The impacts of plant species on the fitness of the tomato potato psyllid (*Bactericera cockerelli*) and the efficacy of its non-chemical management strategies

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Abstract of a thesis submitted in partial fulfilment of the requirements for the Degree of Master of Agricultural Science.

The impacts of plant species on the fitness of the tomato potato psyllid (*Bactericera cockerelli*) and the efficacy of its non-chemical management strategies

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Important vegetables such as tomato and potato, among others are affected by *Bactericera cockerelli* (the tomato potato psyllid; TPP). TPP causes psyllid yellows on these plants. However, in the recent years, it was discovered to be a transmitter of the bacterium *Candidatus liberibacter*, which causes symptoms similar to psyllid yellows to be more pronounced. This causes zebra chip in potatoes, making them undesirable to consume. As a result, farmers are managing the insect with agro-chemicals. This has since disrupted the bio-control strategies for other pests in glasshouse in New Zealand. This study focused on learning more about the insect ecology and research non-chemical approaches to manage the pest.

Several host plants of TPP are present in New Zealand, but the impact of these hosts on the ecological fitness (ability of the insect to adapt to its environment) of the insect is limited. It was evaluated if TPP progeny development and survival were affected when their mothers transferred from non-crop to crop host species. TPP was reared on boxthorn (*Lycium ferocissimum*) and poroporo (*Solanum aviculare*) which are non-crop host species and potato (*Solanum tuberosum*) and tomato (*Lycopersicon esculentum*) which are crop host species. Adults were transferred from each non-crop to each crop host species and allowed to oviposit. Each life stage of the progenies was evaluated for survival (%) and development (time in days). Nymph eclosion was faster on tomato when their mothers were transferred from poroporo or boxthorn compared to if they were from tomato. Total development was faster for 'poroporo to tomato' than 'tomato to tomato'. Total survival and development were also higher for 'poroporo to tomato' than 'tomato to tomato'.

In the third chapter, the coccinellid *Cleobora mellyi,* the parasitoid *Tamarixia triozae,* the mite *Amblydromalus limonicus* and the mirid bug *Engytatus nicotianae,* also '*C. mellyi* + buckwheat' and '*T. triozae* buckwheat' was eveluated in greenhouse conditions for the management of the pest.

These have already proven to be useful in laboratory studies. *A. limonicus* significantly reduced TPP eggs. *T. triozae* reduced nymph numbers by almost a half, but this was not significant. Similarly, *T. triozae, A. limonicus, C. mellyi and C. mellyi* + buckwheat reduced TPP adults numbers by more than a half and *T. triozae* more than two thirds, but neither reduction was significant.

The final research chapter determined in laboratory conditions how aphids colonise potato plants below mesh crop covers of different sizes which are currently used to exclude TPP from potatoes crops successfully. These mesh were touching or not touching potato leaflet. Aphid nymphs were able to breach all the mesh covers commercially available for field use. Aphids circumventing the mesh were not significantly affected whether the leaflet was touching the mesh or not. No adult was found feeding through the mesh.

In conclusion, results obtained in this study showed that host transfer from poroporo to tomato of TPP adults had an impact on the development and survival of its progeny. Some BCAs reduced TPP numbers. However, the pest population was too high for the BCAs to reduce the numbers to a level that would not warrant the use of agro-chemicals. Mesh covers can be used to manage TPP but using a natural enemy to manage aphids below the mesh would aid in successful control. Smaller mesh sizes may obviate this, but the medium term economics of that action needs to be evaluated.

Keywords: tomato, potato, poroporo, boxthorn, psyllid, host plant, ecology, mesh, biological control agent, eggs, nymphs, adults, transfer, non-chemical, aphid and glasshouse.

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Table of Contents

List of Tables

List of Figures

Chapter 1

Introduction

1.1 Overview

Farmers are under increasing pressure to meet the food demands of the world population. More than 800 million people are food insecure (James, 1998; United Nations, 2006) and another 2.7 billion live on less than $2 US daily (United Nations, 2006). What's more is that the world population is 7.3 billion (United Nations, 2015) and by 2050 is projected to reach almost 10 billion, requiring a 50% increase in food production (Food and Agriculture Organization, 2017a; Koscica, 2014; United Nations, 2015). 'Western' agriculture is attempting to intensify to achieve this goal but continues to cause increasing losses of biodiversity and its functions (Farm Animal Investment Risk and Return, 2016; Millennium Ecosystem Assessment, 2005). The increasing food demand in developing countries is partially met by recognised suppliers from countries such as New Zealand who are continuously trying to increase production especially of red meat and dairy (Liefting *et al.,* 2009). However, vegetables are also being produced intensively to meet demands where needed. Among the vegetables that are produced intensively because their demands are potato and tomato (Wassilieff, 2008).

The most important vegetable in New Zealand and the world is potato (*Solanum tuberosum* L. (Solanaceae)) (Food and Agriculture Organization, 2008b, 2015). The tuber adapted well to the conditions in New Zealand (Food and Agriculture Organization, 2008b) after been cultivated by the Europeans (Best, 1976). More than 10,329 hectares of land in New Zealand are cultivated annually with potato. In the 2013 growing season, the industry value was $500 million. These potatoes are used mainly fresh or processed, with some retained for seed (Potatoes New Zealand, 2017). The potato industry is one of New Zealand's most lucrative commercial vegetable ventures (Potatoes New Zealand, 2017). This can be seen in (Table 1) which indicates the two most purchased vegetables in New Zealand. Potato is consistently in the first or second place, and in more recent times it has been first. This is reflected by the fact that there is a steady increase in the cultivation of potato in New Zealand (New Zealand Grown Vegetables, 2017). It is evident that the tuber has a significant socio-economic impact on the country. Therefore, there is a pressing demand for improvement in the product quality and quantity to satisfy demanding markets (Potatoes New Zealand, 2017).

Table 1. Most purchased vegetables In New Zealand based on household expenditure (New Zealand Grown Vegetables, 2017)

Place	Year of assessment				
	1995	2004	2007	2010	2013
1st	potato	tomato	tomato	tomato	potato
2nd	tomato	potato	potato	potato	tomato

Tomato (*Lycopersicon esculentum* Mill. (Solanaceae)) is the second most important vegetable in the world and New Zealand (Food and Agriculture Organization, 2015; New Zealand Grown Vegetables, 2017). It is estimated that more than 100 million tonnes are produced annually from 3.7 million ha of land worldwide (Food and Agriculture Organization, 2015). The demands for tomato continue to increase on the world market as it is used in many diets (Hobson & Grierson, 1993). About 60 to 65% is consumed fresh while 35 to 40% is consumed in other forms (Roselló, Díez, & Nuez, 1996).

Tomato and potato originated from the Andes region. However, they are mostly produced outside of this region (Food and Agriculture Organization, 2008a, 2017c). This practice impacts transboundary pests (Food and Agriculture Organization, 2017b). These pests may have a more significant impact on their new ecosystems because of a reduction in naturally accruing population reducing factors (Food and Agriculture Organization, 2001). Not surprisingly, the arrival of *Bactericera cockerelli* (Ŝulc 1908) (Hemiptera, Triozidae) in New Zealand has negatively affected the production of tomato, potato and some other essential vegetables (N. Martin, 2008).

1.2 *Bactericera cockerelli* (Ŝulc 1908)

B. cockerelli also known as the tomato potato psyllid (TPP) (Figure 1), originated in North America. The insect has caused crop damage in the USA and Mexico dating back to the 18th century (Munyaneza, 2014a) and was later discovered in some Central American countries (Xu & Zhang, 2015). This pest was discovered in New Zealand in 2006 after it was suspected to be introduced in 2005-2006 (Teulon, Workman, Thomas, & Nielsen, 2009), perhaps, involved in smuggling natural enemies of other pests (Thomas *et al.,* 2011). Most recently, TPP has been in Western Australia attracting significant concern (Department of Agriculture and Food Australia, 2017).

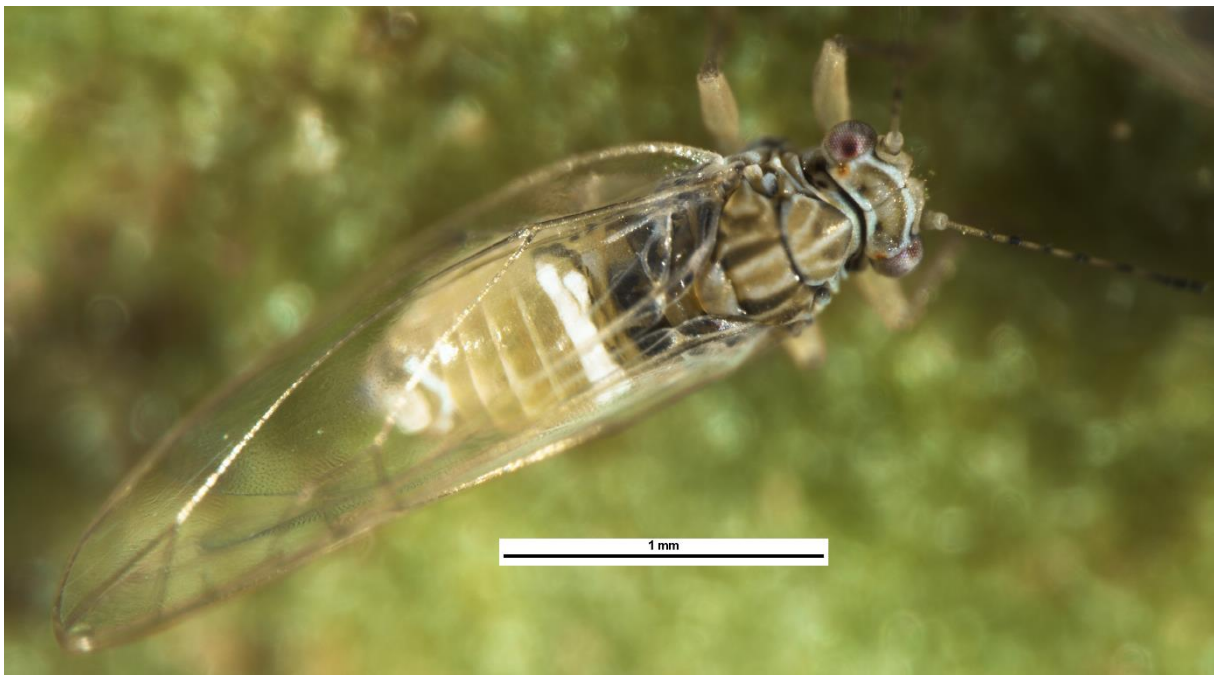

Figure 1. Adult *Bactericera cockerelli*

The insect causes a significant loss in production of potato and tomato in New Zealand and North and Central America (Ferguson & Shipp, 2002; N. Martin, 2016; Teulon *et al.,* 2009). It is, therefore, a key pest in those countries (Munyaneza *et al.,* 2012).

1.2.1 Importance

This insect adults and nymphs have sucking mouthparts, which they use to feed on tomato and potato plants' phloem (N. Martin, 2016). As they feed, they produce honeydew. Honeydew produced by TPP is commonly called "psyllid sugar" (Figure 2) (Cranshaw & Knutson, 2004). It was the consensus that as the nymph feeds, it can release a toxin into the plant, which causes psyllid yellows (Figure 3) (Knowlton & Janes, 1931). However, this is yet to be confirmed (Munyaneza, 2014a). What is certain is after feeding on the plant phloem the insect causes psyllid yellows (Wallis, 1955). These retard plant growth and development, and kill the plant in some cases, resulting in major crop loss (Liefting *et al.,* 2009; Wallis, 1951).

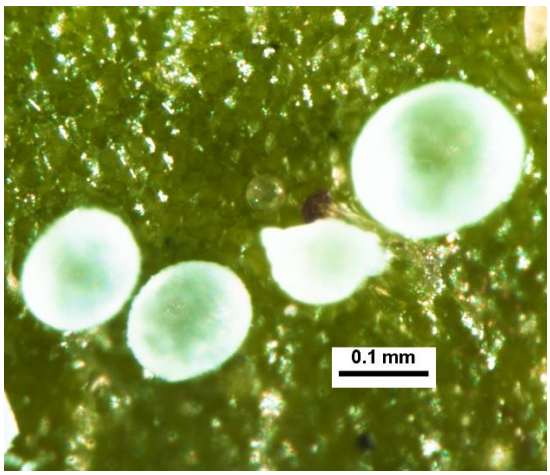

Figure 2. Honeydew produced by *Bactericera cockerelli* is commonly called "psyllid sugars"

The symptoms of psyllid yellows on tomato and potato plants include the upward curling of leaves, chlorosis, slow growth, flattening of young foliage, long internodes, small and poor quality fruits, basal curling and purpling of young leaves and auxiliary branches (Munyaneza, 2013a). Additionally, the below-ground parts of the potato plants can produce many undersized and unusually-shaped tubers, including those that are capable of breaking dormancy early (Munyaneza, 2013a).

Figure 3. Psyllid yellows caused by *Bactericera cockerelli* on tomato (right) and potato (left) (N. Martin, 2016).

In the mid 1990s it was discovered that while feeding, *B. cockerelli* transmits the bacterium *Candidatus liberibacter solanacearum* (Liefting *et al.,* 2008) (Rhizobiales, Phyllobacteriaceae (CLso)) (Munyaneza, 2014b). CLso is gram-negative and limited to the phloem. The bacteria is transmitted vertically and horizontally (Munyaneza, 2013b) and it causes psyllid yellows symptoms to be more heavily expressed (Horton, Miliczky, Munyaneza, Swisher, & Jensen, 2014; Munyaneza, Crosslin, & Upton, 2007; Ogden, Fullerton, & Nitschke, 2011b). Additionally, CLso can cause potato tubers to be affected by stolons to collapse, medullary ray tissues streaking, vascular tissues browning and necrosis of internal tissues (Munyaneza, 2013a). These damage in potato tubers are called zebra

chip, which can be seen on cross-sections of the tuber especially after frying (Figure 4), making it unmarketable (Munyaneza, 2014b; Munyaneza *et al.,* 2007).

This psyllid can cause total crop loss (Munyaneza *et al.,* 2012). In 2009, New Zealand potato growers lost about 16% or $47 million of their crop to the psyllid (Ogden, Fullerton, & Nitschke, 2011a). TPP also caused the loss of lucrative export markets and a significant increase in insecticide input costs, to manage the pest (Teulon *et al.,* 2009). The latter has negative impacts on the environment (Bernanke & Köhler, 2009; Goodman, 1974).

Figure 4. Zebra chip on cooked potato tubers caused by *Candidatus liberibacter* solanacearum transmitted by *Bactericera cockerelli* (N. Martin, 2016)

1.2.2 Biology

The tomato potato psyllid a hemipteran bug and has metamorphosis comprising three life stages eggs, nymphs and adults (Abdullah, 2008; Brewer, 1973). The pest reproduces sexually (Mustafa, 2014).

Adults

TPP wings are long, forming a V over their body (N. Martin, 2016; Munyaneza, 2014a; Wallis, 1955). The hind legs are enlarged, which allows the insect to jump when disturbed, hence, the older name jumping plant lice (Munyaneza & Henne, 2013). Adults measure 2.1-2.55mm in length. At emergence, adult body colour is pale to dark green but as the insect develops the colour changes from green to brown or dark brown and from brown to grey or black (Figure 5) (Munyaneza, 2014a; Wallis, 1955).

There are single transverse white or yellow lines on the head and thorax. Additionally, it has white dorsal lines across the first and final abdominal segments. These lines are typical of *B. cockerelli* and

are essential in identifying the insect (Figure 5) (Cranshaw & Knutson, 2004; N. Martin, 2016; Wallis, 1955).

Figure 5. *Bactericera cockerelli* adult with dorsal lines (L) and newly emerged TPP adult (R) (Martin, 2016).

Males and females have distinctive features on the abdomen. The male has six abdominal segments with one of these bearing the genitalia, while the female also has six abdominal segments and one baring genitalia segment. The male genitalia is blunt while that of the female is round and robust and have a short ovipositor (Figure 6) (Abdullah, 2008)

Figure 6. Underside view of a male (top right) and female (bottom left) *Bactericera cockerelli* (N. Martin, 2016).

Eggs

Eggs are light yellow at oviposition but turn dark yellow or orange with time. They are oval and measures 0.32-0.34 by 0.13-0.15 mm. They are borne on the plant by a stalk 0.48 to 0.51 mm long.

They are oviposited singularly on leaf edges, but they can also be found on any other part of the plant (Figure 7) (Munyaneza, 2013a, 2014a). The incubation period varies from 4 to 8 days on potato plants at 23°C (Tran, Worner, Hale, & Teulon, 2012).

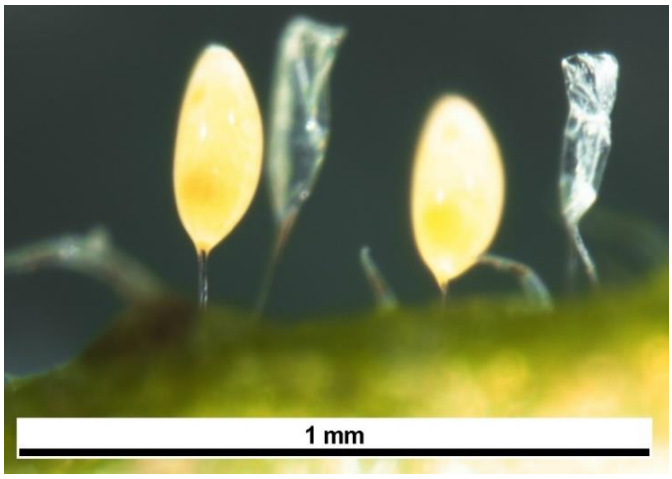

Figure 7. *Bactericera cockerelli* eggs (yellow) and empty eggs (white).

Nymphs

Nymphs can be found on any part of the plant (N. Martin, 2016) including the abaxial and adaxial leaf surfaces but they prefer sheltered locations. Therefore, they are mostly found on the abaxial surface (Cranshaw & Knutson, 2004; Munyaneza, 2013a, 2014a). They are flat and vary in colour between orange and yellow immediately after emerging with changes to pale green in the final instar (Figure 8) (Cranshaw & Knutson, 2004; Wallis, 1955). *B. cockerelli* has five nymphal instars (Wallis, 1955). The main difference between instars is size; they measure 0.23 mm to 1.60 mm (Munyaneza, 2014a). The nymphs can walk short distances but seldom move and usually remain feeding in one position until they moult to adult (Cranshaw & Knutson, 2004; N. Martin, 2016).

Figure 8. *Bactericera cockerelli* nymphs (Martin, 2016).

1.2.3 Thermal requirements

B. cockerelli can survive sub-zero temperatures for short periods (N. Martin, 2016) and can reproduce and develop at the low temperatures (Tran *et al.,* 2012). Therefore, the insect can reproduce throughout the year in New Zealand climatic conditions (N. Martin, 2016; Tran *et al.,* 2012). In New Zealand in warmer conditions, such as glasshouses or during summer, the time required for development is shorter (N. Martin, 2016; Tran *et al.,* 2012). The temperature required for TPP development ranges between 7.1°C and 31°C while the optimum is 23 to 27 °C. The pest development from egg to adult takes 21 to 25 days at the optimum temperature range (Tran *et al.,* 2012).

The insect does not have a diapause induced by photoperiod. Horton et al. (2014) demonstrated that TPP collected from different North American regions and studied in a controlled environment with a photoperiod of 10 L:14 D and 16 L:8 D did not differ in development of ovarian or mating activities. Therefore, development time depends on temperature alone (Horton *et al.,* 2014; Tran *et al.,* 2012)

1.2.4 Host plants

TPP has a wide range of crop and non-crop host plants, mainly Solanaceaes (Barnes, Taylor, & Vereijssen, 2015; Thinakaran, 2014; Wallis, 1955). However, there is limited scientific information to verify that most of the reported non-crop host plants found in New Zealand are true hosts (Barnes *et al.,* 2015; N. Martin, 2008; Wallis, 1955). Many plant species have been listed as hosts (Wallis, 1955), but caution should be taken in pronouncing a plant as a host if only a mobile life stage of an insect is found on it (Burckhardt, Ouvrard, Queiroz, & Percy, 2014; Van Klinken, 2000). TPP adults can fly (Burckhardt *et al.,* 2014) and flying insects can be found on a wide variety of plants (Burckhardt *et al.,* 2014). These are often called "tourists" (Otway, Hector, & Lawton, 2005), which does not mean those plants are true hosts but are colonised casually (Burckhardt *et al.,* 2014). In some cases, the insect can feed and reproduce on them, but their offspring will not develop (Wallis, 1955). A host plant can be defined as a plant on which the insect can complete its life cycle (Burckhardt *et al.,* 2014).

The following weeds that are found in the Canterbury region of New Zealand are host plants of TPP: African boxthorn (*Lycium ferocissimum* Miers. (Solanaceae)) (Barnes *et al.,* 2015; Ember, Acs, Munyaneza, Crosslin, & Kolber, 2011; Taylor & Berry, 2011; Vereijssen *et al.,* 2013b), poroporo (*Solanum aviculare* G.Forst. (Solanaceae)) (Barnes *et al.,* 2015; Taylor & Berry, 2011; Vereijssen *et al.,* 2013a; Wallis, 1955), field bindweed *(Convolvulus arvensis* L. (Convolvulaceae)) (Barnes *et al.,* 2015; Ember *et al.,* 2011; Knowlton & Thomas, 1934; Wallis, 1955), black nightshade (*Solanum nigrum* L. (Solanaceae)) (Knowlton & Thomas, 1934; N. Martin, 2016), and the following crops are suitable hosts: potato (*Solanum tuberosum* L. (Solanaceae)) (Munyaneza *et al.,* 2007; Puketapu, 2011; Walker,

MacDonald, Larsen, & Wallace, 2011; Wallis, 1955), tomato (*Lycopersicon esculentum* L. (Solanaceae)) (Liefting *et al.,* 2009; Teulon *et al.,* 2009; Wallis, 1955). The insect completes its entire life cycle on them. However, it is not known how or if the ecological fitness (ability of the insect to adop to its environment) of the insect is affected after moving from one host plant to the next. It is vital for the management of the pest to know the role of the non-crop host plant in the status of the pest. An ill-informed management technique may include the removal of these plants possibly, ignoring the possible ecosystem services that they provide to agriculture (Wratten, Sandhu, Cullen, & Costanza, 2013).

1.2.5 Dispersal

When disturbed the tomato potato psyllid jumps and flies promptly. With the aid of the wind, the insect can travel long distances (Wallis, 1955). Only the adult of the insect migrate (N. Martin, 2016) but both the nymph and egg can disperse by the movement of plant materials especially in the plant trade (Munyaneza, 2013a, 2014a). A typical case is one by which the insect is thought to have arrived in New Zealand. It is believed that it entered the country on plant materials in its juvenile stages. As a precaution materials of its host plants were banned from entering Australia from New Zealand after the pest was discovered in the later country (Munyaneza, 2013a). Additionally, if after scouting, the pest incidence exceeds 2% of the sampled material, the growers are not allowed to export their fresh produce to Australia (Ministry of Agriculture and Forestry Biosecurity New Zealand, 2008).

1.2.6 Management

The management of TPP is comprised of cultural practices and the use of agrochemicals. Cultural practices include early planting dates when planting outdoor, plant insect free planting materials and the removal of host plants over winter or between crops. Additionally, a rigid scouting system should be adapted to aid in early detection (N. Martin, 2016). As for the use of agro-chemicals, most commercial farmers in New Zealand and the other countries have indicated that the most common, useful and adaptable method of managing the pest is by several applications of various agro-chemicals. In fact, the majority of the research on managing TPP is focussing on the use of the agro-chemicals (Berry, Walker, & Butler, 2009; Gharalari *et al.,* 2009; Guenthner, Goolsby, & Greenway, 2012; Page, Jamieson, Chhagan, Connolly, & Curtis, 2011), of which a wide range is available specifically for this purpose (Tomatoes New Zealand & Vegetables New Zealand, 2012). There are also a few non-chemical approaches (Merfield, Geary, Hale, & Hodge, 2015; Pugh, 2013) but they need further studies to be adopted by many large-scale commercial farmers. Additionally, several natural enemies of TPP are known (González, Flores, Rodrígu, & Ruíz, 2014; MacDonald, Connolly, Larsen, & Walker, 2016; N. Martin, 2016; Pugh, O'Connell, & Wratten, 2015). However, their uses in the management of the pest has not been established (N. Martin, 2016). There is a definite gap in the

knowledge of managing the pest without the use of agrochemicals. Iindicating the need for more research on managing the pest without the use of agro-chemicals.

Taking into consideration the importance of the crops affected by the pest, the pest impact on these crops and the present management techniques, lessons learned from other insects and biological control approaches along with the current knowledge gap, a research approach was designed to investigate the impact of host plants on the fitness and of TPP and further evaluate non-chemical approaches to manage this pest.

1.3 Aim and Objectives

This study aims to quantify the survival and development rate (in time) of TPP progeny's whom parents migrated from non-crop host species to crop host species and to develop non-chemical management approach of TPP in potato and tomato cultivation.

I. To evaluate the impact on the ecological fitness of TPP after transferring from it the non-crop host to tomato and potato.

II. To determine to what extent aphids are breaching insect mesh used for a non-chemical management of TPP.

III. To determine the ability of the Miridae *Engytatus nicotianae,* (Koningsberger, 1903) the Coccinellidae *Cleobora mellyi,* (Mulsant, 1850) the Eulophidae *Tamarixia triozae* (Burks, 1943) and the predatory mite *Amblydromalus limonicus* (Garman & McGregor, 1956) to help manage TPP populations on tomato plants.

Chapter 2

The ecological "fitness" of the tomato potato psyllid after transferring from non-crop host plants to tomato and potato

2.1 Abstract

Plant defence and diet quality affect how well an insect adapts to that plant. Therefore, an insect's development and survival varies on different host plant species. These are also affected by the insect's previous host feeding experience. In New Zealand *Bactericera cockerelli* (the tomato potato psyllid (TPP)) overwinters on non-crop host species and later migrates to crop host plants. How changing host plant species affects the insect "fitness" is unknown. This study evaluated if transferring adult TPP from non-crop to crop host species has an impact on the development and survival of their progeny. TPP was reared on non-crop host species, boxthorn (Lycium ferocissimum) and poroporo (Solanum aviculare), and crop host species, potato (Solanum tuberosum) and tomato (Lycopersicon esculentum). Adults were transferred from non-crop to the crop host species and allowed to oviposit for 48 hours before being removed. Number of counted eggs and nymphs were monitored every 24 hours for the development and survival of each life stage.

The incubation period of eggs from adults transferred from poroporo to tomato was 6.9 days, and for boxthorn to tomato was 7.2 days and these were significantly less than those on tomato to tomato (9.0 days) and potato to potato (9.2 days) ($P < 0.05$). Nymph developmental time was similar for all treatments. Total development time (egg to adult) was substantially faster for progeny of adults from poroporo transferred to tomato (20.5 days) than those from tomato to tomato (23.2). The survival of eggs did not differ significantly across treatments. Fewer nymphs survived when adults were transferred from tomato to tomato (50.4%) than those from poroporo to tomato (92.1 %) ($P < 0.05$). Total survival (egg to adult) was significantly higher for progeny from adults transferred from poroporo to tomato (80.0 %) compared to boxthorn to potato (35.3 %), boxthorn to boxthorn (40.7 %), poroporo to potato (33.9 %) and tomato to tomato (37.6 %) ($P < 0.05$).

2.2 Introduction

The intrinsic rate of increase of a polyphagous herbivorous insect is influenced by its host plant. Host plants selection is determined by ecological (Mira & Bernays, 2002; Nishida, 2014; Schoonhoven, van Loon, & Dicke, 2005; Scriber & Slansky, 1981; Via, 1990) and nutritional factors (Schoonhoven *et al.,* 2005; Scriber & Slansky, 1981) and fertility, survival and development are likely to vary accordingly. Because *Bactericera cockerelli* (Šulc, 1909) ((the tomato potato psyllid (TPP)) immature life stages are

mostly immobile (Nelson, Swisher, Crosslin, & Munyaneza, 2014), the host plant chosen by their mother has to be suitable for their development and survival to maturity (Barnes *et al.,* 2015). However, not all host plant species are equally suitable. Survival of TPP eggs and nymphs differed significantly when reared on *Solanum tuberosum* L.*, Ipomoea batatas* (L.) Lam. and *Solanum aviculare* (G. Forst) in a glasshouse experiment (Puketapu, 2011), and the development rate on *S. tuberosum* and *Solanum elaeagnifolium* Cav. were reported to be significantly different (Thinakaran, Yang, Munyaneza, Rush, & Henne, 2015). Therefore, the ecological "fitness" was affected by the host plant species.

Some parameters that can be measured as proxies for fitness include; growth rate and survival of immature life stages (i.e., eggs and nymphs), and sex ratio, body size and fecundity of adults (Liu & Trumble, 2007a; Lu & Heong, 2009; Sober, 2001). Therefore, the concept adopted for this research is the measurement of how well TPP adapts to a host plant (Lu & Heong, 2009; Sober, 2001). Some known host plants of TPP found in the Canterbury region of New Zealand are: African boxthorn (*Lycium ferocissimum* Miers) (Barnes *et al.,* 2015; Ember *et al.,* 2011; Taylor & Berry, 2011; Vereijssen *et al.,* 2013b), poroporo (*Solanum aviculare* G. Forst.) (Barnes *et al.,* 2015; Taylor & Berry, 2011; Vereijssen *et al.,* 2013a; Wallis, 1955), field bindweed (*Convolvulus arvensis* L.) (Barnes *et al.,* 2015; Ember *et al.,* 2011; Knowlton & Janes, 1931; Wallis, 1955)*,* black nightshade (*Solanum nigrum* L.) (Knowlton & Thomas, 1934; N. Martin, 2016) potato (*Solanum tuberosum* L.) (Munyaneza *et al.,* 2007; Puketapu, 2011; Walker *et al.,* 2011; Wallis, 1955) and tomato (*Lycopersicon esculentum L*.) (Liefting *et al.,* 2009; Teulon *et al.,* 2009; Wallis, 1955).

It is known that TPP ecological fitness differs on host plant species from previous studies. However, changes in the ecological fitness when TPP adults may move from perennial hosts (e.g. African boxthorn or poroporo) to annual host species in spring and summer is unknown. It is essential to understand if the insect progeny suffer changes in ecological fitness after adults transfer from one host plant species to another, given the role different host plant species play at different times of the year (N. Martin, 2008). This information can provide knowledge of the pest's possible intrinsic rate of increase depending on the host plant species of origin and new host plant species. Knowing the intrinsic rate of increase is imperative in planning possible management strategies for the pest. This study evaluated if transferring adult TPP from non-crop to crop host species has an impact on the development and survival of their progeny.

2.3 Materials and methods

2.3.1 Plants

Potato (Ilam Hardy G6, a common cultivar in New Zealand) was grown in a glasshouse at the Plant Nursery, Lincoln University and tomato (Merlice, a common cultivar New Zealand) were sourced from a Zealandia Horticulture (https://www.zealandia.co.nz) a commercial seedling producer. The plants were planted in 0.75 litre planter pots filled with a potting mix comprised of 400L compressed bark, 1500g of Osmocote 3-4 months release (http://www.farmcraft.com.au/), 500g horticultural lime, 500g of hydraflo and 100L pumice.

Cuttings from boxthorn, poroporo, field bindweed and black nightshade were collected from plants in fields around Lincoln. These plant species were selected because they are hosts of TPP (Barnes *et al.,* 2015; Liefting *et al.,* 2009; Taylor & Berry, 2011; Teulon *et al.,* 2009; Vereijssen *et al.,* 2013a; Walker *et al.,* 2011; Wallis, 1955). Cuttings were treated with Rooting hormone (Murphy's) and placed in planting trays with Perlite and situated in a warm, humid glasshouse to root. Periodically the cuttings were supplied with water mist to keep them from drying. After rooting, the cuttings were potted in a similar manner, as were tomatoes and potatoes. All plants were situated in the glasshouse for further development and supplied with water as required.

2.3.2 Psyllid culture

TPP adults were collected from boxthorn in the wild and from a colony kept on potato plants (CV. Swift) at the plant nursery, Lincoln University. Colonies were then established by placing 20 adults TPP each on tomato, potato, poroporo, field bindweed, black nightshade and boxthorn plants kept in separate “BugDorm”-2 Rearing Cages (L60 x W60 x H60 cm and Mesh Size of 96 x 26 cm: 680 µm opening). The colonies were kept in a controlled temperature (CT) room at 23°C with a 4°C range at 60% RH, and a photoperiod of 16:8 (L:D) h, because these are the best conditions for the insect growth and development (Tran *et al.,* 2012). New healthy plants were added to the colonies as older plants begin to senescence and older plants were eventually removed after complete senescence. Plants were watered as needed.

The insect culture did not establish on field bindweed and black nightshade. After serval attempts at infesting these two plants species with TPP, the insect culture failed to establish. It was evident that the insect was feeding and reproducing on the plants because eggs, early instar nymphs and psyllid sugars were observed, but later instar nymphs and newly emerged adults were never observed. The insect was unable to survive through the immature life stages or complete an entire life cycle on these plants. Thus, further experiments with these plant species were not undertaken.

At Plant and Food Research, Lincoln, a subsample of TPP collected from the different host plants were screened for the presence of the bacteria *Candidatus* Liberibacter solanacearum (Liefting *et al.,*2009) (CLso). PrepGEM™ reagents were used to extract DNA from the insect in preparation for CLso measurement using qPCR (Beard & Scott, 2013).

2.3.3 Experimental setup.

Adults were collected from colonies with the aid of an aspirator and sexed under a binocular microscope. The sexing was done concentrating on the apex of the abdomen. The male apex is pointed while that of the female is round and robust and has a short ovipositor (Figure 9) (Abdullah, 2008). Four pairs of adults were placed on plants (Table 2) covered by micro-perforated bread bags. Adults were removed after 48 h, and the number of eggs per plant was recorded. Plants containing no more than 30 eggs were used for observation. There were six replicates per treatment; each plant was a replicate. Plants were placed in a random order in six complete randomised blocks in a CT room as above.

Figure 9. Underside view of *Bactericera cockerelli* male (r) and female (l) (N. Martin, 2016)

Adult psyllids from each non-crop host species were transferred to each crop host species. As controls, adult psyllids cultured on each host species were placed on the same species from which they originated. Eight treatments were evaluated using insects from the four host species (Table 2).

Table 2. The host plant species from which psyllid adults originated and host species on which psyllid progeny was studied.

Host species from which psyllid originate	Host species on which psyllid was studied			
	Potato	Tomato	Poroporo	Boxthorn
Potato	■			
Tomato		■		
Poroporo	■	■	■	
Boxthorn	■	■		■

The ecological fitness was then evaluated by recording the growth rate and survival of immature life stages in each treatment. At 24h intervals, observations were made for the emergence of nymphs from the eggs (nymph eclosion), and the nymphs were observed for their rate of development to the emergence of adults (adult eclosion). Time from ovipositing to adults' emergence was also calculated (total development). The number of nymphs to emerge from eggs was used to calculate the percentage of viable eggs and the number of adults that emerged provided a measure of nymphal survival. Total survival was calculated by analysing the percentage of eggs that survived through to adult. These observations were made until the last adult emerged or all nymphs had died.

The data for development and survival were used to calculate means for each treatment. The data were analysed using two-way ANOVA (factors treatments and blocks) in GenStat 18th edition (VSN International). A least significant difference (LSD) of 5% was used in all analysis.

2.4 Results

All TPP adults sampled for CLso were positive for the presence of the bacterium. The incubation period of eggs (nymph eclosion) from adults transferred from poroporo to tomato were 6.9 days (Table 3). This was similar to poroporo to poroporo (8.2 days) but significantly lower ($P < 0.05$) than for tomato to tomato (9.0 days). For boxthorn to tomato, the incubation period was 7.2 days; this was significantly less ($P < 0.05$) than those on tomato to tomato (9.0 days) ($P < 0.05$). Nymph developmental time (adult eclosion) was similar for all treatments. Total development time (egg to adult) was substantially faster for progeny of adults from poroporo transferred to tomato (20.5 days) than those from tomato to tomato (23.2) ($P < 0.05$). There was no significant difference between the other treatments (Table 3).

Table 3. Development time (days) of the tomato potato psyllid progeny from adults originating from the same or different host plant species. Means with a letter in common within a column did not differ significantly.

Treatment	Nymph eclosion		Adult eclosion		egg to adult	
Boxthorn to boxthorn	8.1	ab	13.5	a	21.7	ab
Boxthorn to potato	8.0	ab	13.8	a	21.6	ab
Boxthorn to tomato	7.2	a	14.3	a	21.7	ab
Poroporo to poroporo	8.2	ab	13.5	a	21.8	ab
Poroporo to potato	7.6	ab	12.9	a	20.8	ab
Poroporo to tomato	6.9	a	13.7	a	20.5	a
Potato to potato	9.2	b	13.3	a	22.9	ab
Tomato to tomato	9.0	b	14.1	a	23.2	b
LSD (5%)	1.8	-	2.5		2.5	

Although not significant, the mean percentage of eggs to eclose ranged from approximately 50% for progeny on potato when adults originated from boxthorn to 87% for eggs on tomato when adults were from poroporo (Table 4). Adult emergence was lowest where host plants were tomato only (tomato to tomato, mean 50% emergence) and highest for poroporo to tomato (92%) ($P < 0.05$).

As for survival of eggs to adults, eggs on tomato from adults reared on poroporo again had the highest survival to adults eclosion (80%), which was significantly higher ($P < 0.05$) than those from boxthorn to boxthorn (41%), tomato to tomato (38%), boxthorn to potato (35%) and poroporo to potato (34%) (Table 4).

Table 4. Survival (percentage) of the tomato potato psyllid progeny from adults originating from the same or different host plant species. Means with a letter in common within a column did not differ significantly.

Treatment	Nymph eclosion		Adult eclosion		egg to adult	
Boxthorn to boxthorn	52.9	a	83.3	ab	40.7	a
Boxthorn to potato	49.8	a	80.4	ab	35.3	a
Boxthorn to tomato	81.4	a	73.1	ab	58.0	ab
Poroporo to poroporo	79.6	a	70.3	ab	51.1	ab
Poroporo to potato	59.7	a	60.3	ab	33.9	a
Poroporo to tomato	87.2	a	92.1	b	80.0	b
Potato to potato	71.5	a	70.2	ab	53.4	ab
Tomato to tomato	70.5	a	50.4	a	37.6	a
LSD (5%)	38.5		33.1		38.2	

2.5 Discussion

2.5.1 Overview

Some host plant species might not always be available to an insect throughout the year, especially for species that utilise annual plant species that are available for only part of the year. Therefore, the insect can survive on various well-distributed perennial non-crop host species which are not always their preferred host species (Awmack & Leather, 2002). These may ultimately serve as refuges for the insect until the annual host species are available, to which they will migrate. An insect changing from one host species to another can have a negative or positive effect on the ecological fitness of the insect and its progeny (Awmack & Leather, 2002). The ability of progeny from migrating insects to survive on the new host species is imperative for it to establish successfully (Awmack & Leather, 2002).

In New Zealand, TPP populations can develop on boxthorn and poroporo during the winter (N. Martin, 2016). Although development at lower temperatures is slow (Tran *et al.,* 2012), these plants

are ideal for the insect to overwinter in small numbers and as temperature increases in spring and summer adults may disperse to annual crop host plants such as potato and tomato (N. Martin, 2016).

Previous studies have examined the development and survival of TPP on host plant species where the host plants of the adults were the same or different to that of the progeny (Abdullah, 2008; Prager, Esquivel, & Trumble, 2014; Puketapu, 2011; Thinakaran *et al.,* 2015; Tran *et al.,* 2012; Yang & Liu, 2009). However, the impact of adults changing from one host plant species to another was not quantified. The present study takes into consideration reproductive adults to transferring from one host plant species to another. The aim was to understand the impacts on the progeny of TPP of adults transferring from non-crop to crop host species.

2.5.2 Development

In this study, eggs developed significantly faster on tomato when TPP females were transferred from boxthorn or poroporo compared to when the adult originated from tomato. The total development time of TPP from egg to adult for the different treatments followed a similar trend to nymph eclosion.

Host plant quality impacts the oviposition of fertile eggs by an insect (Awmack & Leather, 2002; Sadasivam & Thayumanayan, 2003). Fertile eggs are those that produce nymphs (Awmack & Leather, 2002). When an insect has detected a host plant for ovipositioning, it has determined that such plant can provide food suitable for its offspring's development. Additionally, when host plant suitability for development of offspring differs to the previous host plant, resorption of eggs or ovarium can occur to use as energy and produce fewer eggs but of higher quality (Awmack & Leather, 2002; Sadasivam & Thayumanayan, 2003). These high-quality eggs are likely to produce "fitter" offspring, increasing their chances of maintaining the species, therefore, increasing ecological fitness (Awmack & Leather, 2002). Results obtained in the present study supported these conclusions to some extent because the development time of progeny was marginally less when their mothers changed host plant species. This indicates that the offspring were of higher quality as opposed to the offspring of the adults which did not change host plant species. However, the number of eggs produced by these migrating adults is needed to fully adopt this theory.

The reduced development period of TPP offspring when its mother was transferred from non-crop host species to crop host species is essential. It indicates that the intrinsic rate of increase of the pest can be increased (Howe, 1953, 1971) as opposed to if the insect population developed on the same host species over several generations. These results are indicative that life table and forecasting models are needed. Such models help in developing and applying effective pest management strategies (Damos & Savopoulou, 2010). This will help to identify when it may be necessary to apply

agro-chemicals and help reduce the number of applications needed (Ahn, Yang, & Jung, 2012). More research is needed for life table and forecasting models for TPP progenies after their mothers are transferred from non-crop to crop host plant species.

2.5.3 Survival

Results obtained for the survival of nymphs did not show a similar pattern to those obtained for development of nymphs to adults, where there was no statistical difference in development time between treatments. However, with exception a notable interaction is that nymphs from poroporo to tomato survived significantly more than those of tomato to tomato. Additionally, more offspring from adults transferred from poroporo to tomato survived from eggs to adults than those from tomato to tomato.

Survival and development of an insect on a host species is also affected by the defence mechanism of said host species because these have various constitutive and induced defence mechanisms against insects (War *et al.,* 2012). If plant defence mechanisms were having an impact on the fitness of progeny, we would have expected progeny of adults from the same host plant species (i.e. tomato to tomato) to have had higher fitness than those from adults from different host plants. These results did not indicate that the host species defensive mechanism had an impact on the results, given that progeny of adults transferred from poroporo to tomato developed faster and more survived than for any other treatment. Those on tomato of adults originating from tomato developed the slowest and survived the least among all treatments.

Of the many listed non-crop host species of TPP (Barnes *et al.,* 2015; N. Martin, 2008; Wallis, 1955), some are very localised (Barnes *et al.,* 2015). Therefore the use of information provided by developing life table and forecasting models for TPP progeny, considering the natal host species of their mother has to be used in accordance to the host species found in that specific locality taking into consideration that the adults can move as much as 100 m daily (N. Martin, 2016).

The survival of TPP bearing CLso can be lowered by the presence of the pathogen (Nachappa, Shapiro, & Tamborindeguy, 2011). Psyllid samples from all TPP colonies used in this study tested positive for CLso. This indicates that the presence of CLso had no biasing effect on the survival of the insect.

Field bindweed and black nightshade are listed as host plants of TPP (Barnes *et al.,* 2015; Wallis, 1955) However, because the insect progeny were unable to develop on these species in the present study, they may not be suitable as host species for the insect but casual plants. Casual plants are those on which the insect can feed and reproduce, but the progeny will not develop to adults (Burckhardt *et al.,* 2014). Having these plants listed as host plants of TPP can cause some confusion

and have economic and environmental implications especially in formulating a pest management protocol for the insect (N. Martin, 2008). More research in different conditions is needed to ascertain if in fact, these are host plants or not.

2.6 Conclusion

The results from the present study indicated that TPP progeny of adults transferring from poroporo to tomato could have a faster development rate than those developing on the crop host species and may thus accelerate population establishment in crop hosts after migrating to them. This indicates that in these cases the intrinsic rate of increase will be directly affected because of differences observed. Progeny of adults that transfer from boxthorn are unlikely to incur any substantial fitness change relative to those that develop on a host host species. Black nightshade and field bindweed are not host plants of TPP but casual plants because the insect colony did not establish but feed on these.

Chapter 3

Evaluation of the mirid *Engytatus nicotianae*, the ladybird *Cleobora mellyi*, the parasitic wasp *Tamarixia triozae* and the mite *Amblydromalus limonicus* to manage TPP in semi glasshouse conditions

3.1 Abstract

The use of synthetic, agro-chemical insecticides is a significant contributor to the already high negative impact of agriculture on the environment and human health. However, the present management technique for *Bactericera cockerelli* ((the tomato potato psyllid (TPP)) in glasshouses is dominated by insecticides. Laboratory studies have shown that the use of natural enemies to manage pests in glasshouses could provide a viable alternative management strategy. This study evaluated whether predators and a parasitoid of TPP, the coccinellid *Cleobora mellyi,* the parasitoid *Tamarixia triozae,* the mite *Amblydromalus limonicus* and the mirid bug *Engytatus nicotianae,* could reduce TPP eggs, nymphs and adults numbers on tomato plants in a glasshouse, using insect cages. Also, it was evaluated if resource subsidies comprising flowering buckwheat (*Fagopyrum esculentum*) would improve the effectiveness of *T. triozae* and *C. mellyi.*

The mean number of TPP eggs (64) found in the *A. limonicus* treatment was statistically lower ($P < 0.05$), than that of the control (172.9). The other treatments were numerically lower than the control, although not statistically different ($P > 0.05$); *T. triozae* (80.1) was the lowest followed by *C. mellyi* + buckwheat (105.9) then *E. nicotianae* (107.5) then *T. triozae* + buckwheat (110.3) followed by *C. mellyi* (134.1). There was no substantial difference in the mean number of nymphs between the control and all treatments ($P > 0.05$), although fewer TPP nymphs were recorded in cages with *T. triozae* (77.1) followed by *A. limonicus* (109.8), then *C. mellyi* + buckwheat (114.9) and *C. mellyi* without buckwheat (121.4) compared to control (142.8). Fewer adult TPP were found with *T. triozae* (mean = 7.5, $P < 0.05$) compared to the control (mean = 27). Although not significant ($P > 0.05$), fewer TPP adults were found in the following treatments compared to control from lowest to highest number of adults; *C. mellyi* (10.2), *A. limonicus, C. mellyi* + buckwheat (11), *T. triozae* + buckwheat (23.8). Buckwheat did not enhance pest suppression by *T. triozae* nor *C. mellyi*.

3.2 Introduction

Agriculture has a significant level of adverse impacts on the environment and human health (external costs) (Buttel, 2003; Helbling, 2012; Heong, Wong, & Reyes, 2015; Tegtmeier & Duffy, 2004). Among the highest agricultural inputs in the world is the use of synthetic, agro-chemical, pesticides. An estimated 2 million tonnes of pesticides are used annually worldwide (De, Bose, Kumar, & Mozumdar, 2014). These contribute significantly to adverse impacts on ecosystem services and lead to external costs (Boxall, Sinclair, Fenner, Kolpin, & Maund, 2004; Conway, 2002). Never the less, the most common plant pest management strategies are dominated by the use of agro-chemicals (Oerke, 2005). However, plant pest populations can also be managed with biological control agents (BCAs). This practice has been used successfully for many years (Huffaker, 2012) even before the existence of agro-chemicals (Bale, van Lenteren, & Bigler, 2008). BCA success rate has been even higher in controlled environments such as glasshouses (Van Lenteren & Woets, 1988).

The use of BCAs in glasshouses, in regions such as Europe, now dominates pest management, while the use of pesticides is very uncommon. The replacement of pesticides with BCAs is also increasing globally (Pilkington, Messelink, van Lenteren, & Le Mottee, 2010). Despite the overwhelming success of BCAs in glasshouses, the most common practice in managing TPP on glasshouse-grown crops in New Zealand is with the use of synthetic insecticides (Tomatoes New Zealand & Vegetables New Zealand, 2016). It is therefore imperative to explore biological control agent to manage TPP in glasshouse.

Since the discovery of TPP in New Zealand, various studies of naturalised and native natural enemies of the pest have been conducted (Davidson, Nielsen, Butler, & Silberbauer, 2016; Geary, Merfield, Hale, Shaw, & Hodge, 2016; MacDonald *et al.,* 2016; O'Connell, Wratten, Pugh, & Barnes, 2012; Patel & Zhang, 2017; Tran, 2012; Xu & Zhang, 2015). Among the BCAs that achieved positive results for the management of TPP in laboratory studies were *Amblydromalus limonicus* (Garman & McGregor, 1956) (Acari: Phytoseiidae) (Davidson *et al.,* 2016; Patel & Zhang, 2017; Xu & Zhang, 2015), *Cleobora mellyi* (Mulsant, 1850) (Coleoptera: Coccinellidae) (O'Connell *et al.,* 2012) and *Engytatus nicotianae* (Koningsberger, 1903) (Hemiptera: Miridae) (unpublished data in this study). No evidence was found in the literature to use these natural enemies against TPP in commercial glasshouses. However, growers continue to be interested in the potential for biocontrol of TPP.

Laboratory research of *A. limonicus* to reduce TPP showed that the mite consumed a mean of 6.17 eggs and 6.77 1st instar nymphs per day in a non-choice test (Patel & Zhang, 2017). The mite reproduced and developed on the diet of egg, nymphs, and sugars of TPP (Xu & Zhang, 2015). These results confirmed that *A. limonicus* has the potential to be used as prey for eggs and 1st instar of TPP and should be further evaluated.

O'Connell et al. (2012) demonstrated in the laboratory that adults and final instar larvae of *C. mellyi* consumed a mean of 100 TPP nymphs per day. Further laboratory evaluation showed that intraguild predation with *Trialeurodes vaporariorum* (Westwood) had no significant impact on TPP predation rate by *C. mellyi* (Pugh, 2013). These findings showed that *C. mellyi* has considerable potential to manage TPP. It is therefore essential to evaluate this Coccinellid in glasshouse conditions.

A preliminary laboratory experiment was conducted testing the ability of *E. nicotianae* to manage TPP. Results showed that *E. nicotianae* could reduce TPP nymph populations. This naturalised zoophytophagous mirid preditor is easy to culture on plants only in the Solanaceae family and can be made readily available to farmers (unpublished data in this study, 2017). Additional evaluations should be conducted to quantify its potential as a viable BCA for TPP in glasshouse conditions.

The parasitoid wasp, *Tamarixia triozae* (Burks, 1943) (Hymenoptera: Eulophidae) is native to North and Central America. It feeds on 1st and 2nd instars and parasitises 3rd, 4th and 5th instars of TPP (González *et al.,* 2014; Yang, Campos, Silva, & Henne, 2015). Approval was granted by New Zealand Environmental Protection Agency to Horticulture New Zealand Inc., for the importation and release of *T. triozae* as a classical BCA to manage TPP (Kerry, Deborah, Ngaire, Max, & Geoff, 2016). This presents an opportunity for glasshouse growers to use *T. triozae* for biological control of TPP.

There are many reports of floral resources increasing the effectiveness of BCAs (Berndt, 2002; Berndt & Wratten, 2005; Gurr, Wratten, Landis, & You, 2017; Jonsson, Wratten, Robinson, & Sam, 2008; Pugh, 2013; Robinson, Jonsson, Wratten, Wade, & Buckley, 2008). Floral resources provide sugars, amino acids minerals etc. for insects, which can increase their longevity and fecundity. In laboratory studies, floral resources increased the longevity of *C. mellyi* (Pugh *et al.,* 2015) and honey increased the longevity of *T. triozae* (Rojas, Rodríguez, Lomeli, & Liu, 2014). Buckwheat (*Fagopyrum esculentum*, Moench. CV. Katowase) is used as a floral resource in New Zealand for BCAs (Berndt, 2002; Gurr *et al.,* 2017)

This study, therefore further evaluated the potential of *E. nicotianae*, *A. limonicus*, *C. mellyi* and *T. triozae* for the management of all TPP life stages on tomato in insect cages in glasshouse conditions. Buckwheat was evaluated to determine whether it could increase the effectiveness of *C. mellyi* and *T. triozae* for TPP.

3.3 Materials and methods

3.3.1 Plants

Tomato plants (CV. merlice) were grown in 1L pots in a potting mix comprised of 400L compressed bark, 1500g of Osmocote 3-4 months release, 500g horticultural lime, 500g of hydraflo and 100L pumice, for six weeks, in a glasshouse at the plant nursery, Lincoln University.

3.3.2 Tomato Potato Psyllid

With the aid of a beating tray and an aspirator, TPP were collected from African boxthorn growing in and around the farmland near Lincoln. The insects were placed on the tomato plants in a "BugDorm-2120" (https://shop.bugdorm.com) insect rearing cage in a glasshouse. The culture was maintained for 4 months. New plants were added to the cages as the quality of older plants deteriorated.

At the New Zealand Institute for Plant & Food Research Ltd. (Plant & Food Research), Lincoln, with the assistance of Gabby Drayton, TPP from the culture were screened for the presence of the bacterium *Candidatus Liberibacter solanacearum* (CLso). PrepGEM^{TM} reagents were used to extract DNA from TPP with CLso DNA quantified using qPCR (Beard & Scott, 2013).

3.3.3 Cages and irrigation

Due to availability, an equal mixture of BugDorm-2120 and 2120F insect cages (Dimensions: W60 x D60 x H60 cm) were used for the experiment. Each treatment had an equal number of each cage type. BugDorm 2120 is made of a mesh with 680 µm aperture while that of the 2120F is 160 µm. To avoid entering cages regularly to irrigate and possibly cross-contaminating treatments, drip irrigation was installed.

In each tent, a small hole was made to install the irrigation drip lines. Holes were sealed by using tape and paper. Irrigation was on a timer which was adjusted to ensure the plants were irrigated as needed.

3.3.4 Climate management

The glasshouse temperature control systems had a lower set point of 23°C to start heating and an upper set point of 22°C to initiate cooling. Additionally, on hot days the floor of the glasshouse was irrigated to help reduce the temperature. An EasyLog (EL-USB-2-LCD+), data logger, was used to collect actual temperature, relative humidity and dew point at 15-minute intervals cages.

3.3.5 Biological control agents

T. *triozae* were sourced from Plant & Food Research, Auckland and a colony at Lincoln University. *E. nicotianae* was collected from colonies kept on woolly nightshade (Solanum mauritianum) at Lincoln University and Bioforce Limited, Auckland (Bioforce). A. *limonicus* was also sourced from Bioforce. C. *mellyi* was collected from Eucalyptus spp. forest around Marlborough in the winter. They were kept in an insect cage with *Myzus persicae* (Sulzer) as a food source on potato plants in a controlled temperature room kept at 13°C with a 4°C range at Lincoln University.

3.3.6 Experimental design

About 20 TPP adults of unknown age and sex were placed in all BugDorms and left for three weeks. All adults were then removed, and the number of eggs and nymphs on each plant were counted. The combined total of eggs and nymphs had a minimum of 144 and a maximum of 606. Plants with similar numbers of total eggs and nymphs were placed in cages of the same experimental block within the glasshouse. Biological control agents were then added to the bug dorms; (a) Two adult *C. mellyi* of unknown sexes and age. (b) Two adult *C. mellyi* of unknown sexes and age and one flowering buckwheat plant. (c) One male and two female adult *T. triozae.* (less than five days old) (d) One male and two female adult *T. triozae* (less than five days old) and one flowering Buckwheat plant. (e) Approximately 500 *A. limonicus* of unknown sexes and age. The number used were based on the number of mites estimated by the commercial supplier to be in a package and by equally dividing the volume of the mite product. (f) Two adult E. *nicotianae* of unknown sex and age (g) control (no biological control agent). There were seven treatments which were replicated six times in a randomised complete block design (RCBD) (n=42) (Figure 10). After three weeks buckwheat plants were replaced with new plants in flower and a second release of the BCAs, identical to the first, was made.

Figure 10. Experimental setup of the seven treatments including control laid out in six blocks in the glasshouse.

3.3.7 Data collection and statistical analysis

Before replacing the buckwheat plants and the second release of the BCAs at the end of three weeks, four leaflet samples were collected from each plant; one leaflet from the top of each plant, two from the middle and one from the bottom. After six weeks the collection of leaflets was repeated. The number of eggs, nymphs and adults on both samples were counted and combined for each plant. The data were analysed using one-way ANOVA conducting a multifactorial analysis in GenStat 18th edition (VSN International). The means were square root transformed before the analysis and back transformed after the analysis. A least significant difference (LSD) threshold of 5% was used in all analysis.

3.4 Results

All psyllids tested positive for CLso. Additionally, the temperature in the cages varied from 14.5 to 44.5 °C, averaging 25.2°C during the study period. The average relative humidity in the cages was 77% with a minimum of 28.5 and maximum of 92.5%. Dewpoint was recorded at a maximum of 33.4°C, minimum of 9.8°C and average of 18.2°C.

After six weeks, the lowest number of TPP eggs was found on plants with *A. limonicus* (mean = 64, $P < 0.05$) compared to control plants (mean = 172.9) (Table 5). For the other treatments, while the number of TPP eggs was lower than in the control they were not statistically significant. The addition of flowering buckwheat with *T. triozae* or *C. mellyi* made no significant difference to the mean number of eggs (Table 5).

Table 5. Mean square root transformed number of TPP eggs, nymphs or adults found on a subsample of leaves collected from plants of each treatment, with back-transformed means in brackets. Means with a letter in common in the same column did not differ statistically.

Treatment	Eggs			Nymphs			Adults		
Control	13.2	b	(172.9)	120	ab	(142.8)	5.2	ab	(27.0)
E. nicotianae	10.4	ab	(107.5)	13.9	b	(193.5)	5.7	b	(32.5)
A. limonicus	8.0	a	(64.0)	10.5	ab	(109.8)	3.3	ab	(10.7)
C. mellyi	11.6	ab	(134.1)	11.0	ab	(121.4)	3.2	ab	(10.2)
C. mellyi + buckwheat	10.3	ab	(105.9)	10.7	ab	(114.9)	3.3	ab	(11.0)
T. triozae	9.0	ab	(80.1)	8.8	a	(77.1)	2.7	a	(7.5)
T. triozae + buckwheat	10.5	ab	(110.3)	12.5	ab	(155.3)	4.9	ab	(23.8)
LSD	4.41		-	4.78		-	2.58		-

The mean number of nymphs in the *T. triozae* without buckwheat treatment (77.1) was almost half that of the control (142.8), and mean numbers of TPP nymphs on plants with *A. limonicus* (109.8)*, C. mellyi* (121.4) and *C. mellyi* + buckwheat (114.9) were lower than that of the control plants, but none of the results were statistically significant (P > 0.05) (Table 5) Fewer adults were also found on plants with *T. triozae* (7.5), A. *limonicus* (10.7)*, C. mellyi* (10.2) and *C. mellyi* + buckwheat (11) than the control plants (27), but again none of the differences were statistically significant (Table 5).

3.5 Discussion

3.5.1 Eggs

A. limonicus reduced the number of TPP eggs by more than half those recorded on control plants. Patel and Zhang (2017) reported that an adult female mite consumed an average of 6.17 eggs per day on capsicum leaves. Tomato leaves, as used in this study, have considerably more trichomes than that of capsicum (Kim *et al.,* 2011). When glandular trichomes are disturbed by insects, they release a sticky, viscous fluid which can inhibit the insects' movement (Johnson, 1956; Maluf *et al.,* 2007). *A. limonicus* was released on the adaxial leaf surface; however, TPP eggs are mostly found on the leaf edge (N. Martin, 2016), so mite mobility was essential for reaching TPP eggs, but the trichomes could have hindered this. Despite this, the results are indicative of the mites' ability to reduce TPP egg numbers and that it may have a role as a BCA of TPP in glasshouses use but further research is needed.

While the reduction of TPP egg numbers by *T. triozae* was not statistically significant, the mean was less than half of the control. Host feeding of the earlier-instar nymphs of TPP by *T. triozae* is known (González *et al.,* 2014) but there are no records of *T. triozae* feeding on TPP eggs. If *T. triozae* does not feed on TPP eggs, the lower numbers could be due to it is feeding on early instar nymphs and

parasitising older instars, thus reducing the number of adult TPP and as a consequence the subsequent number of eggs present on the plant.

As the treatment with *T. triozae,* the number of eggs for the other treatments showed no statistical difference to the control or *T. triozae*. However, numerically they had more than the *T. triozae* treatment but less than the control so no strong inference can be made.

In studies conducted by O'Connell et al. (2012) using *C. mellyi* for TPP management, only nymphs were evaluated. No evidence was found in the literature showing that *C. mellyi* consumes TPP eggs. However, two other Coccinellidae: *Coccinella undecimpunctata* (Linnaeus, 1758) and *Harmonia conformis* (Boisduval, 1835) were studied in laboratory conditions on eggs, nymphs and adults of TPP and results showed these predated on all life stages (MacDonald *et al.,* 2016). However, while there were fewer eggs in the *C mellyi* treatment than the control, the difference was small and statistically not-significant, so no conclusions can be drawn.

3.5.2 Nymphs

The mean number of TPP nymphs on all treatments were statistically similar to the control. However, *T. triozae* followed by *A. limonicus* had the highest impact on reducing the nymphs. The effects of *T. triozae* are surprising because it feeds on early instar nymphs and parasitises the later instars (González *et al.,* 2014; Patel & Zhang, 2017); giving it more possibilities to reduce nymph numbers.

Interestingly, when buckwheat was present with *T. triozae* the mean number of nymphs found was more than doubled that of when buckwheat was absent. The impacts of floral resources on BCAs have been widely studied (Berndt, 2002; Berndt & Wratten, 2005; Gurr *et al.,* 2017; Pugh *et al.,* 2015; Robinson *et al.,* 2008). It has been demonstrated that floral resources can negatively or positively impact BCAs performance depending on the context (Robinson *et al.,* 2008). Prey consumption can be negatively affected by the presence of alternative food resources (Vangansbeke *et al.,* 2014). Although in the absence of the prey these alternative resources can be beneficial for the longevity of the predator or parasitoid. Therefore, floral resources can assist predator when prey resources are limited, but with prey in abundance and alternative food sources available to the predator, predation rate may be reduced (Robinson *et al.,* 2008). The possibility of buckwheat reducing host feeding of TPP by *T. triozae* is plausible, which will not favour nymph reduction. It is hypothesised that the higher number of nymphs when buckwheat is present can be because of reduced host feeding by *T. triozae*. More research is needed to ascertain if, buckwheat can be used when the wasp needs an additional food source. This can be included sometime after inundation biocontrol, but after TPP population is reduced because the wasp population will need to be sustained when the food source

(TPP) is depleted. Another case is in inoculative biocontrol because the flower can provide a food source for the wasp in the absence of TPP.

The *C. mellyi* and *C. mellyi* with buckwheat treatments were numerically similar and statistically the same as the control. This is unexpected because O'Connell et al. (2012) showed *C. mellyi* could consume almost 100 nymphs in 24 hours on tomato leaflets. However, O'Connell et al. (2012) confined *C. mellyi* in a Petri dish, and when the behaviour of the adult was observed in 15 minutes periods, almost 50% of its time it was recorded roaming and was not observed feeding. In the present study, there was much more space for the BCA to spend roaming rather than feeding, so this could have affected the predation rate.

According to the methodology used by O'Connell et al. (2012) psyllid sugars were not present or were very limited, because the nymphs developed on one leaflet and were placed on a new leaflet during the study rather than developing on the same leaflet. *C. mellyi* can survive equally on the floral resource as on TPP (Pugh *et al.,* 2015), it also feeds on sugars (Mensah & Madden, 1994). Therefore, the presence of psyllid sugars in this study may be providing an additional food source for *C. mellyi*; this could contribute to lower levels of prey consumption when compared O'Connell et al. (2012) findings.

Surprisingly *E. nicotianae* had no significant impact on any life stage of TPP compared to the control. In a no-choice anecdotal laboratory study, *E. nicotianae* reduced TPP nymphs. Mirids are zoophytophagous and will feed on plants by inserting their stylets into the plant and sucking the sap (Mitchell, 2004). It may be that *E. nicotianae* preferred to feed on the tomatoes compared to TPP eggs or nymphs. In the preliminary experiment conducted with *E. nicotianae* and TPP, nymphs were on a leaflet in a Petri dish; it may be that the leaflets were not as turgid and *E. nicotianae* had difficulties feeding on the leaflet and was forced to feed on the TPP nymphs. In contrast, in this study, whole, living plants were used, and *E. nicotianae* may have favoured feeding on the plants over TPP. These results indicate *E. nicotianae*is is a poor choice as a TPP BCA.

3.5.3 Adults

The *C. mellyi*, *C. mellyi* with buckwheat, *A. limonicus*, *T. triozae* and *T. triozae* with buckwheat and the control all had a statistically similar number of adults. While the mean number of adults on the control was more than twice that on the *C. mellyi*, *C. mellyi* with buckwheat and *A. limonicus* treatments. Mean number of adults for the control was three times than that of the *T. triozae* treatment. However, none of the aforementioned were statistically different from the control. Although not significantly different, these treatments also had lower numbers of TPP eggs and

nymphs relative to the control. The lower numbers of adults can be due to BCAs lowering TPP egg and nymph numbers as well as directly reducing adult TPP numbers.

There is no literature supporting any of the BCAs reducing TPP adults. However, there is are some possibilities that *C. mellyi* might be able to because MacDonald et al. (2016) showed two other Coccinellidae did feed on TPP adults. Additionally, from looking at the impact of *A. limonicus* and *T. triozae* on the other life stages of the pest when compared to the *C. mellyi* would suggest that because of the trend the number of adults in *C. mellyi* should be more than is reflected if the beetle was not having a direct impact on TPP adults. This is a clear indicator that some research should probably be done to quantify if *C. mellyi* reduces TPP adults.

3.6 Conclusion

As far as I know, this is the first study comparing four BCA to manage TPP outside of the laboratory. The current glasshouse study disagreed with some laboratory results (O'Connell *et al.,* 2012; Patel & Zhang, 2017).

Despite fewer TPP being recorded on plants with some of the BCAs than control plants, none of the BCAs reduced TPP populations to a level, which may not be low enough to make an economic difference. This may have been due to the relatively high numbers of TPP on the plants before introducing the BCAs. In the present study, the initial eggs and nymphs total varied from 144 to 606 per plant. However, S. Albert (2017, personal communication), who works in commercial tomato production notes that scouting for early detection of TPP on commercially grown greenhouse crops is very intensive due to their inconspicuous nature and the very low numbers of all life stages of TPP. If 1% of the samples have TPP, agro-chemical application is recommended (Tomatoes New Zealand & Vegetables New Zealand, 2016). Additionally, symptoms of the pest appear when there are as few as eight nymphs per plant (Liu & Trumble, 2007b). This further emphasised that the pest population count in this experiment is considerably higher than what occurs in a commercial setup. Thus, further studies using lower initial TPP numbers, especially with combination *A. limonicus* and *T. triozae*, would be worthwhile.

Under the conditions in the present study, the use of buckwheat did not improve the effectiveness of *T. triozae* or *C. mellyi,* so the role of such floral resources remains uncertain. However, since floral resources are known to increase the longevity of some BCA, understanding their role in conserving natural enemies would be warranted, especially for outdoor crops or indoor crops where prey populations are very low.

Chapter 4

Mesh crop covers on potatoes to protect against psyllids: the additional challenge of aphids

4.1 Abstract

Mesh crop covers (mesh) which are used in Europe and Israel to protect crops from insect pests have been used experimentally in New Zealand for *Bactericera cockerelli* the tomato potato psyllid (TPP) management. While the mesh was highly effective for TPP management, the green peach aphid (GPA), *Myzus persicae* was found in large numbers under the mesh. This study investigated the ability of the GPA to penetrate different mesh hole sizes. Experiments using four hole sizes (0.15×0.15, 0.15×0.35, 0.3×0.3 and 0.6×0.6 mm) were carried out under laboratory conditions to investigate: (i) which mesh hole size provided the most effective barrier to GPA; (ii) which morph of adult (apterous or alate) and/or its progeny could breach the mesh; (iii) would leaves touching the underside of mesh, as opposed to having a gap between leaf and mesh, increase the number of aphids breaching the mesh; and (iv) could adults feed on leaves touching the mesh by putting their heads and/or stylets through the mesh?

No adult aphids, either alate or apterous breached the mesh; only nymphs did, with the majority being the progeny of alate adults. Nymphs of the smaller alate aphids breached the three coarsest mesh sizes; nymphs of the larger apterous aphids breached the two coarsest mesh sizes. No nymphs breached the smallest mesh size. For both aphid morphs and all mesh sizes, nymph numbers were lower when the adult aphids were placed on the opposite side of the mesh from the potato leaflet than when the adults were placed inside the mesh directly on the leaflet. Having the leaflet touch the mesh increased the number of aphids breaching the mesh, but this effect was not statistically significant. Adults did not feed through the mesh, though it is believed they were able to sense the potato leaflet using visual and olfactory cues. As mesh is highly effective for managing TPP on field potatoes, alternative measures to manage aphid colonisation of this crop due to aphid nymphs breaching the mesh are required; one option is introducing biocontrol agents under the mesh.

4.2 Introduction

Due to the negative impacts of TPP on potatoes in New Zealand, organic farmers have encouraged researchers to investigate non-chemical management approaches. Biological options such as the mite *Anystis baccarum* L. (Merfield, Geary, Hale, Shaw, & Hodge, 2016), among others, were explored but with little success. In comparison, a physical management technique using high-density

polyethylene insect mesh covers was able reduce in-crop TPP populations to very low levels, even outperforming insecticides (Merfield, 2017; Merfield *et al.,* 2015).

Mesh covers have been used in Europe for many years to protect potatoes and other crops from insects (Hill, 1987). In New Zealand, mesh covers have only recently been implemented experimentally. Mesh with a size up to 0.7 mm (commercial label 0.6 mm) was able to efficiently manage the pest (Merfield *et al.,* 2015). Additional benefits were that plants grown under the mesh had higher yields than the controls grown in the open, and were less affected by potato blight, though it was not determined if this was 'main' blight (*Phytophthora infestans*, Mont. de Bary) or 'early' blight (*Alternaria solani*, Sorauer) (Merfield *et al.,* 2015).

Despite the promising results obtained from using mesh, an unexpected result was that aphids, believed to be mostly the green peach aphid (GPA) (*Myzus persicae* (Sulzer)) appeared in large numbers under the mesh sheets, particularly in the 2016-17 field trials where the edge of the mesh was dug into the soil, creating a complete seal (Merfield, 2017). Aphid populations were significantly higher under all mesh covers when compared to uncovered crops, probably due to the microclimate and the exclusion of the aphid's natural enemies by the mesh (Merfield, 2017). A research was conducted to understand if the aphids are getting through the different mesh but, the results were not conclusive (Hodge, Bluon, & Merfield, In press)

Aphids can significantly affect plant growth and development, which causes reduced yields. They feed from the phloem (Dixon, 1973) causing damage to shoots and leaves (Capinera, 2001), and excreting honeydew (Dixon, 1973), which results in the growth of sooty moulds (Chomnunti *et al.,* 2014) that cover the leaf, causing a reduction in respiration, transpiration and photosynthesis. These factors further reduce plant growth, development, and crop yield (Centre for Agriculture and Bioscience International, 2017; Chomnunti *et al.,* 2014), resulting in significant economic losses (Centre for Agriculture and Bioscience International, 2017). Such damage is more severe in young plants and when the aphid population is high (Capinera, 2001). Also, GPA is a vector of many potato viruses that also cause significant yield losses (Capinera, 2001).

The GPA is the most common aphid on potatoes in New Zealand, and it has hundreds of host plants so is both is common and widespread (Stufkens & Teulon, 2001). It is also the most economically important aphid of potatoes, both in New Zealand and worldwide, because it transmits both potato virus Y and leaflet curl virus, which are among the most damaging of the potato viruses. (Saguez, Giordanengo, & Vincent, 2013; Selvaraj & Ganeshamoorthi, 2012; Srinivasan, Cervantes, & Alvarez, 2013; Syller & Marczewski, 2001; Woodford, 1992). The main management tool for aphids in potatoes is insecticides. However, the GPA has developed resistance to a number of these (Centre for

Agriculture and Bioscience International, 2017; Foster, Denholm, & Devonshire, 2000) which poses challenges to potato farmers and researchers for future aphid management.

With mesh crop covers being highly effective for TPP management on potatoes, the major challenge is understanding how aphids are circumventing the mesh, and if adults can, from outside mesh, feed on leaflets touching the underside of the mesh. If so, this means aphids outside the mesh could transmit viruses to potatoes under the mesh. This could discourage seed potato growers from using the mesh as a management option for TPP because of increased virus transmission to tubers intended for propagation.

With these gaps in knowledge, the present research was therefore designed to investigate (i) if aphids can penetrate different mesh sizes; (ii) if there is a difference between alate or apterous adults and/or if their offspring's have ability to penetrate mesh; (iii) if having potato leaves touching the mesh from below increases the number of aphids penetrating mesh than when the leaves do not touch the mesh; and (iv) if adult aphids are capable of feeding on potato leaves through the mesh.

4.3 Materials and methods

GPA was sourced from a colony cultured on *Brassica rapa* subsp. *chinensis* (L.) pak choi (CV. Mei Qing Choi F1) kept at Lincoln University in a controlled-temperature room. The room was kept at 16 h day length, temperature of 23 with a 4°C range and 60% relative humidity. Potato plants (CV. Ilam Hardy) were grown in a glasshouse at the Lincoln University plant nursery.

For the laboratory work, two Petri dishes were used to create two compartments separated by mesh; the top dish contained the aphids and the bottom one a single potato leaflet (Figure 11). The two Petri dishes were held together with plastic food wrap. The mesh was carefully glued around the full circumference of the opening between the two dishes, because, in previous experiments, could locate and penetrate minimal gaps between the mesh and hard surfaces (C. Merfield, 2017, unpublished observations). A piece of moist tissue paper was placed in the bottom Petri dish to maintain humidity. Leaflets were then collected from potato plants and cotton wool was placed over the petiole of the leaflet, which was inserted into an Eppendorf tube filled with water to maintain leaflet turgidity. The Eppendorf tube with leaflet inserted was placed in the lower dish with the adaxial surface facing up. For the mesh treatments, three adult aphids were inserted through a hole (150 mm diameter) in the top of the upper dish, which was then sealed with insect mesh 0.15 x 0.15 mm held in place by adhesive tape. For the control treatments, three adult aphids were placed inside the lower dish before sealing.

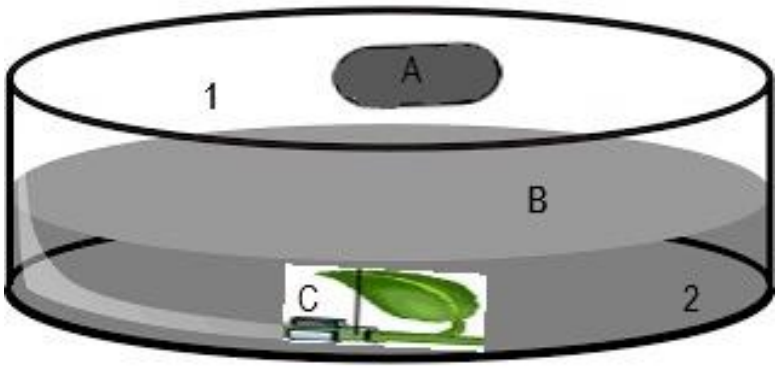

Figure 11. Experiment setup: (1) top Petri dish, (2) bottom Petri dish, (A) hole in Petri dish, (B) mesh between Petri dishes, (C) Eppendorf tube & leaflet.

There were a total of 24 treatments in a 4 x 2 x 3 factorial design: Four mesh sizes × two aphid morph (apterous or alate) × (two leaflet positions plus control). Commercially stated mesh sizes were 0.15 × 0.15 mm, 0.15 × 0.35 mm, 0.3 × 0.3 mm and 0.6 × 0.6 mm. Aphid morphs were apterous or alate, while leaflet positions were touching or not touching the mesh. For the control, aphids (both alate or apterous) were placed directly on the leaflet under the mesh. There were five blocked replicates. The experiment ran for 72 hours, at which point the number of aphids, both adults and nymphs, on the leaflets were counted. The experiment was conducted in a controlled temperature room with 16 hours day length, temperature of 23 ± with 4°C range and relative humidity of 60%.

To investigate whether adult aphids could feed through the mesh, all adults (n=240) used for the study of breaching the insect mesh were lightly probed with a fine artist's brush at 12, 24, 36 and 48 hours through the opening of the top Petri dish. Therefore, 240 individuals were probed four times each, giving a total of 960 tests of feeding. Those that remained in the same position following probing were taken as having their stylets inserted into the leaflet and therefore to be feeding (Auclair, 1963; Giordanengo *et al.,* 2010). Those aphids that moved following probing were considered to have been not feeding.

Mesh sizes 0.15×0.15 mm and 0.15×0.35 mm (hereinafter referred to as 0.15×0.15 and 0.15×0.35 mesh, respectively) were supplied by AB Ludvig Svensson (www.ludvigsvensson.com) as ECONET 1515 and ECONET 1535. Those measuring 0.3×0.3 mm and 0.6×0.6 mm (hereinafter referred to as 0.3×0.3 and 0.6×0.6 mesh, respectively) were supplied by Crop Solutions Ltd. (www.cropsolutions.co.uk) and were the custom made for an earlier field trial (Merfield, 2017). To test the accuracy of the measurement for each mesh size used in this experiment, ten random samples of each mesh morph were selected, and ten holes of each sample were measured under a Nikon SMZ25 microscope (Magnification range 0.63x - 15.75x). The mean, minimum and maximum mesh measurements are presented in (Table 6).

Table 6. Measurements of each mesh morph.

	Mesh size (mm)							
	0.15×0.15		0.15×0.35		0.3×0.3		0.6×0.6	
Mean	0.14	0.13	0.15	0.32	0.37	0.23	0.52	0.52
Max.	0.16	0.15	0.18	0.37	0.53	0.31	0.57	0.55
Min.	0.12	0.10	0.12	0.30	0.27	0.17	0.45	0.47

All data were analysed in a randomised block analysis of variance (ANOVA) (with a factorial treatment structure) using GenStat® 18th edition. The response variable, number of aphids on potato leaflets, was subjected to a square root transformation to normalise the data before analysis. In addition, the analysis was split into two ANOVAs to achieve homogeneity of variance: (1) the 8 control treatments, which were relatively high in variability, were analysed separately as a 4 x 2 factorial with 5 blocks; (2) other treatments which were not all zeroes and hence had non-zero variability, 10 treatments in total, were analysed as a (2 x 2 + 1) x 2 factorial with 5 blocks.

4.4 Results

For the control treatments, with aphids below the mesh, there were no significant differences in nymph numbers between the two aphid morph, nor any significant linear or quadratic components of mesh size (assuming these were in the ratio 1 : 2 : 3 : 6), nor any significant interaction components (Table 7).

In the 16 treatments with adults placed above the mesh, only nymphs, not adult aphids, were able to pass through the mesh. Nymphs of the smaller alate adults breached the 0.15×0.35, 0.3×0.3 and 0.6×0.6 mesh but did not breach the 0.15×0.15 mesh (Table 7). Nymphs of the larger apterous nymphs breached the 0.3×0.3 and 0.6×0.6 mesh but did not breach the 0.15×0.15 and 0.15×0.35 mesh. For the alate aphids, the number of nymphs breaching the mesh increased with mesh size (P=0.098 for linear component of the main effect of mesh size, assuming the ratio of mesh sizes of 2:3:6 (Table 7).

When averaged over the larger 0.3x0.3 and 0.6x0.6 mesh sizes and over leaflet touching or not treatments, more nymphs of alate adults than nymphs of apterous adults get through the mesh, but the difference was not statistically significant (P=0.192). On the transformed scale, main effect means were 0.788 for nymphs of alate adults and 0.491 for those of apterous adults, which back transformed to 0.62 and 0.24 nymphs, respectively.

When leaflets touched the mesh, there were higher numbers of nymphs breaching the mesh than when the leaves did not touch it, but the difference was not statistically significant (*P*=0.612). On a

transformed scale, main effect means were 0.638 when the leaflet and mesh were touching, and 0.536 for not touching, which back transformed to 0.41 and 0.29 nymphs, respectively.

The interaction between aphid morph (alate and apterous) and the leaflet touching mesh or not was 10% significant (P=0.066). For nymphs that circumvented mesh of alate adults, the mean square root transformed number of nymphs was 1.021 for leaflet touching the mesh and 0.556 for not touching, while for nymphs of apterous adults, these means were 0.300 and 0.683 respectively; hence the interaction was (1.021 – 0.556) – (0.300 – 0.683) = 0.848.

Table 7. Mean (√) number of aphid nymphs of apterous and alate parents breaching different mesh sizes when leaflets were touching mesh or not. In a first part of the table, controls were statistically analysed. In a second part of the table, treatments with means in brackets indicate treatments that were omitted because they had zero mean and zero variability. m.e. = main effect.

	Aphid morph	Mesh	Mean of square root of # of nymphs below mesh	Back transformed means
Control	Apterous	0.15×0.15	2.460	6.05
		0.15×0.35	2.202	4.85
		0.3×0.3	1.940	3.76
		0.6×0.6	2.448	5.99
	Alate	0.15×0.15	1.823	3.32
		0.15×0.35	1.673	2.80
		0.3×0.3	2.455	6.03
		0.6×0.6	1.756	3.08
LSD 5%			**1.235**	
Significance of m.e., Apterous vs Alate			not sig.	
Leaflet not touching mesh	Apterous	0.15×0.15	(0.000)	0.00
		0.15×0.35	(0.000)	0.00
		0.3×0.3	0.483	0.23
		0.6×0.6	0.883	0.78
	Alate	0.15×0.15	(0.000)	0.00
		0.15×0.35	0.200	0.04
		0.3×0.3	0.283	0.08
		0.6×0.6	0.829	0.69
Leaflet touching mesh	Apterous	0.15×0.15	(0.000)	0.00
		0.15×0.35	(0.000)	0.00
		0.3×0.3	0.200	0.04
		0.6×0.6	0.400	0.16
	Alate	0.15×0.15	(0.000)	0.00
		0.15×0.35	0.546	0.30
		0.3×0.3	1.012	1.02
		0.6×0.6	1.029	1.06
LSD 5%			**0.905**	

No aphids were found, at any time, to be feeding through the mesh, as all aphids moved following probing with the artist's brush.

4.5 Discussion

4.5.1 Aphid host feeding and host recognition

Alate GPA and other aphids disperse wind currants (Dixon, 1971; Kennedy, 1950) and their first step in finding a host plant is by detecting it by olfactory and visual cues pre-alighting (Döring, 2014). However, the white colour of the mesh used in field trials (Farias & Orozco, 1997; Merfield, 2017) and the absence of the visual cue of green-yellow plants would be expected to reduce aphid alighting on the mesh (Ben, Antignus, Offir, & Shahak, 2012). However, the presence of aphids in all mesh plots in the field trial by Merfield (2017) indicates that adults must be alighting on the mesh. After alighting, aphids examine the plant to determine if it is a suitable host by probing the subepidermal tissues of the plant. Subsequently, they do more deeper probing, and if the plant is suitable, they will evaluate the pholem (Vargas, Troncoso, Tapia, Olivares, & Niemeyer, 2005). When an alate adult determines that a plant is a suitable host they feed and reproduce, they may then disperse to another host (Dixon, 1971; Kennedy, 1950). Adults will start reproducing after feeding for at least 30 minutes (Powell, Tosh, & Hardie, 2006). However, these results in this study found that the aphids did not feed, yet they still reproduced. This appears to contradict previous research that contact with the plant and active feeding is required for reproduction. This indicates that the aphid may be able to detect the host plant without feeding on it, i.e., by olfactory and possibly visual clues through the mesh, resulting in it deciding to reproduce. The results with the leaflet not touching the mesh could be evidence that aphids are detecting the plants by non-physical means. However, to confirm this, a second control treatment in the experiment would have been required: that of putting the aphids on mesh without a potato leaflet to determine the number of nymphs produced and the numbers of the latter penetrating mesh in the total absence of vegetation. In addition to the issue of host detection through the mesh, as the adult aphids are not feeding on the plant, they cannot gain nutrients and energy so would have to reproduce using stored embryos energy and nutrients, which would be expected to limit the number of nymphs produced. A further limitation of this study is that the number of nymphs that did not penetrate the mesh were not counted. It is not therefore possible to determine if the nymphs that did penetrate the mesh represent a minority or majority of those produced by the adults, and therefore provide evidence whether the nymphs can detect the leaf through the mesh and therefore actively penetrate it in search of food.

4.5.2 The role of leaves touching the mesh

The interaction of aphid morph and leaf touching or not touching the mesh was significant at the 10% level, but the direct comparison of leaf touching vs not touching was not significant. This indicates that it does not require potato leaves to touch the mesh for aphid nymphs to penetrate it.

Had aphid penetration of the mesh been reduced when leaves were not touching it, it could have provided an option for commercial growers to set up infrastructure as supports to keep the mesh from touching the plants. This could have been of particular value for potato seed breeders, to reduce GPA numbers, where the area of the crop is comparatively small (tens of square meters to hectares) and of very high value (Bisognin, Storck, da Costa, & Bandinelli, 2006). Therefore, based on these results, raising the mesh off the crop would not reduce aphid ingress and would, therefore, be of no value. However, this study was effectively a no-choice test, with the adults and nymphs confined near the mesh and potato leaflet. In the field, alate aphids that alight on the mesh have the option of flying off in search of other hosts if they do not detect potatoes beneath the mesh. In this situation, lifting the mesh off the crop foliage could produce a different result to these laboratory findings. In addition, the gap between the leaf and mesh was only a few millimetres and future research could investigate various distances between the leaflet and the mesh to determine if there is specific distance over which the adults cannot detect the potatoes under the mesh and that also results in nymphs no longer breaching the mesh. Further studies under more realistic conditions would, therefore, be of more practical value to potato growers and also potentially shed new light on the mechanisms of host finding by aphids (Döring, 2014).

4.5.3 Supplementing the mesh approach

Results obtained in this study showed that GPA could colonise potato crops cultivated beneath insect mesh, and with the rapid clonal reproduction of GPA, populations would reach levels that could destroy crops. However, results from Merfield (2017) for the management of TPP are considered too promising to abandon the use of mesh crop covers due to aphid infestation. Therefore, the mesh should be used to manage TPP, with a second management approach used to manage GPA under the mesh, ideally using a non-chemical approach.

A wide range of commercially available biological controls have been used to successfully manage GPA, particularly in protected environments such as glasshouses. For example, these include *Aphidius matricariae* Haliday (Hymenoptera: Braconidae), *Aphidius colemani* Viereck (Hymenoptera: Braconidae) (Zamani, Talebi, Fathipour, & Baniameri, 2007) *Micromus tasmaniae* Walker (Neuroptera: Hemerobiidae) (Harcourt, 1996; Jonsson *et al.,* 2008) *Adalia bipunctata L.* (Coleoptera, Coccinellidae) (Jalali, Tirry, Arbab, & De Clercq, 2010). However, the use of biological controls has a higher success rate in protected agriculture than in the open field (Van Emden & Harrington, 2007). A form of protecting crops is by using mesh covers, and as the mesh not only keeps pests and naturally occurring biological control agents out of the crop, the covers can also ensure that biological controls introduced under the mesh cannot escape, unlike in open fields. It is therefore believed that the best option for management of aphids that do penetrate the mesh is to use commercially available

biological control agents as used in other forms of protected cropping. Finding the optimum species of BCA to put under the mesh, the numbers and frequency of introductions, and the value of floral resources and banker plants under the mesh is, however, considered to require a substantial amount of research.

4.5.4 Commercial relevance of this work

From a commercial potato production perspective, especially for seed potatoes, that the adults do not feed through the mesh could be a significant finding as it indicates potato viruses will not be transmitted through the mesh. However, this result is not direct evidence for lack of transmission, as it only demonstrated a lack of feeding but not lack of probing. GPA can transmit virus only by probing (Radcliffe & Ragsdale, 2002). Direct testing of virus transmission is required, using virus-infected aphids to test the rates of transmission when the mesh is present and not.

Potato virus Y and potato leafroll virus are not maternally transmitted to nymphs of GPA (Radcliffe & Ragsdale, 2002). If these results that adults do not transmit viruses through the mesh are corroborated, and the new-born nymphs that penetrate the mesh are also virus free, it appears that mesh could prevent virus infection of crops. However, uninfected nymphs and adults become infected by feeding on infected plants (Radcliffe & Ragsdale, 2002). Therefore, should any of the plants underneath the mesh already have a virus, e.g., transmitted via the planted tuber, aphids below the mesh can spread the virus(es) from infected to uninfected plants. As the mesh is believed to act as a barrier for aphid natural enemies (Merfield, 2017), and aphid populations can rapidly increase to very high levels (Merfield, 2017; Winder, Alexander, Woolley, Perry, & Holland, 2014) existing viruses could be spread rapidly to all plants under the same mesh sheet.

In the present study, nymphs produced by alate adults breached the 0.15x0.35 mesh, while those produced by apterous adults did not. This supports the findings of Dixon and Wratten (1971) who found that alate aphids were smaller and produce fewer and smaller nymphs than did apterous aphids. For larger mesh sizes, nymphs of both progenitors can enter the mesh, so both alate and apterous adults are potential threats to the crop. However, apterous aphids, lacking wings, could arrive only on the outside of the mesh from other plants bordering the mesh. In field trials conducted by Merfield (2017) the periphery of mesh was kept free of vegetation with residual herbicides such that apterous aphids walking onto the mesh should have been eliminated, yet aphids infested all mesh plots. It is therefore believed that it was alate adult that were producing the nymphs that infested the mesh treatments in that trial. Alate adults produce smaller nymphs that can penetrate smaller hole sizes in the mesh, so this indicates that only the smallest size mesh (0.15×0.15 mm holes) would be an effective barrier.

In New Zealand and many tropical and subtropical regions around the world, GPA is anholocyclic (females are viviparous parthenogenetic in the absence of males) (Blackman, 2009). This means that one nymph is enough to start a colony, but, the more nymphs that can penetrate a mesh sheet, the faster the population will grow. This study found the 0.15×0.15 mesh was the only size that was entirely impervious to aphids. The next mesh size up, the 0.15×0.35 mesh, prevented colonisation by the larger nymphs of apterous aphids, but not the smaller progenies of alates. This means the mesh sizes capable of protecting potatoes from TPP are insufficient to protect potato crops from aphids. The 0.15×0.15 mesh (ECONET 1515, from Ludvig Svensson) is intended for glasshouse use, not field use, unlike the Crop Solution's mesh crop covers. The finest mesh currently designed for field use is 0.3 x 0.3 mm, (Ian Campbell, Crop Solutions Ltd., personal communication (2017)). Therefore, there are no commercially available field mesh crop covers that would also block GPA from potato crops.

4.6 Conclusion

In summary, because of availability, cost, and usage, it is recommended that the 0.6×0.6 or 0.3x0.3 mesh be used to manage TPP, even though GPA nymphs can breach it (see chapter 5). Biological control agents to manage GPA that penetrate the mesh need to be researched. The potential for the mesh to be an effective barrier to virus spread, by both adults and nymphs, needs to be confirmed. If mesh, combined with BCAs for under-sheet aphid management, are thus an effective means of managing potato viruses, the implications for the potato seed industry are believed to be considerable.

Chapter 5

General discussions and conclusions

As the world population grows, the demand for food is inevitably increasing. To meet these demands, agriculture is intensifying, which is having a negative impact on the environment (Food and Agriculture Organization, 2017b). With such rapid change in the environment, the prevalence of pest and pest resistance is increasing worldwide (Sparks & Nauen, 2015). The problem includes the increased prevalence of the tomato and potato psyllid (TPP). The food crops of high relevance produced in New Zealand, Australia and some countries of the Americas are threatened by TPP. TPP is a vector of CLso that causes psyllid yellows in tomato and potatoes, with the associated zebra chip in potatoes resulting in significant economic loses.

This study aimed to investigate the impact of host-plant change on the "fitness" of TPP and further evaluate non-chemical approaches to manage this pest. To achieve this, a research was designed to quatify (i) if transferring adult TPP from non-crop to crop host species has an impact on the subsiquent development and survival of their progeny; (ii) if aphids are breaching insect mesh used as a non-chemical management of TPP; (iii) the ability of the coccinellid *Cleobora mellyi,* the parasitoid *Tamarixia triozae,* the mite *Amblydromalus limonicus* and the mirid bug *Engytatus nicotianae,* also '*C. mellyi* + buckwheat' and '*T. triozae* buckwheat' to help manage TPP populations on tomato plants.

5.1 Summary of findings

5.1.1 Objective 1

Development and survival were measured as proxies for ecological fitness of TPP progeny after adults were transferred from either poroporo or boxthorn to either tomato or potato. Nymphs took 6.9 days to emerge when their mothers came from poroporo to tomato and 7.2 for boxthorn to tomato; these were significantly less than on tomato to tomato (9 days). The time from nymphal eclosion to adult to eclosion did not differ across treatments. However, the total development time on poroporo to tomato (20.5) was significantly faster than on tomato to tomato (23.2). The mean percentage of eggs that produce nymphs did not differ among all treatments. Additionally, the mean percentage of nymphs that survived to adult on poropopro to tomato (92.1%) was significantly higher than on tomato to tomato (50.4%). Survival from egg to adult for poroporo to tomato (80%) was higher than tomato to tomato (37.6%).

5.1.2 Objective 2

E. nicotianae, *A. limonicus*, *C. mellyi*, *C. mellyi* + buckwheat, *T. triozae* and *T. triozae* + buckwheat were evaluated to manage TPP in the glasshouse. The mean number of eggs found in the control (120) was almost twice that found in the treatment containing *A. limonicus* (64.0). Nymphal mean numbers were 142.8 for control and 77.1 for *T.* triozae. Mean number of adults found in the controls was (27.0), *A. limonicus* (10.7), *C. mellyi* (10.2), *C. mellyi* + buckwheat (11.0), *T.* triozae (7.5). Buckwheat did not improve the performance of *C. mellyi* or *T.* triozae.

5.1.3 Objective 3

GPA adults were not able to bypass the mesh and reach the leaflets. However, their nymphs were able to do this for the two largest of the four meshes types evaluated. Of those, only the largest (0.6×0.6 mm) is commercially available in New Zealand. However, the others can be sourced but at a higher cost (C. Merfield, personal communication, 2017; Hummert International (2017).

Handling of mesh can cause threads to move causing openings to differ from that of the manufacturer's specifications (Table 6). Therefore, there is no guarantee that the small meshes will not sometimes have openings that admit the aphids. Perhaps 0.3x0.3 or 0.6×0.6 mm meshes can be used but with a management approach for the GPA, maybe including the use of biological control agents.

The openings of the four meshes were probably not enough to allow adult aphids to insert their stylet through the mesh. However, such probing was not evaluated. Therefore, further research is needed to know if probing is possible because the insects can transmit viruses by probing (Radcliffe & Ragsdale, 2002). Whether the mesh was touching the leaflet or not did not make a significant difference to nymphs circumventing the mesh.

5.2 Transfer between host plants

One general opinion that TPP moves from one host plant species to another and a management approach for the insect is to reduce all non-crop the host plants in winter (N. Martin, 2016). However, there is no evidence in the literature to show that studies were conducted to demonstrate that the insect could move from one host plant species to another, nor the extent of such movement. Moreover, even if they move, how well can they adapt to the new is unknown. Results in this study showed that in some cases the survival and development of the subsequent generation

could be affected by the change of host species by their mothers. However, this is just a small insight on how little is known about the ecology of TPP.

Only four host plant species were evaluated in this study, but there are many potential host species of TPP in New Zealand (N. Martin, 2008). Additionally, both crop and non-crop host species are distributed in specific localities or throughout New Zealand. An example of the distribution of some host species is that kumara (*Ipomoea Batatas L.* (Convolvulaceae)) is produced mainly in upper north island, potato in all regions, tomato mostly north island and a small amount in south (Horticulture New Zealand, 2017). The apple of Peru (*Nicandra physaloides* L. (Solanaceae)) is mostly in north island and poroporo is widespred (Webb, Sykes, & Garnock, 1988) and African boxthorn is found on the coast of Taranaki and Auckland and ocasionally in areas of the South island (Popay, Champion, & James, 2010).

It might be relevant to understand in a choice test from which host species will TPP migrate to crop host species and what will be the possible rate of increase after migrating. However, because of the distribution of both crop and non-crop host species in New Zealand, studies will need to be conducted with a focus on how plants are distributed in different parts of the country. This information will be relevant to plan a more exact management strategy taking into consideration host species and locality. As it stands, this research is an indicator that there is more to be known surrounding TPP host transfer; it certainly does not lead to the conclusion that field boundary weeds must be removed to manage the pest.

5.3 Biological control of TPP

Developing a successful classical biological control takes about ten years. Many studies are needed to fully understand the target pest and the BCA ecology and biology. Additionally, the BCA(s) and the target organism environment in which they will be encountered (such as a glasshouse) needs to be understood (Bale *et al.,* 2008). Chapter two in this study aimed at understanding more about the ecology of the target pest. The results obtained showed more studies are needed to fully understand how best to manage this pest. In the subsequent chapter, four natural enemies were evaluated to manage the pest in glasshouses. Some of these agents have shown some potential to manage the pest either alone or in combination with another BCA.

Measuring success in managing a pest with a BCA is has several parameters (Gurr & Wratten, 2000). However, success in this study was measured by successful reduction of TPP numbers using four BCAs separately in the glasshouse conditions on tomato plants. This was to achieve some extent for some BCAs, although the starting pest population was high in comparison to the number of BCAs

released. Additionally, we still need to know if the pest population can be kept below an economic threshold by the BCAs. However, such an economic threshold is yet to be established for tomato. Additionally, we need to know release rates and timing of release for these BCAs.

Apart from *A. limonicus*, there is no data to show that the BCAs used in this study are part of glasshouse pest management in New Zealand. This study containing these BCAs is a significant step in developing a possible BCA to be used in the management of TPP. Research planned by others at Lincoln University, after thesis completion, will have lower pest population at the start and will examine possible synergies between BCA species.

5.4 Mesh crop covers

The emerging management approach of mesh covers for TPP has gained favour because of the benefits it brings to the farmer and the environment (Merfield, 2017). Therefore, the practice can be implemented, but the impediment of GPA nymphs bypassing the mesh should be addressed.

Using mesh covers to cover crops grown in the open field from insects is well studied in Europe, Africa, Asia and USA (Cohen, 1981; Franck & Bar, 1992; T. Martin, Assogba, Houndete, Hougard, & Chandre, 2006). Implementing this approach eliminates the use of agro-chemicals, which can have unfavourable effects on the environment see introduction (Chapter 1)

The only mesh size capable of completely protecting the crop from TPP and aphids (0.15×0.15), is sold as a ventilation screen for greenhouses to “keep the good bugs in and the bad bugs out”. This mesh can also endure outdoor conditions for three years (Svensson, 2017). On the other hand, the 0.6×0.6 and 0.3×0.3 mesh are both used for protecting crops from pests in the open field (Crop Solutions, 2017; Merfield, 2017), which is how they are being used in research for TPP management in field potatoes in New Zealand. The latter two mesh sizes are expected to remain durable for 8 to 10 years (Crop Solutions, 2017; Merfield, 2017); however, they are more vulnerable to being breached by GPA which will establish beneath them. The meshes studied are produced and marketed by different entities for different uses, with different materials and durability.

A price evaluation of the different mesh sizes studied showed that as the mesh size decreased, the price increased. The approximate price for 1300 m² of each mesh is as follows: $912 for the 0.6×0.6, $957 for 0.3×0.3 (Merfield, personal communication, 2017), $13,713 for 0.15×0.35 and $15,113 for the 0.15×0.15 (Hummert International, 2017). For farmers in New Zealand, the biggest challenge in using the 0.6×0.6 mesh is the upfront cost (G. Smith, personal communication, 2017), using the mesh for ten years can achieve an estimated annual profit increase of 25 to 75 % (Merfield, 2017). Additionally, agro-chemical application cost for 10 years is significantly higher than using the mesh

for the same period (Merfield, 2017). After considering the cost and long-term benefits, some growers are willing to try this emerging TPP management technique using the expensive but durable 0.6×0.6 mesh, which is the cheapest among those tested in this study. The less durable and more expensive 0.15×0.15 mesh that provides the best protection for potatoes from aphid infestation is not likely to be adopted by farmers if only of immediate economics are considered.

Providing the ideal management strategy below the mesh covers for GPA is recommended, preferably using a generalist predator such as the brown lacewing, which can manage both GPA and TPP. Biological control of GPA is widely known in controlled planting environments such as shade house and greenhouse (Andorno & López, 2014; Van Lenteren & Woets, 1988; White, Wratten, Berry, & Weigmann, 1995). Laboratory and field research should be conducted to quantify the suitability of these biological control agents for GPA below a mesh.

Chapter 6

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