°C as same as at 25°C).

The research in this thesis contributes new knowledge about the life cycle of this psyllid species and has identified areas in the knowledge base for further research. In addition to continuing to increase understanding of TPP biology and ecology, future research needs to develop action thresholds for the control of this species appropriate for the various crop management systems. Also accumulating more detailed knowledge about the interactions of the psyllid, the disease it vectors and its host plants and natural enemies will be important. Such research, should lead to more sustainable management of this pest. For example, in the present study I estimated the developmental threshold of *B. cockerelli* to be 7.1°C reared on potato and 7.5 °C for psyllids reared on tomato, with a thermal budget of 358 degree days on potato and 368 degree days on tomato. Using this data we can estimate approximately how many generations of *B. cockerelli* might occur per year for specific sites throughout New Zealand. Figure 6.1 shows the number of generations of TPP in different potato growing sites in New Zealand. For early crop potatoes at Pukekohe only 0.8 generations occur from July 1st until potato emergence (Fig. 6.1) and 1.8 generations on the crop (emergence to harvest). For main crop potatoes at Pukekohe, 2 generations occur from July 1st until potato emergence and 5.2 generations on the crop. In contrast, for the main crop in the cooler temperatures in Canterbury only 0.7 generations occur before potato emergence, and only 3.8 generations on the crop. Note that Pukekohe has potato hosts available much longer than that in Canterbury due to an early crop in addition to main crop.



Based on weather data from 2002-2012
Pukekohe - early: emergence 15 Sep, harvest 15 Dec
Pukekohe - main: emergence 21 Nov, harvest 31 May
Manawatu – main: emergence 27 Oct, harvest 7 Apr
Canterbury – main: emergence 27 Oct, harvest 15 Apr

Figure 6.1: Degree days available and number of generations of TPP on potato crops at different sites in New Zealand. Degree days are calculated from July 1st.

To show the potential variability of TPP phenology, the estimated dates on which each generation (egg to adult) completes for Pukekohe over a range of years is shown in Figure 6.2. For the 2011-12 season, TPP development is nearly 1 month ahead compared with other years. For example, the third generation occurs on 30th December for the 2011-12 season compared with 24th January in the 2009-2010 season.

Because the economic threshold for TPP is low due to rapid transmission of *Liberibacter* as discussed in Chapter 5, the predictions of the first and second peak of adult TPP in the field may be of limited practical application. In other words, the limitation of the forecasting models in this thesis is the inability to forecast the first occurrence of adult TPP in the field. Accurate prediction of the first occurrence of TPP is essential for its management. To overcome this limitation, clearly more data is required to refine and validate the degree day and other forecasting models described in Chapter 5. More long term monitoring data of adult TPP and plant phenology (including phenology of secondary hosts) is needed at various locations and years. Since plant development is also temperature dependent, monitoring potato plant phenology, such as emergence dates can be used to track

and adjust degree day accumulation, as well as provide potential biofix to predict TPP activity. Additionally, there may be opportunities to use the detailed life cycle parameters in a more detailed population model that can show projections and possibilities of population dynamics under different environmental conditions.

2009-10	-	-	-	1 (17 th)	-	2 (15 th)	3 (24 th)	4 (23 rd)	5 (31 st)
2010-11	-	-	-	1 (18 th)	-	2 (6 th)	3 (7 th)	4 (6 th)	5 (8 th)
2011-12	-	-	-	1 (5 th)	2 (24 th)	3 (30 th)	-	4 (2 nd)	5 (7 th)
Month	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar

Generations from 1 July based on Degree Days Accumulation for Pukekohe

Figure 6.2 Estimated dates on which each generation (egg to adult) completes for Pukekohe based on accumulated degree days.

6.6 SUMMARY

With regard to the objectives of this thesis which were given in the introduction (Section 6.1) the following conclusions were reached:

- Various details of the temperature-dependent development of TPP have been elucidated. These include the thermal constant, the optimum temperature, and the upper and lower temperature thresholds of the egg, nymph, and total development (egg to adult) (Chapter 2).
- From the life tables constructed using the data obtained from laboratory experiments, important information on the life history parameters that regulate the population dynamics of TPP has been determined and discussed in Chapter 3.
- The Type I and II functional responses of predatory bug *O. vicinus* feeding on TPP at various stages were determined. This study also indicated that *O. vicinus* has a preference for thrips over TPP but that preference is not strong.
- The timing of adult psyllid population development in the field at various locations in New Zealand has been investigated by using phenology models. A bimodal model

described and estimated two peaks of TPP flights as indicated by trap captures, with the first peak occurring from 722 to 749 DD, and the second peak from about 1189 to 1264 DD after biofix for the data available in this study.

6.7 RECOMMENDATIONS FOR FUTURE RESEARCH

- Studies of the temperature-dependent development of TPP on various plant hosts such as bell pepper and eggplant are required because these plants are hosts of TPP and this thesis suggested that development of TPP varied depends on host plant species.
- There is evidence that TPP can vector *Liberibacter* throughout a crop very rapidly. As TPP is an important vector of *Liberibacter* and a significant proportion of some TPP populations will be infected with *Liberibacter* it is important that the temperature-dependent development of TPP infested with *Candidatus Liberibacter* in laboratory conditions is determined.
- The detailed life cycle parameters could be used in a more detailed population model that can show projections and possibilities of population dynamics under different environmental conditions.
- To better predict the impact of *O. vicinus* on psyllid populations, the functional response of this predator bug and its preference on thrips and TPP should be studied under more natural laboratory conditions or in the greenhouses where the predator is allowed to determine their movement and residence time in particular areas. Additionally, so that the true effectiveness of this predator can be determined or modeled, the numerical response of *O. vicinus* to predation needs to be quantified.
- Because the economic threshold for TPP is low due to apparent rapid transmission of *Liberibacter*, the timing of first flight of TPP in the field is the most important for future work to determine. Despite the potential of the DD method for forecasting, particularly the first flight, and pest management, further research on TPP development at varying temperatures is required to establish more precisely DD requirements in the field. The development and refinement of effective forecasting

systems requires large amounts of both accurate long-term data on pest incidence and climate variables, collected over a wide geographic area.

References

- Abad, J.A., M. Bandla, R.D. French-Monar, L.W. Liefing, and G.R.G. Clover. 2009. First report of the detection of '*Candidatus Liberibacter*' species in zebra chip disease-infected potato plants in the United States. *Plant Dis.* 93: 108-109.
- Abernathy, R.L. 1991. Investigation into the nature of the potato psyllid toxin. M.S. thesis, Colorado State University, Fort Collins, CO.
- Aghdam, H.R., Y. Fathipour, G. Radjabi, and M. Rezapanah. 2009. Temperature-dependent development and temperature thresholds of codling moth (Lepidoptera: Tortricidae) in Iran. *Environ. Entomol.* 38: 885-895.
- Akotsen-Mensah, C., R.T. Boozer, A.G. Appel, and H.Y. Fadamiro. 2011. Seasonal occurrence and development of degree-day models for predicting activity of *Conotrachelus nenuphar* (Coleoptera: Curculionidae) in Alabama peaches. *Ann. Entomol. Soc. Am.* 104: 192-201.
- Anderson, D. R. 2008. Model based inference in the life sciences: Primer on evidence. NewYork: Springer.
- Arbab, A., and M.R. Mcneill. 2011. Determining suitability of thermal development models to estimate temperature parameters for embryonic development of *Sitona lepidus* Gyll. (Coleoptera: Curculionidae). *J Pest Sci.* 84: 303-311.
- Arnold, C.Y. 1960. Maximum-minimum temperature as a basic for computing heat units. *Am. Soc. Hort. Sci.* 76: 682-692.
- Baek, S., C. Kijong, Y.H. Song, and J.H. Lee. 2008. Degree-day based models for forecasting the flight activity of adult *Helicoverpa assulta* (Lepidoptera: Noctuidae) in hot pepper fields. *Int. J. Pest Manage.* 54: 295-300.
- Beggs, J. 2001. The ecological consequences of social wasps (*Vespula* spp.) invading an ecosystem that has an abundant carbohydrate resource. *Biol. Conserv.* 99: 17-28.
- Begon, M., and M. Mortimer. 1981. Population ecology: A unified study of animals and plants. Massachusetts, USA: Sunderland Sinauer Associated Inc.
- Bentz, B.J., J.A. Logan, and G.D. Amman. 1991. Temperaturedependent development of the mountain pine beetle (Coleoptera: Scolytidae) and simulation of its phenology. *Can. Entomol.* 123: 1083-1094.

- Bergant, K., and S. Trdan. 2006. How reliable are thermal constants for insect development when estimated from laboratory experiments? *Entomol. Exp. Appl.* 120: 251-256.
- Berry, N.A., M.K. Walker, and R.C. Butler. 2009. Laboratory studies to determine the efficacy of selected insecticides on tomato/potato psyllid. *N.Z. Plant Protect.* 62: 145-151.
- Berryman, A.A. 1992. The origins and evolution of predator-prey theory. *Ecology.* 73: 1530-1535.
- Biosecurity New Zealand Website. (<http://www.biosecurity.govt.nz/media/16-02-06/clover-root-weevil>) (Accessed on 09/2012).
- Birch, L.C. 1948. The intrinsic rate of natural increase of an insect population. *J. Anim. Ecol.* 17: 15-26.
- Blanco, C. A., and G. Hernandez. 2006. Prediction of masked chafer, *Cyclocephala pasadenae*, capture in light traps using a degree-day model. *J. Insect Sci.* 6: 36-42.
- Borchert, D.M., R.E. Stinner, J.F. Walgenbach, and G.G. Kennedy. 2004. Oriental fruit moth (Lepidoptera: Tortricidae). Phenology and management with methoxyfenozide in North Carolina Apples. *J. Econ. Entomol.* 97: 1353-1364.
- Briere, J., P. Pracros, A.L. Roux, and J. Pierre. 1999. A novel model of temperature-dependent development for arthropods. *Environ. Entomol.* 28: 22-29.
- Broatch, J.S., L.M. Dosdall, G.W. Clayton, K.N. Harher, and R.C. Yang. 2006. Using degree-day and logistic models to predict emergence patterns and seasonal flights of the cabbage maggot and seed corn maggot (Diptera: Anthomyiidae) in Canola. *Environ. Entomol.* 35: 1166-1177.
- Buchman, J.L., V.G. Sengoda, and J.E. Munyaneza. 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. *J. Econ. Entomol.* 104: 1486-1495.
- Buckley, Y.M., M. Rees, A.W. Sheppard, and M.J. Smyth. 2005. Stable coexistence of an invasive plant and biocontrol agent: a parameterized coupled plant-herbivore model. *J. Appl. Ecol.* 42: 70-79.
- Burckhardt, D., and P. Lauterer. 1997. A taxonomic reassessment of the trioqid genus *Bactericera* (Hemiptera: Psylloidea). *J. Nat. Hist.* 31: 99-153.

- Butler, C.D., and J.T. Trumble 2012. The potato psyllid, *Bactericera cockerelli* (Sulc) (Hemiptera: Triozidae): life history, relationship to plant diseases, and management strategies. *Terre. Arthropod Rev.* 5: 87-111.
- Butts, R.A., and F.L. McEwen. 1981. Seasonal populations of the diamondback moth, *Plutella xylostella* (Lepidoptera: Plutellidae), in relation to day-degree accumulation. *Can. Entomol.* 113: 127-131.
- Cameron, P.J., M.R. Surrey, P.J. Wigley, J.A.D. Anderson, D.E. Hartnett, and A.R. Wallage. 2009. Seasonality of *Bactericera cockerelli* in potatoes (*Solanum tuberosum*) in South Auckland, New Zealand. *New. Zeal. J. Crop Hort.* 37: 295-301.
- Campbell, A., B.D. Frazer, N. Gilbert, A.P. Guitierrez, and M. Mackauer. 1974. Temperature requirements of some aphids and their parasites. *J. Appl. Ecol.* 11: 431-438.
- Carey, J. R. 1993. Applied demography for biologists, with special emphasis on insects. 211 pp. Oxford University Press, U.K.
- Casas, J., and B. Hulliger. 1994. Statistical analysis of functional response experiments. *Biocontrol Sci. Technol.* 4: 133-145.
- Cawley, G.C., and N.L.C. Talbot. 2004. Fast exact leave-one-out cross-validation of sparse least-squares support vector machines. *Neural Networks* 17: 1467-1475.
- Chesson, J. 1989. The effect of alternative prey on the functional response of *Notonecta hoffmani*. *Ecology.* 70: 1227-1235.
- Cock, M.J.W. 1978. The assessment of preference. *J. Anim. Ecol.* 47: 805-816.
- Collett, N. 2000. Biology and control of psyllids, and the possible causes for defoliation of *Eucalyptus camaldulensis* Dehnh. (river red gum) in south-eastern Australia-a review. *Aust. Forestry.* 64: 88-95.
- Collier, R.H., and S. Finch. 2001. Forecasting attacks by pest insects of cruciferous crops. The management of diamondback moth and other crucifer pests. Proceedings of the Fourth International Workshop, Melbourne, Victoria, Australia, 26-29 November 2001. 163-168 pp.
- Cranshaw, W.S. 1993. An annotated bibliography of the potato/tomato psyllid *paratrioza cockerelli* (Sulc) (Homoptera: Psyllidae). Colorado State University, Agric. Exp. Sta. Bull. TB93-5.Ft. Collins, CO. 52 pp.

- Cranshaw, W.S., and G.L. Hein. 2004. High Plains IPM Guide. Potato XXII. Potato Psyllid. <http://scarab.msu.montana.edu/HpIPMSearch/Docs/potatopsyllidpotato.pdf> (accessed 25 March 2009, updated 12 April 2004). Crop Prot. 29: 1190-1199.
- Crawford, D. L. 1910. American Psyllidae I. (Triozinae). Pomana J. Entomol. 2: 228-237.
- Crawford, D. L. 1911. American Psyllidae III. (Triozinae). Pomana J. Entomol. 3: 421-453.
- Crosslin, J.M., G. Bester. 2009. First report of '*Candidatus Liberibacter psyllaureus*' in Zebra Chip symptomatic potatoes from California. Plant Dis. 93: 551.
- Damos, P.T., and M. Savopoulou-Soultani. 2010. Development and statistical evaluation of models in forecasting moth phenology of major lepidopterous peach pest complex for integrated pest management programs. Crop Prot. 29: 1190-1199.
- Davis, A.C. 1937. Observations on the life history of *Paratrioza cockerelli* (Sulc) in southern California. J. Econ. Entomol. 30: 377-378.
- De Clercq, P., F. Merlevede, I. Mestdagh, K. Vandedurpel, J. Mohanghegh, and D. Degheele. 1998. Predation on tomato looper *Chrysodeixis chalcites* (Esper) (Lep. Noctuidae) by *Podisus maculiventris* (Say) and *Podisus nigrispinus* (Dallas) (Het. Pentatomidae). J. Appl. Entomol. 122: 93-98.
- Diaz, M. B., M. Muniz, L. Barrios, and A. Fereres. 2007. Temperature thresholds and thermal requirements for development of *Nasonovia ribisnigri* (Hemiptera: Aphididae). Environ. Entomol. 36: 681-688.
- Drankin, S.M., J.O. Palmer, L. Larocque, and A.L. Risser. 1995. Life history characteristics of ringlegged earwig (Dermaptera: Labiduridae): Emphasis on ovarian development. Ann. Entomol. Soc. Am. 88: 887-893.
- Dransfield, R.D. 1979. Aspect of host parasitoid interactions of two aphid parasitoids, *Aphidius urticae* (Haliday) and *Aphidius uzbekistanicus* (Luzhetski) (Hymenoptera: Aphidiidae). Ecol Entomol. 4: 307-316.
- Eckenrode, C.K., and R.K. Chapman. 1972. Seasonal adult cabbage maggot populations in the field in relation to thermal unit accumulations. Ann. Entomol. Soc. Am. 65: 151-156.
- ESA, Entomological Society of America. 2012. Common names of insects database. Entomological Society of America at: <http://www.entsoc.org/common-names> (Accessed on 11/2012).

- Eubanks, M.D., and R.F. Denno. 2000. Health food versus fast food: the effects of prey quality and mobility on prey selection by generalist predator and indirect interactions among prey species. *Ecol. Entomol.* 25: 140-146.
- Fan, Y., and F.L. Pettit. 1994. Parameter estimation of the functional response. *Environ. Entomol.* 23: 785-794.
- Fathi, S.A.A., and G.N. Ganbalani. 2009. Assessing the potential for biological control of potato field pests in Ardabil, Iran: functional responses of *Orius niger* (Wolf.) and *O. minutus* (L.) (Hemiptera: Anthocoridae). *J. Pest Sci.* 83: 47-52.
- Fathipour, Y., A. Hosseini, and A. A. Talebi. 2004. Some behavioral characteristics of *Diaeretiella rapae* (Hym., Aphidiidae), parasitoid of *Brevicoryne brassicae* (Hom., Aphididae). *Iran. J. Agric. Sci.* 35: 393-401.
- Fellowes, M.D.E., J.J.M. van Alphen, and M.A. Jervis. 2005. Foraging behavior. In *Insects as natural enemies: A practical perspective* (ed M.A. Jervis). 1-71 pp. Springer, Dordrecht, The Netherlands.
- Ferguson, G., and L. Shipp. 2002. New pests in Ontario greenhouse vegetables. Working Group "International Control in Protected Crops, Temperate Climate". Proceedings of the Working Groups meeting, Victoria, British Columbia. 6-9 May 2002. *Bulletin OILB/SROP.* 25: 69-72.
- Fernández-Arhex, V., and J.C. Corley. 2003. The functional response of parasitoids and its implications for biological control. *Biocontrol Sci. Tech.* 13: 403-413.
- Flinn, P.W., A.A. Hower, and R.A.J. Taylor. 1985. Preference of *Reduviolus americanoferus* (Hemiptera: Nabidae) for potato leafhopper nymphs and pea aphid. *Can. Entomol.* 117: 1503-1508.
- Flint, M.L., and S.H. Dreistadt. 1998. *Natural enemies handbook*. University of California Press.
- Flint, M. L., and P. Gouveia. 2001. *IPM in practice: principles and methods of integrated pest management*. University of California Press, Oakland, CA.
- Gao, F., J. Jifon, X. Yang, T.X. and Liu. 2009. Zebra chip disease incidence on potato is influenced by timing of potato psyllid infestation, but not by the host plants on which they were reared. *Insect Sci.* 16: 399-408.

- Gharalari, A.H., C. Nansen, D.S. Lawson, J. Gilley, J.E. Munyaneza, and K. Vaughn. 2009. Knockdown mortality, repellency, and residual effects of insecticides for control of adult *Bactericera cockerelli* (Hemiptera:Psyllidae). J. Econ. Entomol. 102: 1032-1038.
- Gill, G. 2006. Tomato psyllid detected in New Zealand. Biosecurity. 69: 10-11.
- Gitonga, L.M., W.A. Overholt, B. Lohr, J.K. Magambo, and J.M. Mueke. 2002. Functional response of *Orius albidipennis* (Hemiptera: Anthocoridae) to *Megalurothrips sjostedti* (Thysanoptera: Thripidae). Biol. Control. 24: 1-6.
- Godfray, H.C.J., and J.K. Waage. 1991. Predictive modeling in biological control: the mango mealy bug (*Rastrococcus invadens*) and its parasitoids. J. Appl. Ecol. 28: 434-453.
- Golizadeh, A., and J. Razmjou. 2010. Life table parameters of *Phthorimaea operculella* (Lepidoptera: Gelechiidae), Feeding on tubers of six potato cultivars. J. Econ. Entomol. 103: 966-972.
- Golizadeh, A., and M.P. Zalucki. 2012. Estimating temperature-dependent developmental rates of potato tuberworm, *Phthorimaea operculella* (Lepidoptera: Gelechiidae). Insect Sci.19: 609-620.
- Goolsby, J.A., J. Adamczyk, B. Bextine, D. Lin, J.E. Munyaneza, and G. Bester. 2007a. Development of an IPM programme for the management of the potato psyllid to reduce incidence of zebra chip disorder in potatoes. Subtrop. Plant. Sci. 59: 85–94.
- Goolsby, J.A., B. Bextine, J.E. Munyaneza, M. Setamou, J. Adamczyk, and G. Bester. 2007b. Seasonal abundance of sharpshooters, leafhoppers, and psyllids associated with potatoes affected by zebra chip disorder. Subtrop. Plant. Sci. 59: 15-23.
- Greenberg, .S.M., T.W. Sappington, B.C. Legaspi, T.X. Liu, and M. Setamou. 2001. Feeding and life history of *Spodoptera exigua* (Lepidoptera: Noctuidae) on different host plants. Ann. Entomol. Soc. America 94: 566-575.
- Grout, T.G., and K.C. Stoltz. 2007. Development rates at constant temperatures of three economically important *Ceratitis spp.* (Diptera: Tephritidae) from Southern Africa. Environ. Entomol. 36: 1310-1317.
- Haghani, M., Y. Fathipour, A.A. Talebi, and V. Baniamერი. 2006. Comparative demography of *Liriomyza sativae* Blanchard (Diptera, Agromyzidae) on cucumber at seven constant temperatures. Insect Sci. 13: 477-483.

- Haghani, M., Y. Fathipour, A.A. Talebi, and V. Baniameri. 2009. Estimating development rate and thermal requirements of *Hemiptarsenus zilahisebessi* (Hymenoptera: Eulophidae) parasitoid of *Liriomyza sativae* (Diptera: Agromyzidae) using linear and nonlinear models. *Pol Pismo Entomol.* 78: 3-14.
- Hansen, L.S., H. Skovgard, and K. Hell. 2004. Life table study of *Sitotroga cerealella* (Lepidoptera: Gelechiidae), a strain from West Africa. *Econ. Entomol.* 97: 1484-1490.
- Hansen, A.K., J.T. Trumble, R. Stouthamer, and T.D. Paine. 2008. A new Huanglongbing Species, “*Candidatus Liberibacter psyllaurosus*”, found to infect tomato and potato, is vectored by the psyllid *Bactericera cockerelli* (Sulc). *Appl. Environ. Microbiol.* 74: 5862-5865.
- Harari, A. R., D. Ben-Yakir, M. Chen, and D. Rosen. 1997. Life- and fertility-tables of *Maladera matrida* (Coleoptera: Scarabaeidae). *Environ. Entomol.* 27: 45-48.
- Harcourt, D.G. 1969. The development of life tables in the study of natural insect populations. *Ann. Rev. Entomol.* 14: 175-191.
- Hassell, M.P. 1978. The dynamic of arthropod predator-prey systems. Princeton University Press, Princeton, New Jersey. 237 pp.
- Holling, C.S. 1959. Some characteristics of simple types of predation and parasitism. *Can. Ent.* 91: 385-398.
- Holling, C.S. 1966. The functional response of invertebrate predators to prey density. *Mem. Ent. Soc. Can.* 48: 1-86.
- Huey, R. B., G.W. Gilchrist, M.L. Carlson, D. Berrigan, and L. Serra. 2000. Rapid evolution of a geographic cline in size in an introduced fly. *Science* 287: 308–309.
- Huffaker, C., A. Berryman, and P. Turchin. 1999. Dynamics and regulation of insect populations. *Ecological Entomology* (eds. C.B. Huffaker & A.P. Gutierrez). 269-305 pp. Wiley, New York.
- Huffaker, C.B., and P.S. Messenger. 1976. Theory and practical of biological control. Academic, New York, USA.
- Hughes, R.D., L.T. Woolcok, and M.A. Hughes. 1992. Laboratory evaluation of the parasitic Hymenoptera used in attempts to biologically control aphid pests of crops in Australia. *Entomol. Exp. Appl.* 63: 177-185.

- Isikber, A.A. 2005. Functional response of two coccinellid predators, *Scymnus levaillanti* and *Cycloneda sanguinea*, to the cotton aphid, *Aphis gossypii*. Turk. J. Agric. 29: 347-355.
- Jalali, M.A., L. Tirry, A. Arbab, and P. De Clercq. 2010. Temperature-dependent development of the two-spotted ladybeetle, *Adalia bipunctata*, on the green peach aphid, *Myzus persicae*, and a factitious food under constant temperatures. J. Insect. Sci. 10: 1-14.
- Jalalizand, A., M. Modaresi, S.A. Tabeidian, and A. Karimy. 2011. Functional response of *Orius niger niger* (Hemiptera: Anthocoridae) to *Tetranychus urticae* (Acari: Tetranychidae): effect of host plant morphological feature. IPCBEE. 9: 92-96.
- Juliano, S.A. 2001. Nonlinear curve fitting: predation and functional response curves. In: Scheiner SM, Gurevitch J (eds) Design and analysis of ecological experiments. Oxford University Press, Oxford. 159-182 pp.
- Kasap, I., and R. Atlihan. 2011. Consumption rate and functional response of the predaceous mite *Kampimodromus aberrans* to two-spotted spider mite *Tetranychus urticae* in the laboratory. Exp. Appl. Acarol. 53: 253-261.
- Kim, D.S., J.H. Lee, and M.S. Yiem. 2000. Spring Emergence Pattern of *Carposina sasakii* (Lepidoptera: Carposinidae) in Apple Orchards in Korea and its Forecasting Models Based on Degree-Days. Environ. Entomol. 29: 1188-1198.
- Kim, H., and J.H. Lee. 2008. Phenology simulation model of *Scotinophara lurida* (Hemiptera: Pentatomidae). Environ. Entomol. 37: 660-669.
- Knowlton, G.F., and M.J. James. 1931. Study on the biology of *Paratrioza cockerelli* (Sulc). Ann. Entomol. Soc. Am. 24: 283-291.
- Kontodimas, D.C., P.A. Eliopoulus, G.J. Stathas, and L.P. Economou. 2004. Comparative temperature-dependent development of *Nephus includens* (Kirsch) and *Nephus bisignatus* (Boheman) (Coleoptera: Coccinellidae) preying on *Planococcus citri* (Risso) (Homoptera: Pseudococcidae): evaluation of a linear and various nonlinear models using specific criteria. Environ. Entomol. 33: 1-11.
- Krebs, C.J. 1994. Ecology: The Experimental Analysis Distribution and Abundance. HarperCollins College Publishers, New York.

- Krips, O.E., P.W. Kleijn, P.E.L. Willems, G.J.Z. Gols, and M. Dicke. 1999. Leaf hairs influence searching efficiency and predation rate of the predatory mite *Phytoseiulus per similis* (Acari: Phytoseiidae). *Exp. Appl. Acarol.* 23: 119-131.
- Kuhrt, U., J. Samietz, H. Hohn, and S. Dorn. 2006. Modelling the phenology of codling moth: Influence of habitat and thermoregulation. *Agric. Ecosyst. Environ.* 117: 29-38. *Agri. Eco. Environ.*
- Kumral, N.A., B. Kovanci, and B. Acbudak. 2007. Life tables of the olive leaf moth, *Palpita unionalis* (Hübner) (Lepidoptera: Pyralidae), on different host plants. *J. Biol. Environ. Sci.* 1: 105-110.
- Kumral, N.A., B. Kovanci, and B. Akbudak. 2008. Using degree-day accumulations and host phenology for predicting larval emergence patterns of the olive psyllid, *Euphyllura phillyreae*. *J. Pest Sci.* 81: 63-69.
- Lacey, L.A., F. de la Rosa, and D.R. Horton. 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 Sci. Tech.* 19: 957-970.
- Lacey, L.A., T.X. Liu, J.L. Buchman, J.E. Munyaneza, J.A. Goolsby, and D.R. Horton. 2011. Entomopathogenic fungi (Hypocreales) for control of potato psyllid, *Bactericera cockerelli* (Sulc.) (Hemiptera: Triozidae) in an area endemic for zebra chip disease of potato. *Biol. Control.* 56: 271-278.
- Lactin, D. J., N. J. Holliday, D. L. Johnson, and R. Craigen (1995). Improved rate model of temperature-dependent development by arthropods. *Environ. Entomol.* 24: 68-75.
- Lamb, R.J. 1992. Developmental rate of *Acyrtosiphon pisum* (Homoptera: Aphididae) at low temperatures: implications for estimating rate parameters for insects. *Environ. Entomol.* 21: 10-19.
- Lankin-Vega, G.O., S.P. Worner, and D.A.J. Teulon. 2008. An ensemble model for predicting *Rhopalosiphum padi* (Hemiptera: Aphididae) abundance. *Entomol. Exp. Appl.* 129: 308-315.
- Lariviere, M.C., and C.H. Wearing. 1994. *Orius vicinus* (Ribaut) (Heteroptera: Anthocoridae), a predator of orchard pests new to New Zealand. *N. Z. Entomol.* 17: 17-21.

- Legaspi, J. C., A. M. Simmons, and B. C. Legaspi. 2006. Prey preference by *Delphastus catalinae* (Coleoptera: Coccinellidae) on *Bemisia argentifolii* (Homoptera: Aleyrodidae): effects of plant species and prey species. Fla. Entomol. 89: 218-222.
- Lemos, W.P., F.S. Ramalho, and J.C. Zanuncio. 2003. Age-dependent fecundity and life-fertility tables for *Euborelliaannulipes* (Lucas) (Dermaptera: Anisolabididae) a cotton boll weevil predator in laboratory studies with an artificial diet. Environ. Entomol. 32: 592-601.
- Lester, P.J., H.M.A. Thistlewood, and R. Harmsen. 2000. Some effects of pre-release host-plant on the biological control of *Panonychus ulmi* by the predatory mite *Amblyseius fallacies*. Exp. Appl. Acarol. 24: 19-33.
- Lester, P.J., and R. Harmsen. 2002. Functional and numerical responses do not always indicate the most effective predator for biological control: an analysis of two predators in two-prey system. J. Appl. Ecol. 39: 455-468.
- Lewis, T.M., and J.D. Lattin. 2010. *Orius* (Heterorius) *vicinus* (Ribaut) (Hemiptera: Heteroptera: Anthocoridae) in western north America, a correction of the past. Proc. Entomol. Soc. Wash. 112: 69-80.
- Liefting, L.W., Z.C. Rez-Egusquiza, G.R.G. Clover, and J.A.D. Anderson. 2008. A new ‘*Candidatus Liberibacter*’ species in *Solanum tuberosum* in New Zealand. Plant Dis. 92: 1474.
- Liefting, L.W., P.W. Southerland, L.I. Ward, K.L. Paice, B.S. Weir, and G.R.G. Clover. 2009. A new “*Candidatus Liberibacter*” species associated with diseases of solanaceous crops. Plant Dis. 92: 208-214.
- List, G. 1939a. The potato and tomato psyllid and its control on tomatoes. Colorado Agric. Exp. Sta. Bull. 454: 33 pp.
- List, G. 1939b. The effect of temperature upon egg deposition, egg hatch, and nymphal development of *Paratrioza cockerelli* (Sulc.). J. Econ. Entomol. 32: 30-36.
- Liu, D., and J.T. Trumble. 2004. Tomato psyllid behavioral responses to tomato plant lines and interactions of plant lines with insecticides. J. Econ. Entomol. 97: 1078-1085
- Liu, D., and J.T. Trumble. 2005. Interaction of plant resistance and insecticides on the development and survival of *Bactericera cockerelli* [Sulc] (Homoptera:Psyllidae). Crop Prot. 24: 111-117.

- Liu, D., and J.T. Trumble. 2006. Ovipositional preferences, damage thresholds, and detection of the tomato-potato psyllid *Bactericera cockerelli* (Homoptera: Psyllidae) on selected tomato accessions. *Bull. Entomol. Res.* 96: 197-204.
- Liu, D., L. Johnson, and T.J. Trumble. 2006. Differential responses to feeding by the tomato/potato psyllid between two tomato cultivars and there implications in establishment of injury levels and potential of damaged plant recovery. *Insect Sci.* 13:195-204.
- Liu, D., and J.T. Trumble. 2007. Comparative fitness of invasive and native populations of the potato psyllid (*Bactericera cockerelli*). *Entomol. Exp. Appl.* 118: 177-183.
- Liu, S.S., G.G. Shang, and J. Zhu. 1995. Influence of temperature variation on rate of development in insects: Analysis of case studies from entomological literature. *Ann. Entomol. Soc. Am.* 88: 107-119.
- Liu, Z.D., D.M. Li, P.Y. Gong, and K. Wu. 2004. Life table studies of the cotton bollworm, *Helicoverpa armigera* (Hubner) (Lepidoptera: Noctuidae), on different host plants. *Environ. Entomol.* 33: 1570-1576.
- Logan, J.A., D.J. Wolkind, S.C. Hoyt, and L.K. Tanigoshi. 1976. An analytical model for description of temperature-dependent rate phenomena in arthropods. *Environ. Entomol.* 17: 359-376.
- Mack, R.N., D. Simberloff, W.M. Lonsdale, H. Evan, M. Clout, and F. Bazzaz. 2000. Biotic invasions: Cause, epidemiology, global consequences, and control. *Ecol. Appl.* 10: 689-710.
- Madriz, H.V., Martinez, N.B., Graziano, J.V., Gutierrez, C.G., and Palacio C.C. (2011). Life and fertility table of *Bactericera cockerelli* (Sulc) on two varieties of tomato in a greenhouse. *Southwest. Entomol.* 36: 413-422.
- Maia, A.H., A.B. Luiz, and C. Campanhola. 2000. Statistical inference on associated fertility life table parameters using jackknife technique, computational aspects. *J. Econ. Entomol.* 93: 511-518.
- Manly, B.F.J. 1974. A model for certain types of selection experiments. *Biometrics* 30: 281-294.
- Marin-Jarillo, A., J.A. Garzon-Tiznado, A. Becerra-Flora, C. Mejia-Avila C, R. Bujanos-Muniz, and K.F. Byerly-Murphy. 1995. Biology and morphological of the potato

- psyllidae *Paratrioza cockerelli* (Sulc) (Homoptera: Psyllidae) vector of the “Permanent Jitomate” disease in Bahio. Manejo Integrado de Plagas (Costa Rica) 38: 25-32.
- McBrien, H.L., and G.J.R. Judd. 1998. Forecasting emergence, flight, and oviposition of *Spilonota ocellana* (Lepidoptera: Tortricidae), in British Columbia. Environ. Entomol. 27: 1411-1417.
- Medeiros, R. S., F. S. Ramalho, W. P. Lemos, and J. C. Zanuncio. 2000. Age-dependent fecundity and life fertility tables for *Podisus nigrispinus* (Dallas) (Het., Pentatomidae). J. Appl. Entomol. 124: 319-324.
- Meyer, J.S., C.G. Ingersoll, L.L. McDonald, and M.S. Boyce. 1986. Estimating uncertainty in population growth rates: Jackknife vs. bootstrap techniques. Ecology. 67: 1156-1166.
- Meyling, N. V., A. Enkegaard, and H. Brodsgaard. 2003. Two *Anthocoris* bugs as predators of glasshouse aphids-voracity and prey preference. Entomol. Exp. Appl. 108: 59-70.
- Mills, N.J. 1982. Satiation and functional response: a test of a new model. Ecol. Entomol. 7: 305-315.
- Mohammad, A.A. 1999. Integrated Pest Management of TPP, *Paratrioza cockerelli* (Sulc) (Homoptera: Psyllidae) with emphasis on its importance in greenhouse grown tomatoes. PhD Thesis in Colorado State University, CO, USA.
- Mooney, H.A., and E.E. Cleland. 2001. The evolutionary impact of invasive species. Proceedings of the National Academy of Science, U.S.A.
- Munyanza, J.E., J.M. Crosslin, and E.J. Upton. 2007a. Association of *Bactericera cockerelli* (Homoptera: Psyllidae) with “Zebra Chip,” a new potato disease in Southwestern United States and Mexico. J. Econ. Entomol. 100: 656-663.
- Munyanza, J.E., J.A. Goolsby, J.M. Crosslin, and E.J. Upton. 2007b. Further evidence that Zebra Chip potato disease in the Lower Rio Grande Valley of Texas is associated with *Bactericera cockerelli*. Subtrop. Plant Sci. 59: 30-37.
- Munyanza, E.J., M.J. Crosslin, and L.J. Buchman. 2009. Seasonal occurrence and abundance of the potato psyllid, *Bactericera cockerelli*, in South Central Washington. Am. J. Pot Res. 86:513-518.

- Munyaneza, J.E. 2012. Zebra Chip Disease of Potato: Biology, Epidemiology, and Management. *Am. J. Pot Res.* 89: 329-350.
- Murdoch, W.W. 1969. Switching in general predators: Experiments on predator specificity and stability of prey populations. *Ecol. Monogr.* 39: 335-354.
- Murdoch, W.W., A. Oaten. 1975. Predation and population stability. *Adv. Ecol. Res.* 9: 1-132.
- Musthapa, W.F.Z.W. 2010. The influence of mosquito predators on population dynamics of endemic and exotic mosquitoes. PhD thesis in The Victoria University of Wellington, Wellington, New Zealand.
- Nachappa, P., S.K. Braman, L.P. Guillebeau, and J.N. All. 2006. Functional Response of the Tiger Beetle *Megacephala carolina Carolina* (Coleoptera: Carabidae) on Twolined Spittlebug (Hemiptera: Cercopidae) and Fall Armyworm (Lepidoptera: Noctuidae). *J. Econ. Entomol.* 99: 1583-1589.
- Nahrung, H.F., G.R. Allen, and V.S. Patel. 2004. Day-degree development and phenology modeling of the immature stages of *Chrysophtharta agricola* (Chapuis) (Coleoptera: Chrysomelidae), a pest of eucalypt plantations. *Aust. J. Entomol.* 43: 177-183.
- Nahrung, H.F., M.K. Schutze, A.R. Clarke, M.P. Duffy, E.A. Dunlop, and S.A. Lawson. 2008. Thermal requirements, field mortality and population phenology modeling of *Paropsis atomaria* Olivier, an emergent pest in subtropical hardwood plantations. *Forest Ecol. Manage.* 255: 3515-3523.
- Norris, R.F., E.P. Caswell-Chen, and M. Kogan. 2003. Concepts in integrated pest management. Upper Saddle River, New Jersey 07458.
- Nowatzki, T.M., J.J. Tollefson, and D.D. Calvin. 2002. Development and validation of models for predicting the seasonal emergence of corn rootworm (Coleoptera: Chrysomelidae) beetles in Iowa. *Environ. Entomol.* 31: 864-873.
- Nylin, S. 2001. Life history perspectives on pest insects: What's the use? *Austral Ecol.* 26: 507-517.
- Omer, A. D., Johnson, M. W. & Tabashnik, B. E. (1996) Demography of the leafminer parasitoid *Ganaspidium utilis* Beardsley (Hymenoptera, Eucoilidae) at different temperatures. *Biol. Control.* 6: 29-34.

- Parajulee, M.N., R.B. Shrestha, J.F. Leser, D.B. Wester, and C.A. Blanco. 2006. Evaluation of the functional response of selected arthropod predators on bollworm eggs in the laboratory and effect of temperature on their predation efficiency. *Environ. Entomol.* 35: 379-386.
- Pedigo, L.P., and M.E. Rice. 2006. *Entomology and pest management*. Hamilton Printing, Upper Saddle River, NJ.
- Pervez, A. and Omkar. 2005. Functional responses of coccinellid predators: An illustration of a logistic approach. *J. Insect Sci.* 5:1-6.
- Pinder III, J.E., J.G. Wiener, and M.H. Smith. 1978. The Weibull distribution: a new method of summarizing survivorship data. *Ecology.* 59: 175-179.
- Pletsch, D.J. 1947. The potato psyllid *Paratrioza cockerelli* (Sulc), its biology and control. *Montana Agric. Expt. Stn. Bull.* 446: 95 pp.
- Pratt, P.D., R. Rosetta, and B.A. Croft. 2002. Plant related factors influence the effectiveness of *Neoseiulus fallacies* (Acari: Phytoseiidae), a biological control agent of spider mites on landscape ornamental plants. *J. Econ. Entomol.* 95: 1135-1141.
- Propp, G.D. 1982. Functional response of *Nabis americanoferus* to two of its prey, *Spodoptera exigua* and *Lygus hesperus*. *Environ. Entomol.* 11: 670-674.
- Punya, N., L. Julien, and T. Cecilia. 2012. Transcriptome analyses of *Bactericera cockerelli* adults in response to “*Candidatus Liberibacter solanacearum*” infection. *Mol. Genet. Genomics.* 287: 803-817.
- R Version 2.9.2. 2009. The R foundation for statistical computing ISBN 3-900051-07-0.
- Ramvalho, F.S., P.A. Wanderley, J.B. Malaquias, K.C.V. Rodrigues, J.V.S. Souza, and J.C. Zanuncio. 2009. Temperature – dependent development rates of *Bracon vulgaris*, a parasitoid of boll weevil. *Phytoparasitica.* 37: 17-25.
- Rees, M., and Q. Paynter. 1997. Biological control of Scotch broom: modeling the determinants of abundance and the potential impact of introduced insect herbivores. *J. Appl. Ecol.* 34: 1203-1222.
- Régnière, J., and J.A. Logan. 2003. Animal life cycle models. In: Schwartz M (ed) *Phenology: an integrative environmental science*. Kluwer, Dordrecht, pp 237-254.
- Riechert, S.E. and T. Lockley. 1984. Spiders as biological control agents. *Annu. Rev. Entomol.* 29: 299-320.

- Roy, M., J. Brodeur, and C. Cloutier. 2002. Relationship between temperature and development rate of *Stethorus punctillum* (Coleoptera: Coccinellidae) and its prey *Tetranychus mcdanieli* (Acarina: Tetranychidae). *Environ. Entomol.* 31: 177-187.
- Roy, M., J. Brodeur, and C. Cloutier. 2003. Effect of temperature on intrinsic rate of natural increase (r_m) of a coccinellid and its spider mite prey. *Biol Control.* 48: 57-72.
- Sabaghi, R., A. Sahragard, and R. Hosseini. 2012. Functional and numerical responses of *Scymnus syriacus marseul* (Coleoptera: Coccinellidae) to the black bean aphid, *Aphis fabae scopoli* (Hemiptera: Aphididae) under laboratory conditions. *J. Plant Protect. Res.* 51: 423-428.
- Sabelis, M.W. 1992. Predatory arthropods. In: *Natural Enemies: The Population Biology of Predators, Parasites and Diseases*, (Ed.: M.J. Crawley). Blackwell, Oxford, pp. 225-264.
- Sanchez-Pena, S.R., E. Casas-De-Hoyo, R. Hernandez-Zul, and K.M. Wall. 2007. A comparison of the activity of soil fungal isolates against three insect pests. *J. Agric. Urban Ecol.* 24: 43-48.
- Sandhu, H.S., G.S. Nuessly, S.E. Webb, R.H. Cherry, and R.A. Gilbert. 2010. Temperature-dependent development of *Elasmopalpus lignosellus* (Lepidoptera: Pyralidae) on sugarcane under laboratory conditions. *Environ. Entomol.* 39: 1012-1020.
- Satpute, N.S., S.D. Deshmukh, N.G.V. Rao, and S.A. Nimbalkar. 2005. Life tables and the intrinsic rate of increase of *Earias vittella* (Lepidoptera: Noctuidae) reared on different hosts. *Int. J. Trop. Insect Sci.* 25: 73-79.
- Schaub, L., B. Graf, and A. Butturini. 2005. Phenological model of pear psylla *Cacopsylla pyri*. *Entomol. Exp. Appl.* 117: 105-111.
- Schenk, D., and S. Bacher. 2002. Functional response of a generalist insect predator to one of its prey species in the field. *J. Anim. Ecol.* 71: 524-531.
- Schowalter, T.D. 2006. *Insect ecology: An Ecosystem approach*. 2nd edition. Tokyo: Academic Press, 572.
- Secor, G.A., V. Rivera-Varas. 2004. Emerging diseases of cultivated potato and their impact on Latin America. *Revista Latinoamericana de la Papa (Suppl)* 1: 1-8.

- Sengoda, V.G., J.E. Munyaneza, J.M. Crosslin, J.L. Buchman, and H.R. Pappu. 2010. Phenotypic and etiological differences between Psyllid Yellows and Zebra Chip Diseases of Potato. *Am. J. Pot. Res.* 87: 41-49
- Sharpe, P.J.H., and D.W. DeMichele. 1977. Reaction kinetics of poikilothern development. *J. Theor. Biol.* 64: 649-670.
- Shea, K., and D. Kelly. 1998. Estimating biocontrol agent impact with matrix models: *Carduus nutans* in New Zealand. *Ecol. Appl.* 8: 824-832.
- Shea, K., P. Amarasekare, P. Kareiva, M. Mangel, J. Moore, W.W. Murdoch, E. Noonburg, A.M. Parma, M.A. Pascual, H.P. Possingham, C. Wilcox, and D. Yu. 1998. Management of populations in conservation, harvesting and control. *Trends Ecol. Evol.* 13: 371-375.
- Shea, K., D. Kelly, A.W. Sheppard, and T.L. Woodburn. 2005. Context-dependent biological control of an invasive thistle. *Ecol.* 86: 3174-3181.
- Shea, K., A. Sheppard, and T. Woodburn. 2006. Seasonal life-history, models for the integrated management of the invasive weed nodding thistle *Carduus nutans* in Australia. *Appl. Ecol.* 43: 517-526.
- Sherratt, T. N., and I. F. Harvey. 1993. Frequency-dependent food selection by arthropods: a review. *Biol. J. Linn. Soc.* 48: 167-186.
- Siddique, M.A.B. 1985. Biology and Predation of Pacific damsel bug, *Nabis kinbergii* Reuter, (Hemiptera : Nabidae). The PhD thesis in The University of Canterbury, Canterbury, New Zealand.
- Siswanto, R. Muhamad, D. Omar, and E. Karmawati. 2008. Life tables and population parameters of *Helopeltis antonii* (Hemiptera: Miridae) reared on cashew (*Anacardium occidentale* L.). *J. Bioscience.* 19: 91-101.
- Skinner, L.C., D.W. Ragsdale, R.W. Hansen, M.A. Chandler, and G. Spoden. 2006. Phenology of first and peak emergence of *Aphthona lacertosa* and *A. nigriscutis*: Two flea beetles introduced for biological control of leafy spurge, *Euphorbia esula* L. *Biol. Control.* 37: 382-391.
- Smits, N., J.F. Briere, and J. Fargues. 2003. Comparison of non-linear temperature-dependent development rate models applied to in vitro growth of entomopathogenic fungi. *Mycol. Res.* 107: 1476-1484.

- Solomon, M.E. 1949. The natural control of animal populations. J. Anim. Ecol. 18: 1-35.
- Southwood, T. R.E. 1978. Ecological methods with particular reference to the study of insect populations. 2nd edition. London: Chapman and Hall, 524.
- Southwood, T.R.E. 1995. Ecological methods, 2nd ed., Chapman and Hall, London, United Kingdom.
- Stewart, C.D., S.K. Braman, and A.F. Pendley. 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). Environ. Entomol. 31: 1184-1190.
- Strauss, S. Y. 1991. Indirect effects in community ecology: their definition, study and importance. Trends Ecol. Evol. 6: 206-210.
- Sulc, K. 1909. *Trioza cockerelli* n.sp., a novelty from North America, being also of economic importance. Acta Soc. Entomol. Bohemiae. 6: 102-108.
- Tahriri, S., A. A. Talebi, Y. Fathipour, and A. A. Zamani. 2007. Host stage preference, functional response and mutual interference of *Aphidius matricariae* (Hym.: Braconidae: Aphidiinae) on *Aphis fabae* (Hom.: Aphididae). Entomol. Sci. 10: 323-331.
- Teulon, D.A.J., P.J. Workman, K.L. Thomas, and M.C. Nielsen. 2009. *Bactericera cockerelli*: Incursion, dispersal and current distribution on vegetable crops in New Zealand. NZ Plant Prot. 62: 136-144.
- Thomas, K.L., D.C. Jones, L.B. Kumarasinghe, J.E. Richmond, G.S.C. Gill, and M.S. Bullians. 2011. Investigation into the entry pathway for tomato-potato psyllid *Bactericera cockerelli*. N.Z. Plant. Protect. 64: 259-268.
- Toft, S. 1995. Value of the aphid *Rhopalosiphum padi* as food for cereal spiders. J. Appl. Ecol. 32: 552-560.
- Tran, L.T., S.P. Worner, R.J. Hale, and D.A.J. Teulon. 2012. Estimating development rate and thermal requirements of *Bactericera cockerelli* (Hemiptera: Triozidae) reared on potato and tomato by using linear and nonlinear models. Environ. Entomol. 41: 1190-1198.
- Trexler, J.C., E.M. Charles, and J. Travis. 1988. How can the functional response best be determined? Oecologia. 76: 206-214.

- Tschanz, B., L.F. Bacher, S. Bacher. 2007. Functional responses: A question of alternative prey and predator density. *Ecology*. 88: 1300-1308.
- Van Baalen, M., V. Krivan, P.C.J. Van Rijn, and M.W. Sabelis. 2001. Alternative food, switching predators, and persistence of predator-prey systems. *Am. Nat.* 157: 1-13.
- Van Lenteren, J. C., and K. Bakker. 1977. Behavioral aspects of the functional response of a parasite (*Pseudeucoila bochei* Weld) to its host (*Drosophila melanogaster*). *Netherlands J. Entomol.* 28: 213-233.
- Vargas, R.I., W.A. Walsh, D.T. Kanehisa, E.B. Jang, and J.W. Armstrong. 1997. Demography of four Hawaiian fruit flies (Diptera: Tephritidae) reared at five constant temperatures. *Ann. Entomol. Soc. Am.* 90: 162-168.
- Varley, G.C., and G.R. Gradwell. 1970. Recent advances in insect population dynamics. *Annu. Rev. Entomol.* 15: 1-24.
- Veeravel, R., and P. Baskaran. 1997. Functional and numerical responses of *Coccinella transversalis* and *Cheilomenes sexmaculata* Fabr feeding on the melon aphid, *Aphis gossypii* Glov. *Insect Sci. Appl.* 17: 335-339.
- Vollset, S. E., K. F. Hirji, and A. A. Afifi. 1991. Evaluation of exact and asymptotic interval estimators in logistic analysis of matched case-control studies. *Biometrics* 47: 1311-1325.
- Vucetich, J.A., R.O. Peterson, and C.L. Schaefer. 2002. The effect of prey and predator densities on wolf predation. *Ecology*. 83: 3003-3013.
- Wagner, T. L, Wu, P.J.H. Shraper, and R. N. Coulson. 1984. Modeling distribution of insect development time: a literature review an application of Weibull function. *Ann. Entomol. Soc. Am.* 77: 475-487.
- Walgama, R.S., and M.P. Zalucki. 2006. Evaluation of different models to describe egg and pupal development of *Xyleborus fornicatus* Eichh. (Coleoptera: Scolytidae), the shot-hole borer of tea in Sri Lanka. *Insect Sci.* 12: 109-118.
- Walker, G.P., F.H. MacDonald, N.J. Larsen, and A.R. Wallace. 2011. Monitoring *Bactericera cockerelli* and associated insect populations in potatoes in South Auckland. *NZ Plant Prot.* 64: 269-275.

- Walker, G.P., F.H. MacDonald, A.J. Puketapu, H.A. Fergusson, P.G. Connolly, P.J. Wright, and J.A.D. Anderson. 2012. A field trial to assess damage by *Bactericera cockerelli* to early potatoes at Pukekohe. N. Z. Plant Protect. 65: 148-154.
- Wallis, R. 1951. Potato psyllid selection of host plants. J. Econ. Entomol. 44: 815-817.
- Wallis, R.L. 1955. Ecological studies on the potato psyllid as a pest of potatoes. USDA Tech. Bull. 1107: 25 pp.
- Wearing, C.H., and K. Colhoun. 1999. Development of *Orius vicinus* (Ribaut) (Heteroptera: Anthracoridae) on different prey. Biocontrol Sci. Tech. 9: 327-334.
- Welch, S.M., B.A. Croft, J.F. Brunner, M.F. Michels. 1978. PETE: an extension phenology modeling system for management of multi-species pest complex. Environ. Entomol. 7: 482-494.
- Welch, S. M., B. A. Croft, and M. F. Michels. 1981. Validation of pest management models. Environ. Entomol. 10: 425-432.
- Wells, M.L., and R.M. McPherson. 1999. Population dynamics of three coccinellids in flue-cured tobacco and functional response of *Hippodamia convergens* (Coleoptera:Coccinellidae) feeding on tobacco aphids (Homoptera: Aphididae). Environ. Entomol. 28: 768-773.
- White, P.C.L., A.E.S. Ford, M.N. Clout, R.M. Engeman, S. Roy, and G. Saunder. 2008. Alien invasive vertebrates in ecosystems: Pattern, process and the social dimension. Wildlife Res. 35: 171-179.
- Win, S.S., R. Muhamad, Z.A.M. Ahmad, and N.A. Adam. 2011. Life table and population parameters of *Nilaparvata lugens* Stal. (Homoptera: Delphacidae) on rice. Trop. Life Sci. Res. 22: 25-35.
- Wold, S.J., and W.D. Hutchison. 2003. Phenology of *Lygus lineolaris* (Hemiptera: Miridae) in Minnesota June-Bearing strawberries: Comparison of sampling methods and habitats. J. Econ. Entomol. 96: 1814-1820.
- Workman, P.J., and G. Walker. 2009. Current research on the tomato/potato psyllid. In: Proceedings of the 7th World Potato Congress workshop on Solanaceous crops: Psyllids and Liberibacter, 16 March 2009, Christchurch, New Zealand.
- Workman, P.J., and G. Whiteman. 2009. Importing *Tamarixia triozae* into containment in New Zealand. N. Z. Plant Protect. 62: 412.

- Worner, S.P., and D.R. Penman. 1983. Analysis of thermal summation models. Pp.250-254. Proceedings of the 46th New Zealand Weed and Pest Conference, Palmerston North.
- Worner, S.P. 1988. Evaluation of Diurnal Temperature Models and Thermal Summation in New Zealand. J. Econ Entomol. 81: 9-13.
- Worner, S.P. 1992. Performance of phenological models under variable temperature regimes: consequences of the Kaufmann or rate summation effect. Environ. Entomol. 21: 689-699.
- Worner, S.P., G.M. Tatchell, and I.P. Woiod. 1995. Predicting spring migration of the damson-hop aphid *Phorodon humuli* (Homoptera: Aphididae) from historical records of host-plant flowering phenology and weather. J. Appl. Ecol. 32: 17-28.
- Xu, X., and A. Enkegaard. 2009. Prey preference of *Orius sauteri* between Western Flower Thrips and spider mites. Entomol. Exp. Appl. 132: 93-98.
- Xu, X., and A. Enkegaard. 2010. Prey preference of the predatory mite, *Amblyseius swirskii* between first instar western flower thrips *Frankliniella occidentalis* and nymphs of the twospotted spider mite *Tetranychus urticae*. J. Insect Sci. 10: 149.
- Yang, X., and T.X. Liu. 2009. Life history and life tables of *Bactericera cockerelli* (Homoptera: Psyllidae) on eggplant and bell pepper. Environ. Entomol. 38: 1661-1667.
- Yang, X.B., Zhang, Y.M., Hua, L., and Liu, T.X. (2010). Life history and life tables of *Bactericera cockerelli* (Homoptera: Psyllidae) on potato under laboratory and field conditions in the Lower Rio Grande Valley of Texas. J. Econ. Entomol. 103: 1729-1734.
- Zamani, A., A. Talebi, Y. Fathipour, and V. Baniamiri. 2006. Temperature-dependent functional response of two aphid parasitoids, *Aphidius colemani* and *Aphidius matricariae* (Hymenoptera: Aphididae), on the cotton aphid. J. Pest Sci. 79: 183-188.
- Zar, J.H. 1999. Biostatistical analysis, 4th ed. Prentice Hall, Upper Saddle River, NJ.
- Zied, E.M.A., R.M. Gabre, and H. Chi. 2003. Life table of the Australia sheep blow fly *Lucilia cuprina* (Wiedemann) (Diptera: Calliphoridae). Egypt. J. Zool. 41:29-45.
- Zilahi-Balogh, G.M.G., S.M. Salom, and L.T. Kok. 2003. Temperature-dependent development of the specialist predator *Laricobius nigrinus* (Coleoptera: Derodontidae). Environ. Entomol. 32: 1322-1328.

Acknowledgements

I would first like to thank my university supervisor Associate Professor Sue Worner of the Bio-Protection Research Center at Lincoln University. The door to Prof. Worner's office was always open whenever I ran into a trouble spot or had a question about my research or writing. She consistently allowed this paper to be my own work, but steered me in the right direction whenever she thought I needed it.

My sincere thanks go to Dr. David Teulon my co-supervisor at Plant & Food Research and Dr. Roddy Hale my university associate supervisor for their valuable guidance, careful editing, advice and constructive critique throughout this project.

I acknowledge the technical assistance of Myles MacIntosh and Andrew Holyoake, my go-to men for equipment and space related issues; Brent Richards, the long suffering nursery manager who was always open to my pestering requests for nursery related materials and advice.

I greatly appreciate the support from Graham Walker, Nadine Berry, Jessica Dohmen-Vereijssen, Melanie Davidson, Melanie Walker, Mette Nielsen, Nina Jorgensen, Gabby Drayton, and John Fletcher at Plant & Food Research who helped me with equipment, insect colonies, plants, data and documents.

Thanks are also due to staff at The Biological Husbandry Unit Organic Training College who granted me the permission to collect field data in organic potato crops.

My special thanks to staff and friends in and outside of the Bio-Protection Research Center who made my life and study here an interesting and unforgettable experience.

I am very grateful to the Ministry of Education & Training, Vietnamese Government for providing me with a scholarship to pursue my PhD study at Lincoln University. I would also like to acknowledge the financial support from Plant & Food Research, and the Horticulture New Zealand Product Groups - Potatoes NZ, Vegetables NZ, and Tomatoes NZ.

I wish to dedicate this thesis to my wife Bui Thi Thu Trang and my son Tran Phuc Bao, who have sacrificed a lot during my four years intensive study. This thesis is a present for them.

Appendices

Appendix 1: Number of *B. cockerelli* per trap for one week at Pukekohe 2009-2010.

Week ending	TPP/Trap	Cumulative proportion	ADD
22/12/09	2.458333	0.538125	354
30/12/09	4.958333	1.623495	427
5/1/10	4.625	2.635899	482
12/1/10	4.458333	3.611821	538
19/1/10	22.625	8.564393	612
26/1/10	52.16667	19.98358	688
02/02/10	60.75	33.28165	775
9/2/10	51.125	44.47282	856
16/2/10	39.83333	53.19227	940
24/2/10	64.75	67.36593	1034
02/3/10	77.875	84.41263	1102
09/3/10	45.20833	94.30865	1170
16/3/10	26	100	1235

ADD is accumulated degree days started from biofix 1st November.

Appendix 2: Number of *B. cockerelli* per trap for one week at Pukekohe 2010-2011.

Week ending	TPP/Trap	Cumulative proportion	ADD
02/11/10	1	0.0815	11.9
09/11/10	1.5	0.203749	53.3
16/11/10	1.25	0.305623	109.2
23/11/10	0.25	0.325998	171.4
30/11/10	3	0.570497	236.9
7/12/10	4.75	0.95762	307.7
14/12/10	6.75	1.507742	382.5
21/12/10	8.25	2.180114	471.4
30/12/10	15.25	3.422983	567.2
06/01/11	23.5	5.338223	650.6
11/01/11	107.25	14.07905	711.6
18/01/11	119	23.77751	799.8
25/01/11	44.75	27.42461	876.4
01/02/11	36.75	30.41972	954.9
08/02/11	39.5	33.63896	1048.1
15/02/11	16	34.94295	1123.7
22/02/11	72.5	40.85167	1218
01/03/11	174.75	55.09372	1294.2
08/03/11	286.5	78.44336	1363.7
15/03/11	159.5	91.44254	1430.7
22/03/11	17	92.82804	1505.4
29/03/11	23.5	94.74328	1577.3
06/04/11	7.5	95.35452	1642.5
12/04/11	17	96.74002	1688.1
19/04/11	19.5	98.32926	1740.3
26/04/11	10.5	99.185	1794.8
03/05/11	6	99.674	1843.5

(Continued on next page)

Appendix 2 *(continued)*

Week ending	TPP/Trap	Cumulative proportion	ADD
10/05/11	3.5	99.95925	1896.6
17/05/11	0.5	100	1952.8

ADD is accumulated degree days started from biofix 1st November.

Appendix 3: Number of *B. cockerelli* per trap for one week at Pukekohe 2011-2012.

Week ending	TPP/Trap	Cumulative proportion	ADD
29/11/11	0	0	229
6/12/11	1	0.454588	301
13/12/11	0.75	0.795529	372
18/12/11	2.1	1.750163	419
22/12/11	2.138889	2.722476	456
27/12/11	6.65	5.745485	508
30/12/11	2.916667	7.071366	544
4/1/12	4.59375	9.159629	601
6/1/12	17.9375	17.3138	625
10/1/12	6.5625	20.29703	668
12/1/12	21	29.84337	691
17/1/12	6.825	32.94594	743
20/1/12	21.29167	42.62487	775
24/1/12	11.59375	47.89525	812
1/2/12	12.35938	53.51367	895
7/2/12	12.25	59.08237	959
13/2/12	25.08333	70.48495	1027
21/2/12	30.40625	84.30726	1118
29/2/12	13.5625	90.4726	1204
6/3/12	9.333333	94.71542	1246
13/3/12	11.625	100	1317

ADD is accumulated degree days started from biofix 1st November.

Appendix 4: Number of *B. cockerelli* per trap for one week at Manawatu 2009-2010.

Week ending	TPP/Trap	Cumulative proportion	ADD
28/12/09	0.25	0.108342	421
4/01/10	0.75	0.433369	489
11/01/10	1	0.866739	548
18/01/10	4.5	2.816901	605
25/01/10	31.75	16.57638	686
1/02/10	18.25	24.48537	772
8/02/10	42.25	42.79523	852
15/02/10	15.75	49.6208	930
22/02/10	11	54.38787	1008
1/03/10	10.75	59.04659	1086
8/03/10	16.25	66.08884	1154
15/03/10	31	79.52329	1211
22/03/10	20.5	88.40737	1267
29/03/10	8	91.87432	1329
5/04/10	16.75	99.13326	1380
12/04/10	2	100	1405

ADD is accumulated degree days started from biofix 1st November.

Appendix 5: Number of *B. cockerelli* per trap for one week at Waikato 2009-2010.

Week ending	TPP/Trap	Cumulative proportion	ADD
21/12/09	0.25	0.2331	393
28/12/09	0.5	0.699301	464
4/01/10	0.75	1.398601	538
11/01/10	0.33	1.706294	599
18/01/10	1.67	3.263403	673
25/01/10	8.5	11.18881	757
1/02/10	6.75	17.48252	848
8/02/10	2.25	19.58042	942
15/02/10	2	21.44522	1035
22/02/10	3	24.24242	1120
1/03/10	4	27.97203	1204
8/03/10	27	53.14685	1283
15/03/10	21	72.72727	1351
22/03/10	3	75.52448	1410
29/03/10	13.25	87.87879	1475
5/04/10	13	100	1532

ADD is accumulated degree days started from biofix 1st November.

Appendix 6: Number of *B. cockerelli* per trap for one week at Lincoln 2009-2010.

Week ending	TPP/Trap	Cumulative proportion	ADD
8/2/10	1.4	1.02221	727.5
15/2/10	2.6	2.534501	792
22/2/10	3.8	4.826446	849.5
1/3/10	4.4	8.907833	918.5
8/3/10	7.2	12.23441	991.5
15/3/10	27	20.36546	1048
22/3/10	19	27.77113	1100.5
29/3/10	20.6	41.1713	1157
5/4/10	39.4	60.47976	1218
12/4/10	18.4	72.56317	1261.5
19/4/10	36	90.0648	1298.5
26/4/10	22.2	100	1349.5

ADD is accumulated degree days started from biofix 1st November.

Appendix 7: Number of *B. cockerelli* per trap for one week at Lincoln 2010-2011.

Week ending	TPP/Trap	Cumulative proportion	ADD
1/2/11	7.4	2.957634	799.5
8/2/11	7.6	5.995204	873
15/2/11	8.4	9.352518	947
22/2/11	8	12.54996	1017
1/3/11	18	19.7442	1081.5
8/3/11	19	27.33813	1140.5
15/3/11	25.6	37.56994	1203
22/3/11	58.8	61.07114	1260.5
29/3/11	43	78.25739	1310.5
5/4/11	32.6	91.28697	1354
12/4/11	9	94.88409	1389
19/4/11	12.8	100	1419

ADD is accumulated degree days started from biofix 1st November.