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# Insect biological control of the tomato-potato psyllid *Bactericera cockerelli*, a review

Emiliano R. Veronesi <sup>a</sup>, Christopher J. Thompson<sup>c</sup> and Stephen L. Goldson <sup>a,b</sup>

<sup>a</sup>Bio-Protection Research Centre, Lincoln University, Lincoln, New Zealand; <sup>b</sup>AgResearch, Christchurch, New Zealand; <sup>c</sup>Bioforce Limited, Karaka, New Zealand

## ABSTRACT

The tomato-potato psyllid (TPP) *Bactericera cockerelli* is a polyphagous herbivore and a renowned pest of solanaceous crops found in America and the Pacific region. Over the last fifteen years, several strategies have been tested worldwide to successfully manage this species, but these have been mostly unsuccessful. While IPM (Integrated Pest Management) programs for the management of TPP remain lacking, associated research on biological options has continued to progress. This review classifies and summarises world's current TPP biological control endeavour and discusses the potential and limits of identified biocontrol agents.

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Biocontrol; TPP; predators; parasitoids; beneficials; *Tamarixia triozae*; *Engytatus nicotianae*

## Introduction

Ongoing human population growth, climate instability and environmental degradation continue to increase the need for reliable food supplies; these circumstances are now placing unprecedented pressure on conventional agricultural systems (GSDR 2019, Nicolopoulou-Stamati et al. 2016). This particularly applies to large monocultures that typically require constant inputs of synthetic fertilisers and pesticides (De Schutter 2010; Godfray et al. 2010; Pretty et al. 2018; Springmann et al. 2018). Upscaling of food production practices to meet and protect projected demand is problematic, as this would seem to be incompatible with the Paris Agreement and many of the associated Sustainable Development Goals (SDGs) (Nicolopoulou-Stamati et al. 2016). In short, agriculture and food systems urgently need to change if they are to reach such standards while minimising demands for additional land (Willett et al. 2019).

Part of the solution must be the adoption and adaptation of more environmentally friendly technologies and techniques. This must include the optimal use of invertebrate predators and parasitoids (Assessment 2005) as alternatives to synthetic pesticides (Gurr et al. 2000; Bengtsson 2015; Naranjo et al. 2015; Gurr et al. 2016; Gurr et al. 2017; Ingerslew and Finke 2018; LaCanne and Lundgren 2018; Shields et al. 2019; Wyckhuys et al. 2019).

The availability of already-established natural enemies for the biological control of pests can be determined by geographical region. In addition to this, allochthone

natural enemies from the pest's area of origin may be imported to offer more targeted options (classical biological control).

In the case of the tomato-potato psyllid, *Bactericera cockerelli* Šulc (Hemiptera: Trioziidae) (TPP) its biological control has proven to be particularly challenging, due to its highly fecundity and polyphagy. Further, the pest is a vector of the damaging bacterium *Candidatus liberibacter solanacearum* (CLso). Such characteristics raise the undesirable possibility of complete abandonment of potential IPM (Integrated Pest Management) strategies against TPP in favour of approaches based entirely on synthetic pesticides. That said however, a recent study has suggested that CLso-positive TPP may account for only a small fraction of the total TPP population (only 0.22–6.25% (Djaman et al. 2019)). Consequently, IPM of (uninfected) TPP can be considered.

In this review, we discuss new studies on the potential of several insect biocontrol agents active against *B. cockerelli* and in doing so, we consider different spatial scales (Petri dishes, cages, and greenhouse/field trials) and the associated implications for greenhouse tomato (*Solanum lycopersicum* L.) production. Further, we emphasise how most of the research on beneficials has been largely via laboratory studies, with only a small proportion being conducted under conditions approaching those of commercial production.

### **The tomato-potato psyllid – an overview of the pest**

The tomato-potato psyllid (TPP) is a phloem-feeding insect native to North and Central America and has been recognised as a severe pest of Solanaceae for over a hundred years (Liefting et al. 2008; Butler and Trumble 2012a). The species is hemimetabolous with three different life stages: eggs, nymphs and adults. TPP eggs are yellow, oval shaped measuring on average 0.3 mm in length and 0.1 mm in width. They can be laid everywhere on the plant (depending on the intensity of the infestation) but they are more often found on the leaves (Lehman 1930; Knowlton and Janes 1931; Abdullah 2008). The nymphs are flat and scale-like being yellow-orange when young, whereas the fifth instars are green (Wallis 1955). TPP nymphs are not very mobile, and they tend to move a matter of mm, and then only when disturbed (Lehman 1930). Conversely, the adults are winged, reactive to disturbance, and jump to escape predation (Knowlton and Janes 1931). The adults are less than 3 mm long and appear green shortly after eclosion, but turn darker within 2–3 days when they assume their typical grey-black colour with a characteristic white band on the abdomen (Knowlton and Janes 1931). Young TPP adults become sexually mature within 2 days after eclosion, but they usually don't mate until they reach six days old (Abdullah 2008; Guédot et al. 2012). Female adults reach the peak of oviposition at 15–18 days old and the oviposition period lasts up to when they are 53 days old (Abdullah 2008). A single female can lay up to 500 eggs (Wallis 1955) with an average of c.230 eggs (Abdullah 2008). The eggs take 3–8 days to hatch, depending on temperature. The first instar nymphs need an average of 15.4 days (at 27°C) to go through all five nymphal stages before turning into adults. Development (from egg to adult) can occur after only 22 days in warmer regions (at 27°C), whereas in cooler areas up to 97 days may be required (Lehman 1930; Knowlton and Janes 1931; Abdullah 2008; Yang and Liu 2009; Yang et al. 2010).

Recent studies suggest the optimum temperature range for the reproduction of TPP to be 24°C–27°C (Tran et al. 2012; Lewis et al. 2015).

In the 1930s and 1940s, TPP was sporadically reported as a pest in Utah, Idaho, Colorado, Wyoming and Mexico (Richards 1928; Pletsch 1947). Today, TPP is considered to be an occasional pest as far north as Canada (Ferguson and Shipp 2002; King 2014). However, in the United States the species is regarded as one of the severest pests of both tomatoes and potatoes (*Solanum tuberosum* L.) (Liu and Trumble 2005; Liu et al. 2006, 2007; Munyaneza et al. 2007; Hansen et al. 2008; Butler and Trumble 2012a). The same applies to the North and Central Mexican production systems (Munyaneza et al. 2007; Munyaneza et al. 2009; Butler and Trumble 2012a). In 2019, TPP was found for the first time in South America (Ecuador), on potatoes (Carrillo et al. 2019).

TPP was first observed in New Zealand in 2005 (Gill 2006; Thomas et al. 2011), where it is now a significant pest of field potatoes, greenhouse capsicums and tomatoes, and tamarillos (*Solanus betacea* Sendt) (Teulon et al. 2009). It is thought that the accidental distribution of infected seedlings played an important role in the dispersal of this pest (Teulon et al. 2009). In February 2017, it was also reported for the first time in Western Australia (DAFWA 2017).

Both adults and nymphs of TPP cause direct feeding damage, as their saliva is toxic to the plant; further, the honey dew produced by TPP feeding leads to the growth of sooty mould (Munyaneza et al. 2007; Sengoda et al. 2010). However, most of the economic damage occurs because TPP is able to vector the bacterial pathogen CLso, detected for the first time in New Zealand in 2006 (Gill 2006), which causes foliar damage, stunting, and reduced yield (Hansen et al. 2008; Liefting et al. 2008). CLso causes zebra chip (ZC) disease in potatoes, causing brown patches and stripes in fresh tubers (Munyaneza et al. 2007). After being fried these blemishes become darker (commonly referred to as ‘zebra chips’), causing consumers and processors to reject the tubers (Munyaneza 2012). CLso also leads to the early decline and death of infected plants, sometimes resulting in complete crop losses (Sengoda et al. 2010).

Management of TPP is challenging due to its high reproductive rate and cryptic oviposition habits (Butler and Trumble 2012a). Further, this pest is extremely polyphagous and can feed on plants from more than 20 different families. Because of this, TPP can survive and even complete its life cycle on several non-crop plants, such as the African boxthorn (*Lycium ferocissimum* Miers), a solanaceous perennial weed found throughout New Zealand (Knowlton and Thomas 1934; Butler and Trumble 2012a; Barnes et al. 2015). This wide range of potential host-plants allows TPP to persist even when commercial crops have been removed from the field, as it can establish on the surrounding margins on other non-crop plants which then become reservoirs for future TPP infestations.

### **The biological control of TPP**

Research on TPP biological control has many dimensions. An important consideration when studying potential agents is how to isolate and study parameters of interest separately. This review of recent literature on the biological control of TPP identifies three levels of experimental research, each representing a different scale, these being Petri dishes, cages, and field trials.

With regard to Petri dish studies (also referred to as ‘arenas’), each dish is considered to represent a single experimental unit. By ‘cage studies’, we refer to those conducted either in controlled environments or in the field and rely on the use of relatively small enclosures typically consisting of fine mesh to control the experimental variables. Usually, in this type of experiment, each cage contains a single plant and represents a single experimental unit, although sometimes larger cages may contain multiple plants. Finally, ‘field studies’ comprise experiments conducted either in the field (in case of crops) or commercially scaled greenhouses. Essentially such work does not use simplified proxies for productive environments.

## **Petri dish studies**

Understandably, Petri dish studies are the most commonly occurring biocontrol-based research found in the literature. Petri dishes are cheap, easy to handle, don’t require much space and offer evaluation of simple parameters (e.g. predatory consumption, oviposition, survival) and are easy to assess. However, these studies are obviously gross oversimplifications of reality, and the insights provided, while valuable, are unlikely to be reliable predictors of what happens under more complex circumstances.

## **Parasitoids**

Although there are reports of at least two parasitoids active against TPP these being *Methaphycus psyllidus* (Compere) (Encyrtidae) and *Tamarixia triozae* (Burks) (Eulophidae) (Compere 1943; Pletsch 1947; Jensen 1957), only the latter is well-represented in the literature. Research on this species has covered a wide range of aspects such as fecundity and development (Cerón-González et al. 2014; Rojas et al. 2015; Chen et al. 2022, 2023), parasitism and feeding rates (Cerón-González et al. 2014; Rojas et al. 2015; Tamayo-Mejía et al. 2015; Yang et al. 2015; Ramírez-Ahuja et al. 2017; Chen et al. 2022, 2023), the effects of diets on its longevity and performance (Veronesi et al. 2021; Chen et al. 2022, 2023), and how different tomato varieties can also affect the performance of this wasp (Mayo-Hernández et al. 2022; notably this was based on a ‘Y tube’ olfactometer study, and not P. dishes). Some of these studies have also combined *T. triozae* with other biocontrol agents such as entomopathogenic fungi (Tamayo-Mejía et al. 2015) and mirid predators (Ramírez-Ahuja et al. 2017), usually finding that such combinations are more effective than single biocontrol agents. Overall, such studies have pointed to the potential of *T. triozae* for the biological control of TPP.

## **Predators**

Laboratory studies to test the efficacy of different predators for the biological control of TPP have included a variety of species, which typically have been evaluated based on their consumption rates of the TPP life stages (eggs and/or nymphs, sometimes adults).

Coccinellidae (Coleoptera) are known to feed on a number of psyllid species (Pluke et al. 2005; Hodek and Honěk 2009), and their potential to suppress TPP has been

assessed in many Petri dish studies. O'Connell et al. (2012) tested the feeding potential of three different coccinellids, *Cryptolaemus montrouzieri* Mulsant, *Cleobora mellyi* Mulsant and *Scymnus loewii* Mulsant on tomato and potato leaflets. All three species showed feeding on mixed instars of TPP nymphs. *C. mellyi* showed the highest rate of psyllid consumption (up to 100 over 24 h), followed by *C. montrouzieri* (up to 30 over 24 h), and *S. loewii* (<10 over 24 h). Here it was shown that the host plant substrate can greatly influence the amount of feeding as indicated by the clear preference of *C. mellyi* and *C. montrouzieri* for no-leaflet arenas, suggesting that tomato plants are probably not a desirable substrate for these two control agents. More recently, another study conducted on potato leaflets (Pugh et al. 2015) investigated further the potential prey preference of *C. mellyi* and found that the species did not show any particular preference for TPP or two aphid species *Myzus persicae* (Sulzer) (Hemiptera: Aphididae) or *Macrosiphum euphorbiae* (Thomas) (Hemiptera: Aphididae). MacDonald et al. (2016) evaluated two other coccinellid species these being the 11-spotted ladybird beetle *Coccinella undecimpunctata* Linnaeus and large spotted ladybird beetle *Harmonia conformis* Boisduval. These researchers showed that both species exhibited the capacity to prey upon all TPP life stages with eggs being the least favoured. Sarkar et al. (2022) investigated the development and reproduction of *Coccinella transversalis* Fabricius, an Australian native generalist predator, which has been found to feed, develop, and reproduce on the TPP. *Hippodamia variegata* (Goeze) has also shown its ability to successfully develop and oviposit when feeding on TPP, although its survival and developmental rates were not as high as when feeding on *M. persicae* (Sarkar et al. 2023).

MacDonald et al. (2016) also tested the voracity of three additional insect predators (other than the two coccinellids mentioned above) when feeding on different TPP stages under laboratory conditions (Petri dish). These were the brown lacewing *Microgaster tasmaniae* (Walker) (Neuroptera: Hemerobiidae), the small hoverfly *Melanostoma fasciatum* (Macquart) (Diptera: Syrphidae) and the Pacific damsel bug, *Nabis kinbergii* (Reuter) (Hemiptera: Nabidae). All these predators consumed all TPP life stages offered and when choice was established between TPP and the green peach aphid, *M. persicae*, no preference was apparent. The green lacewing, *Chrysoperla carnea* (Stephens) (Neuroptera: Chrysopidae), has also shown potential for the biological control of TPP. This species is a voracious generalist predator which has been widely adopted in several biocontrol programs (Li et al. 2023). Salas-Araiza et al. (2015) investigated the effect of *C. carnea* larvae on TPP eggs and nymphs, all of which were found to be susceptible. The functional response of *C. carnea* on TPP was further studied by Ail-Catzim et al. (2018) who focused on the predatory response of the three *C. carnea* larval instars to first and second instar TPP nymphs. They found that the third larval instar of *C. carnea* consumed more nymphs than the first and second instar larvae. However, analyses revealed a type-II functional response by the first and second larval instar of the predator and a type-III response by the third larval stage. Analysis of the attack coefficient of first two *C. carnea* larval stages suggested that, although both instars have an equal capacity of finding the prey, the second larval instar can consume it more rapidly. Ail-Catzim et al. (2018) therefore suggested the value of first instar larvae of *C. carnea* larvae for dealing with the TPP first and second instar nymphs.

The existing literature on predatory mirids (Heteroptera: Miridae) indicates opportunity for further systematic exploration of this family as a source of biocontrol agents



against the TPP. *Engytatus varians* (Distant) (Hemiptera: Miridae) is a generalist predator whose potential for the control of TPP has been investigated in a number of studies. Martínez et al. (2014) tested for the first time the feeding capacity of *E. varians* on TPP nymphs and reported that fourth instar *E. varians* nymphs preyed on 46% of 10–20 TPP nymphs in over 24 h. In a later study Mena Mociño (2016) focussed on the influence of *E. varians* sex ratios, and on different TPP life stages. Overall, this work showed that *E. varians* (nymphs and adults of both sexes) preferred second instar nymphs of TPP. Further to this Pineda et al. (2016) used small plastic cylinders each containing one small tomato plant (as opposed to Petri-dishes) and found that during its nymphal developmental stages *E. varians* could consume 80 to 85 TPP third instar nymphs. Mena-Mociño et al. (2021) continued their investigations by examining the effect of sex ratio on different life traits of *E. varians*, as well as the prey preference of the species. Here, 3rd, 4th and 5th instar nymphs of *E. varians* as well as adults of both sexes were tested against 2nd, 3rd, 4th and 5th instar nymphs of TPP. All *E. varians* stages preferred younger TPP nymphs over older TPP nymphs, in the following order  $N2 > N3 > N4 > N5$ . A similar preference for younger TPP nymphs by *E. varians* was observed in another study by Pineda et al. (2020), who showed that female *E. varians* consumed more TPP than males. Overall, the above-mentioned studies on *E. varians* suggest the species has potential as a biological control agent against TPP.

*Dicyphus hesperus* (Knight) (Heteroptera: Miridae) is another mirid that shows potential against TPP. This predator can suppress populations of several greenhouse tomato pests and is capable of feeding on plant sap without causing significant damage to plants (Shipp and Wang 2006; Shipp et al. 2007). However, only one published laboratory study has been conducted to investigate the potential of this mirid against TPP (Ramírez-Ahuja et al. 2017). This work showed that combined releases of *D. hesperus* and *T. triozae*, increased TPP mortality. Furthermore, intra-guild predation was observed in that *D. hesperus* consumed *T. triozae*-parasitised TPP nymphs. This predation risk appeared to be greatest when TPP nymphs contained the egg of the parasitoid, and diminished throughout the development of the parasitoid, to the point where TPP nymphs containing *T. triozae* pupae suffered almost no predation at all.

Veronesi et al. (2021, 2022a) showed that *Engytatus nicotianae* (Koningsberger) (Hemiptera: Miridae) is a useful generalist mirid predator active against TPP in New Zealand greenhouses. Veronesi et al. (2021), assessed the consumption of TPP by *E. nicotianae* adults (males and females), using no-choice tests, against eggs and the first four nymphal instars. Here, they found female *E. nicotianae* to be more voracious than males with both sexes consuming more younger TPP nymphs. Veronesi et al. (2022a) extended this study using choice-essays to compare the feeding preferences of male and female *E. nicotianae* TPP. This work showed a clear preference for the first three TPP instars and TPP eggs versus the fourth instar. The fourth TPP instar was relatively unattractive to both sexes of *E. nicotianae*. Overall, such findings were consistent with studies conducted on the related mirid, *E. varians* (Pineda et al. 2016, 2020; Mena-Mociño et al. 2021).

Predatory mites have also been considered as potential candidates for the biological control of TPP. Xu and Zhang (2015) tested the efficacy of *Amblydromalus limonicus* (Garman and McGregor) (Acari: Phytoseiidae) and showed that the mite can feed on TPP eggs as well as the first three nymphal stages. This might also benefited from psyllid sugar. However, prey size was found to be key in determining the success of

predation. The average TPP consumption per mite over 24 h was 2.5 for eggs, 2.0 for 1st instar nymphs, 0.5 for 2nd instar nymphs and only 0.03 for 3rd instar nymphs. Further, over a 16-day period, *A. limonicus* again showed limited effect, with only 30% exhibiting successful attacks. Xu and Zhang (2015) suggested the possibility of mass-rearing the mite and their inundative release may be effective. However, Bioforce Limited (pers. comm) found that mass rearing of this mite is problematic and expensive, largely because of cannibalism when population densities are high.

Geary et al. (2016) investigated the potential of another predatory mite, *Anystis baccarum* (Linnaeus) (Trombidiformes: Anystidae), against TPP. This aligned with the findings of Xu and Zhang (2015) who found that the mite's efficacy appeared to be limited by the orientation of the psyllid nymphs, in that successful predation occurred only when the mite was able to force its mouthparts into softer tissue on the ventral surface. The study concluded that densities of mites need to be high to achieve significant consumption of TPP and is in line with the findings of Xu and Zhang (2015).

## Cage studies

Cage studies present a more reliable proxy of reality than Petri dishes in that they usually involve whole plants rather than just leaflets. This allows investigations at a higher level of complexity, factoring aspects such as predator searching time and plant-related variables. Cage studies represent a good compromise between the need to control variables and allowing in-depth studies without being too demanding in terms of facilities and access to adequate funds.

## Parasitoids

Although the parasitic wasp *T. triozae* is well-studied at the Petri dish level, the literature on its caged performance is scarce. Butler and Trumble (2012b) investigated the combined effects of several natural enemies on TPP population growth including *T. triozae*. However, the study did not focus specifically on the parasitoid directly but instead, compared the TPP population growth between plants in closed cages (where naturally occurring enemies could not enter and attack TPP) and on plants contained in frame-only cages (where naturally occurring enemies did have access to the TPP). The first attempt to describe the potential of *T. triozae* against TPP based on cage trials was carried out in Veronesi et al. (2021). This study evaluated the performance of *T. triozae* against TPP either alone or combined with other agents. Veronesi et al. (2021) observed that *T. triozae* was not particularly successful in suppressing TPP populations (nor were any other biocontrol agents tested in the study), probably because the numbers of biocontrol agents released were too low compared to the levels of TPP infestation at the commencement of the experiment. However, significant results were subsequently obtained by Veronesi et al. (2022b), where *T. triozae* was successfully combined with the mirid *E. nicotianae* for the suppression of TPP on greenhouse tomatoes. While this study highlighted the differences between the use of *E. nicotianae* alone or combined with *T. triozae*, it provided no data upon the impact of *T. triozae* alone.



## Predators

As discussed above, several predatory insect species have been identified as predators of TPP and tested in Petri dish experiments (MacDonald et al. 2010, 2016; O'Connell et al. 2012; Veronesi et al. 2021). However, only a few of these insect species have had their potential assessed in larger controlled environments (cages). In a cage-based assay, Sarkar et al. (2022) found that *H. variegata* larvae reduced the number of TPP nymphs by up to 59% and 66% based on initial densities of 8 and 16 *H. variegata* per tomato plant, respectively. This result also positively influenced the plant chlorophyll content and biomass. Sarkar et al. (2023) similarly showed that *C. trasveralis* has demonstrable potential for the biocontrol of TPP, achieving up to 59% suppression of the pest population at a density of just 8 *H. trasveralis* per plant.

Amongst the mirids, *E. varians* and *E. nicotianae* have also shown good potential in cage trials. Pérez-Aguilar et al. (2019) showed that *E. varians* reduced the populations of TPP by up to 80% and 90% with release rates of 1 and 4 per tomato plant, respectively. Similarly, Veronesi et al. (2022a) investigated the potential of *E. nicotianae* as a control agent able to prevent TPP incursion and build-up. In this work they showed that a background population of the predator at the time of TPP arrival can effectively prevent it from establishing on tomato plants. In another contribution by Veronesi et al. (2022b) they showed that when *E. nicotianae* is used in the classical way (i.e. released after the pest's arrival) to reduce already-established TPP population it has limited potential, but a combination of *E. nicotianae* and *T. triozae* can successfully suppress TPP populations.

Liu et al. (2019), investigated the potential of combining predatory mites with entomopathogenic fungi and/or pollen against TPP. The mites tested were *A. limonicus* and *Neoseiulus cucumeris* (Oudemans) (Acari: Phytoseiidae) and the fungus was *Beauveria bassiana* Balsamo. Their study showed that the combined use of *A. limonicus* with *B. bassiana* resulted in significantly decreased TPP populations and greater crop yield (on bell peppers). The authors therefore suggested that synergistic combinations of *A. limonicus* with *B. bassiana* could usefully control TPP in greenhouses. In study into the potential of *A. limonicus* Kean et al. (2019) found that plant species and cultivar can significantly affect the ability of this mite to suppress TPP. In their study, on average, *A. limonicus* performed better on pepper rather than tomato plants. These authors hypothesised that their results might have been due to differences in leaf morphology between the plant species and TPP development takes longer on pepper than on tomato thus resulting in a higher predator/prey ratios on pepper.

## Field/greenhouse studies

Field and greenhouse trials offer the most realistic and reliable basis for experimentation beyond what can be determined using laboratory or cage experiments. However, this level of realism inevitably comes with complications. Field and greenhouse trials are much more expensive, and require more space etc.

## Parasitoids

Field and greenhouse studies on *T. triozae* are sparse. However, the potential of *T. triozae* has been assessed in the few published field studies. For instance, Pletsch (1947) reported

only 23% parasitism of TPP by *T. triozae* in one field. More recently, a broad field survey was conducted in Southern California on potatoes, tomatoes, and bell peppers fields; this showed parasitism rates of TPP by *T. triozae* to be on average, below 20% (Butler and Trumble 2012b). The most recent published field study on *T. triozae* was conducted in New Zealand over a period of three years and involved the release of the parasitoid in three different regions (Davidson et al. 2023). This work revealed that *T. triozae* can successfully overwinter and survive on non-crop plants in areas in the vicinity of potato fields. However, the average percentage of parasitism recorded in this study was 15.6%, in line with findings described in Pletsch (1947) and Butler and Trumble (2012b).

Such results have indicated that biological control of TPP by *T. triozae* may well be prohibitive, due to the large releases required to achieve parasitism levels sufficient to impart adequate control (Calvo et al. 2016). Nonetheless, the parasitoid has demonstrated good potential when used in combination with other biocontrol agents. A study conducted in greenhouse sections reached parasitism levels of between 40% and 60% through the release *T. triozae* in combination with the mirid predator *D. hesperus* (Calvo et al. 2018a).

### **Predators**

Under greenhouse conditions, amongst the range of reported predators of the TPP, only a few have been tested under commercial production systems. Al-Jabr (1999) tested *Chrysoperla carnea* against TPP, but it was deemed unsuccessful. Conversely, the mirid *D. hesperus* has been evaluated for the control of TPP in greenhouses, with encouraging results; (Calvo et al. 2016). These authors showed that *D. hesperus* can survive and reproduce effectively feeding on a TPP-based diet. The species has also been tested in combination with *T. triozae*, where better control of the psyllid was achieved compared to use of the species alone (Calvo et al. 2018b).

The two predatory mites *A. limonicus* and *N. cucumeris* have been tested in the greenhouse environment for the biological control of TPP (Patel and Zhang 2017). Both species were found to be equally effective in controlling TPP and significantly reduced damage on capsicum plants. Further, Patel and Zhang (2017) noted that *N. cucumeris* can be more easily mass reared than *A. limonicus* indicating a possibly cost-effective biological control agent against TPP.

### **Discussion**

According to the literature, only 10% of classical field biological control introductions (Greathead and Greathead 1992; Gurr et al. 2000; Cock et al. 2016) and about 16% of field augmentative biological control introductions (Collier and Van Steenwyk 2004) have succeeded in delivering useful pest management. However, even with such low success percentages biological control is estimated to be worth billions of US dollars per year (Losey and Vaughan 2006) and its benefit/cost ratio can be as high as 1000/1 (Naranjo et al. 2015). With the low success rates, there remains plenty of room for improvement leading to reduced costs and protection of the productive environment. Here the low frequency of success calls for a focus on when and why it fails (e.g. Goldson et al. 2014). According to Stiling (1993), one of the main reasons for the low

success rates is insufficient understanding of how pests and biocontrol agents associate in exotic ecological communities and environments, as described by Goldson et al. (2020). Hoelmer and Kirk (2005) identified several factors such as (a) the inadequate taxonomic knowledge of pests and their natural enemies (Rosen 1986; Clarke and Walter 1995), (b) failure to address the importance of climate matching relating to the ecoclimatic area from which the biocontrol agents are taken versus the ecoclimatic area into which they are released, and (c) the fact that even the most promising data from candidate agents obtained while they are still in quarantine often do not translate directly into field performance. This may reflect the complexity of the ecosystem into which they are introduced. Irrespective, it is clear how knowledge gaps play a major role in biological control failure and given globally how valuable biological control is, there is an incontrovertible need to keep researching with the aim to increase its success rate as well as its efficacy.

Based on the published literature, this review has highlighted the significant difference between the number of laboratory experiments versus more realistic tests, such as cage and field trials. While the essential importance of simplified experiments is recognised, such tests alone are usually not to be considered reliable predictors of insect dynamics in productive systems. As it happens, more complex experiments need to be conducted to follow up preliminary results obtained through simple laboratory-based trials.

This is reflected by work on *T. triozae* in its entirety. The literature on this wasp is extensive and covers the species' developmental (Cerón-González et al. 2014; Rojas et al. 2015; Chen et al. 2022, 2023), feeding and reproductive potential (Cerón-González et al. 2014; Rojas et al. 2015; Tamayo-Mejía et al. 2015; Yang et al. 2015; Ramírez-Ahuja et al. 2017; Chen et al. 2022, 2023), circadian rhythm (Chen et al. 2020), the role of diet (Veronesi et al. 2021; Chen et al. 2022, 2023) and the effects of host plants (Mayo-Hernández et al. 2022). The common denominator in all these studies is that they all point to the potential role that *T. triozae* could have in the management of TPP. However, many of these studies have been laboratory-based and could only approximate such fundamental aspects such as prey handling time under field conditions. In some ways an abundance of encouraging laboratory data can contribute to the creation of over-optimistic expectations of the field performance of this control agent. In the case of *T. triozae* in New Zealand expectations were such that permission was granted to release the species in September 2016 as part of a TPP biological control release programme, upon the completion of host specificity and host range studies. Over the ensuing year the parasitoid was systematically released at multiple sites in Hawke's Bay, Canterbury and Auckland (Barnes 2017; Davidson et al. 2023), as well as into tomato greenhouses, potato fields, tamarillo orchards and their surrounding areas (<https://www.hortidaily.com/article/9069529/new-zealand-second-round-of-tamarixia-triozae-biological-control-releases-underway/>). In 2020, the release and study were concluded having demonstrated that *T. triozae* overwinters successfully. However, where *T. triozae* was recovered, the percent TPP parasitism ranged between 4 and 40% with an average of 15% ([https://issuu.com/hortnz/docs/nzgrower\\_august\\_2020\\_/s/11312855](https://issuu.com/hortnz/docs/nzgrower_august_2020_/s/11312855); Davidson et al. 2023). Such percentage of parasitism is insufficient to achieve significant control of the TPP, in fact, it was found that large releases of the parasitoid were necessary to obtain adequate control (Calvo et al. 2016). The relatively low rates of field parasitism found in New Zealand were in line with previous work described by Pletsch (1947) and Butler and Trumble (2012b).

Arguably, a more reliable overview of the true potential of this wasp may have been obtained through larger scale experiments, such as caged trials. While the field release of *T. triozae* resulted in disappointing results regarding its potential to suppress TPP populations in the field, the programme itself has provided valuable information on the ability of *T. triozae* to establish under field conditions and insight into its dispersal (Davidson et al. 2023). Further, this work on *T. triozae* has been valuable in that the wasp is now available to be used in IPM systems in tomato greenhouses (Veronesi et al. 2022a).

In general, while laboratory studies and assessment of biological control agents' efficacy do not necessarily translate into useful impacts under field conditions, nonetheless such studies do provide very important insights into control agent biology and life-history traits. This information can be used effectively to screen for potentially suitable biocontrol agents, which can then be selected for further testing under staged conditions.

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## ORCID

Emiliano R. Veronesi  <http://orcid.org/0000-0002-1659-8786>

Stephen L. Goldson  <http://orcid.org/0000-0003-0057-6969>

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