

The Population Dynamics of the Thrips
Species Assemblage in French bean,
Lettuce, Tomato and Zucchini
Agro-Ecosystems

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Abstract

Management of insect pests is one of the most important aspects of crop agronomy in the agricultural industry. This has become increasingly sophisticated as new approaches based on a greater understanding of individual pests and their biology are developed and used in Integrated Pest Management (IPM) programs to target pest populations at critical development periods to reduce potential injury to the crop. Our understanding of Thysanoptera biology and ecology in vegetables is restricted to a few key pest species, and very little attention has been given to other thrips species that dwell within these systems. This has produced a large gap in our understanding of the population dynamics of pest and non-pest species in vegetable agro-ecosystems. This deficit restricts the capacity to develop IPM strategies for the important pest thrips species. To contribute to our understanding of the Thysanoptera and the relationship of this insect order with the vegetable agro-ecosystem, this study determined the thrips species assemblage in French bean (*Phaseolus vulgaris*, var. 'Labrador'), lettuce (*Lactuca sativa*, var. 'Rador'), tomato (*Solanum lycopersicum*, indeterminate trial variety courtesy of Syngenta©) and zucchini (*Cucurbita pepo*, var. 'Amanda') agro-ecosystems, and further investigated: the temporal distribution of thrips populations on a crop phenological scale; the variability of the spatial distribution of thrips clusters; the effect of weather on thrips relative abundance; and the reproductive host association between thrips and the four crops.

Investigations undertaken in this three-year study (27th December 2011 to 3rd June 2012; 24th December 2012 to 4th June 2013; 27th December 2013 to 17th June 2014) determined that four thrips species assemblages exist in each of the four agro-ecosystems. These comprised of key thrips species including *Frankliniella occidentalis* (Pergande) and *Megalurothrips usitatus* (Bagnall) in French bean, *Desmothrips tenuicornis*

(Bagnall), *F. occidentalis* and *F. schultzei* (Trybom) in lettuce, *F. occidentalis*, *F. schultzei* and *Pseudanaphothrips achaetus* (Bagnall) in tomato and *F. occidentalis*, *F. schultzei* and *Tenothrips frici* (Uzel) in zucchini. French bean and zucchini supported the greatest diversity and abundance of thrips, whilst tomato supported the least within the assemblage. This study represents the first published description of thrips species assemblages in these important vegetable crops.

Frankliniella occidentalis and *F. schultzei* were the two most commonly occurring species. Field studies assessed the differences in their temporal distribution and abundance on a phenological growth scale among the four crops. *Frankliniella occidentalis* were temporally segregated by crop age (weeks since planting), with significantly higher levels present in zucchini compared to French bean, lettuce and tomato between weeks three and six, followed by significantly higher levels in French bean between weeks eight and ten. *Frankliniella schultzei* were temporally separated by crop age between zucchini and lettuce, with significantly higher levels present in zucchini between weeks four and six, and in lettuce between weeks eight and ten.

A reproductive host association was found between French bean and *F. occidentalis*, *F. schultzei*, *M. usitatus* and *T. tabaci*, between lettuce and zucchini and *F. occidentalis*, *F. schultzei* and *T. tabaci*, and *F. occidentalis* and *F. schultzei* and tomato. The reproductive association varied; *M. usitatus* and *T. tabaci* displayed a primary reproductive association with French bean, and *F. occidentalis* and *F. schultzei* with lettuce. All other reproductive associations found in this study were secondary. This is the first recorded evidence for a reproductive association between *F. occidentalis*, *F. schultzei* and *T. tabaci* and lettuce or zucchini.

Temperature, rainfall and relative humidity played an important role in regulating thrips populations in French bean, lettuce, tomato and zucchini. *Megalurothrips usitatus* displayed a negative relationship with temperature, *D. tenuicornis* displayed a positive relationship with

temperature but a negative relationship with relative humidity, while *F. occidentalis* had a positive association with temperature, relative humidity and rainfall. Individual species however displayed variation in their relationship with weather in relation to individual crops, particularly *F. schultzei*, which had a positive relationship with temperature, relative humidity and rainfall in tomato and zucchini, but was negatively affected in lettuce.

Further investigation into the combined effects of variation in crop phenological stage and weather on thrips populations demonstrated an aggregated spatial distribution of *F. occidentalis*, *F. schultzei*, *M. usitatus* and *P. achaetus* in a crop. The probability of species forming a cluster was largely dependent on the age, or phenological growth stage, of the crop. Most species had an increased probability of cluster formation one or two weeks after seeding and transplanting. For *M. usitatus*, probability of cluster formation was much more pronounced in the later stage of French bean growth, coinciding with full flowering. The size and subsequent spatial growth of populations was largely dependent on temperature and rainfall. For *F. occidentalis* in French bean, this was directly related to warm temperatures. For *F. schultzei* in lettuce, probability of cluster formation and growth increased almost from the point of transplanting, and was particularly pronounced during the cool and low rainfall periods. As *F. schultzei* abundance increased in lettuce, there was an increase in gradual spatial spreading of the clusters throughout the agro-system, to accommodate the larger abundance in crop. In tomato, warmer temperatures were associated with an increased chance of *F. schultzei* cluster formation in crop. For *F. occidentalis* and *F. schultzei* in zucchini, the clear dependence on crop age indicates that their presence and growth is reliant on flowering, increasing and decreasing according to flower formation and drop.

The statistical modelling that described the aggregated spatial distribution of the key thrips species in the vegetable crop has not previously been possible as multi-season sampling programs have not

been conducted. The ability to describe the spatial and temporal changes in thrips abundance through statistical models offers the potential for better prediction of likely thrips infestations in the vegetable crops. While further validation research is required for practical application, the statistical model developed in this study offers the potential to improve the management of thrips in crops through better timing of control measures.

This study has demonstrated the benefits of conducting multi-year research on thrips population dynamics in vegetable agro-ecosystems by identifying the assemblage differences in each of the four-vegetable agro-ecosystems, the reproductive association between species and crop, and the behaviour of thrips populations in the vegetable agro-ecosystems in relation to the phenological stage of the crop and the weather conditions. This information is critical to the management of thrips populations in vegetable production through the development of integrated pest management programs.

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Declaration of authorship and originality

The work contained in this thesis has not been previously submitted either in whole or in part for a degree at CQUniversity or any other tertiary institution. To the best of my knowledge and belief, the material presented in this thesis is original except where due reference is made in text.

Signed:

Date: 4th November, 2016

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List of publications and presentations

Publications relevant to the thesis

Healey, MA, Senior, LJ, Senior, PH, Brown & J, Duff 2016, 'Relative abundance and temporal distribution of *Frankliniella occidentalis* (Pergande) and *Frankliniella schultzei* (Trybom) on French bean, lettuce, tomato and zucchini in relation to crop age', *Journal of Asia Pacific Entomology*, 20 (3), 859-865.

Presentations relevant to the thesis

Healey, MA, Senior, LJ, Senior, PH, Brown & J, Duff 2016, 'The predation potential of *D. tenuicornis* in French bean and Lettuce', Annual Entomological Society Meeting, Hobart, Tasmania, October 2012.

Healey, MA, Senior, LJ, Senior, PH, Brown & J, Duff 2016, 'Seasonal dynamics of thrips in vegetables in the Lockyer Valley', Crawford Seminar, Brisbane, Queensland, August 2013.

Chapter One: Thrips in horticulture

General introduction

The management of insect pests is one of the most important aspects of crop agronomy in the agricultural industry. This has become increasingly sophisticated as new approaches based on a greater understanding of individual pests and their biology is developed and used in Integrated Pest Management (IPM) programs to target pest populations at critical development periods to reduce potential injury to the crop. For Thysanoptera, our understanding of their biology and ecology in agricultural systems is restricted to a few key pest species; very little attention has been given to other thrips species that dwell within these systems. Development of alternative management strategies to chemical control is dependent on understanding the ecological systems that thrips inhabit. This literature review documents what is currently known about the biology and ecology of key thrips species in relation to field grown vegetable production, and highlights the research gaps to be investigated in this research project.

Thrips in vegetables

The adaptive diversity of many thrips has enabled members of the order Thysanoptera to successfully exploit more than 300 species of cultivated plants (Ainsworth 1991; Ananthakrishnan 1993). The polyphagous nature of many thrips coupled with their ability to use a wide range of hosts for shelter and reproduction has seen some species classified as important economic plant pests. In vegetable production, thrips cost vegetable growers billions of dollars annually in lost productivity and costs of control measures (Ullman et al. 1997). Many pest species have become increasingly damaging in recent decades with increasing intensification of agricultural systems and reliance on chemical control measures. Knowledge of population dynamics of pest thrips in vegetable production is, therefore, desirable to better understand interactions

between thrips and crop plants. However, there is limited research on the population dynamics of thrips in many field-grown vegetable production systems. This has produced a large gap in the understanding of the ecological dynamics of thrips populations in field-grown vegetable agro-ecosystems.

Infestation by pest species contributes directly to the injury of many horticultural crops through feeding or oviposition and indirectly by transmission of plant diseases such as Tospoviruses (Ullman et al.1997). This has led to an increased body of research focused on pest species to better predict and manage incursion in horticultural production. While such research has led to better management of pest thrips, this focus has made a lesser contribution to understanding the ecology of all other thrips species that dwell within a crop, including pest species in crops where they are otherwise not considered to cause injury. A vegetable crop can support an assemblage of thrips species (pest, non-pest and transient thrips species) using the crop for shelter as opposed to reproduction or feeding. With the vegetable industry looking for more precise and effective methods of pest control through integrated pest management, understanding the diversity of thrips species that exist within these assemblages in a crop, and understanding the factors that influence the dynamics of these populations, will allow for more strategic pest control planning. Importantly, understanding the fluctuation in the dynamics of these populations based on seasonal and phenological changes contributes to our knowledge of thrips ecology in agro-ecosystems.

Impact of thrips on vegetable production

The vegetable industry contributes 6% to the gross value of Australian agricultural production (ABARES 2016) which was valued at approximately \$9.3 billion dollars in 2014 to 2015; with the states, South Australia, Victoria and Queensland accounting for most vegetable production (ABARES 2016). Crop damage due to pest insects is a major constraint to vegetable production, and management practices to control pests represents a significant cost to producers. In a 2014 national survey, vegetable growers indicated that

productivity loss as a direct result of insect pests causing injury to the crop was a major concern along with other issues including water, climate and soil suitability (ABARES 2014). An industry report compiled in 2003 identified pest incursion and control as a key threat to Queensland vegetable production (QLDFVG 2003) as the subtropical/tropical climate in the state is particularly favourable for the development of pest populations in vegetable crops. Queensland vegetable production is centralised in the Lockyer Valley and Darling Downs, Bundaberg and Burdekin regions, with the top commodities by value listed as pumpkins, beans, onion and potatoes (ABARES 2014).

Many thrips are phytophagous. It is these species that cause extensive damage to vegetable production, having the ability to move from one crop to another, using the crop for food and for reproduction. The western flower thrips, *Frankliniella occidentalis* (Pergande), onion thrips, *Thrips tabaci* (Lindeman) and melon thrips, *Thrips palmi* (Karny), are three key economic thrips pests in vegetable crops globally. These cosmopolitan thrips cause damage to a wide range of crops through feeding, breeding and transmission of plant viruses. For example, in Canada, production loss attributed to heavy infestation of *T. tabaci* was estimated to be more than 40% in field grown onions (Fournier et al. 1995). Losses of petals, fruit malformation and scarring by *F. occidentalis* and *T. palmi* caused a loss in tomato crop production and product quality that exceeded US \$10 million in Florida (Nuessly & Nagata 1995). These examples highlight the damage caused by these important pests, reinforcing the idea that Thysanoptera is as a major pest.

Control of thrips can prove difficult due to the rapid rate populations colonise and establish themselves in a crop and the challenge of identifying these small insects in the field. This leads to incorrect insecticide application and unnecessary sprays on non-pest thrips that cause no damage to a crop. It also increases the risk of insecticide resistance development; particularly *F. occidentalis* and *T. tabaci* that have the potential to develop resistance to a range of commonly used insecticides. For example, in Florida, control of the *F. occidentalis* in fruiting vegetables such as tomatoes, capsicums and chillies has been largely based on calendar applications of broad-spectrum insecticides

since the 1980's (Demirozer et al. 2012). The result has been an increase in insecticide resistance development in thrips, the resurgence of thrips populations as a direct result of knock down of naturally occurring enemies, and the subsequent replacement by other pests (Demirozer et al. 2012; Funderburk et al. 2011). This situation prompted the development of well-executed integrated management strategies based on an understanding of the seasonal distribution of *F. occidentalis* populations by gathering critical information on their biology and ecology in different vegetable crops. Growers now use knowledge-based systems, tailoring control measures to coincide with critical seasonal periods to reduce pest impact based on verified seasonal distribution information (Demirozer et al. 2012).

The economic importance of some pest thrips has meant that there has been extensive research on understanding the biology and ecology of these pests in cropping systems. However, this has meant that there is a poor understanding of all the other species that dwell within a crop, including the interaction between these species assemblages and the agro-ecosystems within which they dwell. Agro-ecological studies documenting the species assemblage within a vegetable agro-ecosystem and understanding the changes of the dynamics of these populations allow us to further develop our knowledge of thrips ecology. With an emphasis on accurate and sustainable pest control, understanding the thrips ecology in vegetable agro-ecosystems is vital for integrated pest management development. This also includes understanding the relationship between important pest species, such as *F. occidentalis*, in crops where they are not considered major pest species. This project aims to improve our understanding of the seasonal composition and population dynamics of thrips species assemblages in four field grown vegetable agro-ecosystems. The results can potentially be used to develop targeted management strategies in the future.

Project overview

This thesis is composed of nine chapters documenting the research methodology, results and conclusions drawn from the PhD project. The second chapter examines the literature on thrips populations in Australian vegetable production, including analysis of the factors that affect the dynamics of thrips in a range of vegetable cropping systems globally. Chapter three describes the general research methods used in the project for collecting empirical data on the thrips populations in French bean, lettuce, tomato and zucchini, and includes the examination of past ecological studies on insect populations in agricultural eco-systems. Chapter four presents research data that establishes the species assemblage within each crop and examines the diversity of these populations between the four crops. Chapter five presents research assessing the effect of crop phenology on the distribution and relative abundance of *F. occidentalis* and *F. schultzei*, between the four vegetable agro-ecosystems. Chapter six assesses the reproductive suitability of each crop, to determine the reproductive host association between thrips and crop. Chapter seven examines the relationship between weather and thrips abundance in the four vegetable agro-ecosystem species assemblages. Chapter eight looks at the spatial distribution characteristics of two dominant species from each crop species assemblage, by investigating the evolution of thrips clusters in relation to crop age and distribution throughout the experimental area as influenced by temperature and rainfall. General discussion and conclusions are drawn in Chapter nine, including recommendations for future research.

Project aim

This study titled ‘The population dynamics of the thrips species assemblage in French bean, lettuce, tomato and zucchini agro-ecosystems’ was designed with the following objectives:

- To identify the thrips species assemblage in field grown French bean, lettuce, tomato and zucchini crops.

- To investigate the temporal distribution of thrips populations among the four vegetable agro-ecosystems on a crop phenological scale.
- To examine the spatial distribution of thrips populations in the four vegetable agro-ecosystems.
- To investigate the reproductive host association of thrips on French bean, lettuce plants, tomato and zucchini.
- To understand the relationship between weather and the relative abundance of thrips in each vegetable agro-ecosystem.

By investigating the relationship between the thrips that exists within each of the four agro-ecosystems, this research aims to contribute to a fundamental understanding of the ecology of Thysanoptera in field grown vegetable agro-ecosystem

Chapter Two: Thrips in vegetable production

Introduction

Of the approximate 5,850 described Thysanoptera species only a small number cause economic damage to plant crops (CSIRO 2015). In Australia, 36 thrips species are recognised as pests of a range of horticultural, ornamental and forestry crops (Oz Thrips 2016). The propensity of some species to colonise, establish and use a wide range of crops for reproduction and food, has meant that the order Thysanoptera has been labelled as a pest order. However, not all thrips species are equal in their ability to use and, potentially, injure vegetable crops, with less than 1% of all known thrips species considered pests (Mound & Teulon 1995). Many thrips are transient, moving in and out of these agro-ecosystems, using the area for shelter until a more suitable host plant becomes available. Some thrips will feed within a crop without causing damage, some are recognised as pollinators and some thrips are considered predators of immature thrips and other small arthropods and their eggs. One or many thrips species can co-exist within an agro-ecosystem without causing injury to the crop. Knowing the thrips species that comprise an assemblage provides crucial information as to the potential for injury to occur. Using this information in relation to the crop, the phenology of the crop, and the season provides much needed pre-planting information to prepare for potential injury, reducing the risk of incursion, and in some cases reducing the need to apply unnecessary chemical insecticide. But most importantly, this information contributes to our understanding of the dynamics of these thrips populations that dwell within field grown vegetable agro-ecosystems, around which there is limited research data available.

As a result of the importance of pest thrips in horticulture, and the need for better control options and prediction strategies to reduce the likelihood of incursion, research has focused largely on key pest species. The result has led to poor documentation of the other, often many, species that are supported in

vegetables, and the interaction between these species assemblages and the crop, particularly as the economic literature only focuses on four pest species (*F. occidentalis*, *Scirtothrips dorsalis* (Hood), *T. palmi* and *T. tabaci*) (Mound & Teulon 1995). As many vegetables are planted as annual mono-cropped systems, they provide an island landscape of available nutrients and shelter for insects, both pest and non-pest species. These production systems are considered agro-ecosystems, an ecosystem that exists within the horticultural landscape, supporting a wide range of arthropod and other communities, which all play a vital role within this complex system from nutrient cyclers, pollinators, predators and pests. The literature shows that there are very few complete records of thrips species assemblages within vegetable agro-ecosystems and almost no understanding of the population dynamics of these assemblages.

From an ecological perspective, our knowledge of the relationship between all thrips species that dwell in a vegetable agro-ecosystem is very poor. There has been a limited determination of thrips species assemblages in many field grown vegetable crops. This also includes a poor understanding of the dynamics of some of the key pest species in a range of vegetable agro-ecosystems. This chapter discusses thrips in vegetable production, including the economic importance of key pest species and examines the importance of identifying a thrips species assemblage and understanding the dynamics of these populations in relation to the vegetable agro-ecosystems and vegetable production.

The Thysanoptera

Thrips are small, vagile and ubiquitous insects found across the globe in tropical, temperate and arctic regions. They belong to the order Thysanoptera (Parker et al. 1995). Their size ranges from 0.5 mm to 14 mm in length with a cylindrical or conical body shape, the head is narrow anteriorly forming a conical mouth opening. Adults and larvae have asymmetrical mouthparts with only one mandible. Thysanoptera are the only insects that have asymmetrical

mouthparts, with two of their three feeding stylets derived from the maxillae and one derived from the left mandible. The mandible on the right side of the body is resorbed during embryogenesis (CSIRO 2015). The antennae are short with six to ten segments and adults may be winged or wingless (Figure 2.1). When present, front and hind wings are slender, with long marginal fringes. The word Thysanoptera is derived from the Greek word “*thysanos*” meaning fringe and “*ptera*” meaning wings, referring to the distinct setae, or fringed hairs on winged thrips. Immature thrips are structurally similar to adults and always wingless.

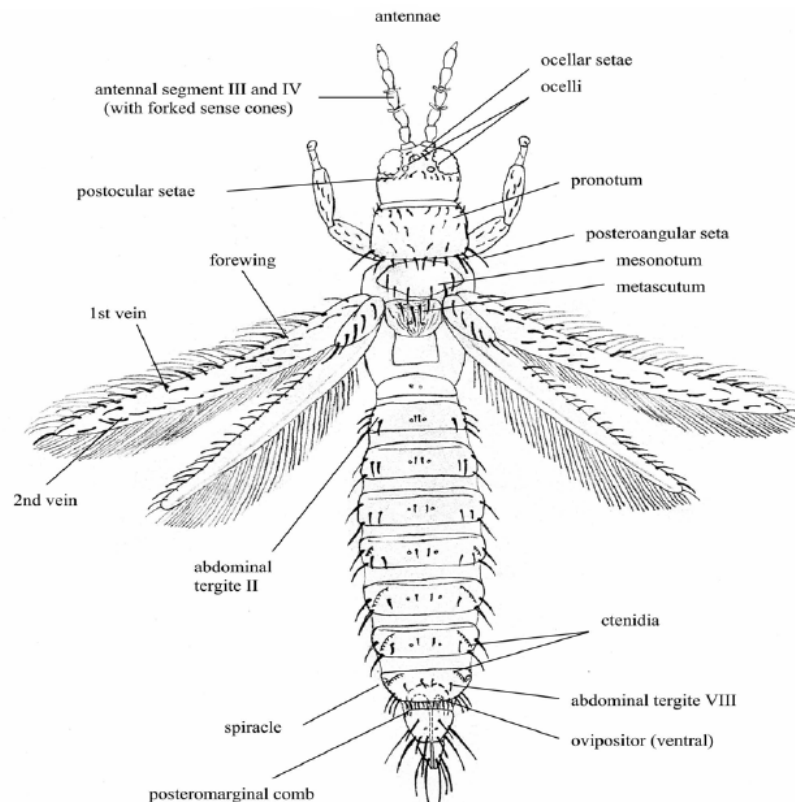


Figure 2.1. General characteristics of Terebrantia (female dorsal view) (Source: ISPM 2010).

Within the order Thysanoptera, there are two sub-orders encompassing nine families, eight in the sub-order Terebrantia and one in Tubulifera; and 750 genera (Mound & Teulon 1995). To date, five of these nine families have been recorded in Australia, four within Terebrantia and the Tubulifera (Mound & Teulon 1995; Oz Thrips 2016) (Table 2.1). Thrips in the sub-order Terebrantia have veins and setae present on the forewing, which is covered in microtrichia, a characteristic that Tubulifera lack. The most distinguishing characteristic between the two sub-orders is the tube-like abdominal segment present in Tubulifera and absent in Terebrantia. Thrips in the sub-order Terebrantia cause the most extensive economic damage to vegetable crops (Kirk 2002).

Table 2.1 Thysanoptera family classification.

Sub-order	Family	Sub-family	Genera	Species
Terebrantia	Merothripidae*		3	15
	Melanothripidae*		4	65
	Aeolothripidae*		23	190
	Fauriellidae		4	5
	Adiheterothripidae		3	6
	Heterothripidae		4	70
	Thripidae*	Panchaetothripinae	38	130
		Dendrothripinae	16	100
		Sericothripinae	3	140
		Thripinae	230	1600
	Uzelothripidae*		1	1
Tubulifera	Phlaeothripinae*	Plaeothripinae	370	2800
		Idolothripinae	80	700

(Source: CSIRO 2015)

*Present in Australia

Of all the known species, very few are considered serious pests, with many species feeding on fungi, dead branches and found in leaf litter (Tree & Walter 2012). Of the total described species, over half (approximately 50

species) are fungal feeders (Morse & Hoddle 2006). In horticulture, the challenge with managing thrips is correctly identifying those species that are pests of a particular crop. The identification process is difficult due to the large number of species that can dwell in a monoculture at any given time and the minute size of thrips (many of which are around 1 mm long).

Thrips biology

Thrips progress through an intermediate metamorphic lifecycle. There is much debate around whether they are holometabolous or hemimetabolous (Arèvalo-Rodriguez 2006). Hemimetabolic insects undergo an incomplete or gradual metamorphosis, where the insect emerges from the egg generally resembling the form of the adult and progressively develops through to maturity. Homometabolic insects undergo a complete metamorphosis lifecycle, where there is a reorganisation of the body in the single pupal stage from larva to adult. However, Thysanoptera have two or three pupal stages, despite going through two larval stages in which the larva resemble the adults. The first two instars are wingless externally, with the wings developing internally, and are often referred to as larvae, resembling holometabolous metamorphosis (Triplehorn & Johnson 2005). Thrips go through two more distinct non-feeding immature stages. The first stage is called the propupa, which show vestigial wings (with the exception of Tubulifera). This is followed by a true pupa stage, which morphologically resembles the adults. Compared to adults, the pupa are inactive and immobile, with two vestigial wings, and fewer antennal segments. Adults are macropterous with well-formed wings and six to nine antennal segments (Moritz 1997).

Reproduction

The lifecycle of the eight Terebrantian families are similar, consisting of an egg, two active feeding larval instars, the propupa and pupa, and adult (Reitz et al. 2011) (Figure 2.2). Females use a saw-like ovipositor to make an incision into the plant tissue or flower, and the egg is embedded in the incision (Lewis 1973). To avoid the eggs being crushed by the expanding cells of the plant,

thrips prefer to lay their eggs in mature non-expanding tissue (Terry 1997). Development progresses through two larval stages (instars). The first larval stage is short, lasting between two and four days. The second instar transforms into a pro-pupal non-feeding stage, which can last several hours or a few days before progressing to the pupal stage. Some species have an extended metamorphosis in the pupal stages, where the pupa rests within a silken cocoon in the soil (CSIRO 2015). Pupation can take place in the soil or on the plant. Female Tubulifera have no ovipositor and eggs are deposited onto the plant surface. The adult is the only migratory stage, colonising other habitats through various modes of dispersal such as the wind, walking and hitchhiking. This sub-order includes a second pupal stage in the lifecycle (Mound & Gillespie 1997).

Thrips generally have a short life cycle and high reproductive capacity (Lewis 1997). However, the length of the lifecycle is dependent on temperature, food quality and food source (Mound & Gillespie 1997). In warm conditions around 30°C, the lifecycle of *F. occidentalis* can be completed in as little as 10 to 12 days; at 20°C the lifecycle takes around 19 days (Duff 2012; Pearsall 2002; Reitz 2008). Tsai et al. (1995) reported that mean generation time of *T. palmi* reared on winter melon, *Cucumis sativus* L., was 80.2 days at 15°C and 20.5 days at 30°C, further highlighting the temperature lifecycle dependence. Parthenogenesis is also common in some species of thrips, where fertilisation is not needed for females to reproduce (Kerruish & Unger 2003). Mating does not result in fertilisation of all the eggs; unfertilised eggs produce males while fertilised eggs produce females (Kumar et al. 2013). Sex ratio is in favour of female progeny.

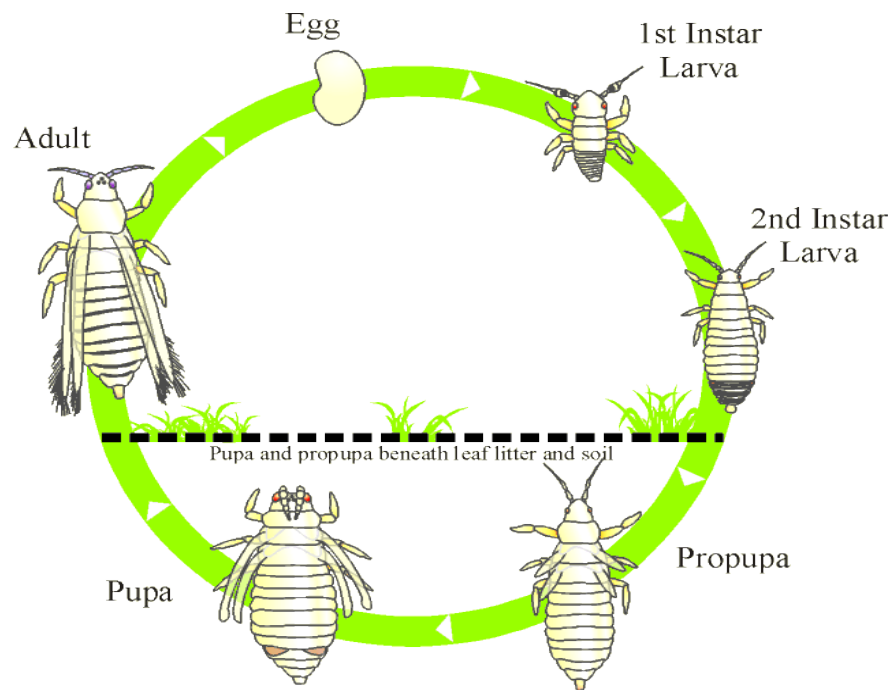


Figure 2.2 Terebrantia lifecycle (Source: Hoddle 2011).

Feeding

With the exception of the non-feeding pre-pupal stage, all other phytophagous thrips stages feed on various parts of the plant. Members of both sub-orders probe vegetation with their stylets, using their piercing-sucking mouthparts to pierce individual cells, emptying the contents into the feeding channel through which the liquid contents are sucked up (van Lenteren & Loomans 1998). Some species of thrips also feed on exposed nectar and water and some feed on fungal tissue such as spores and hyphae. Some thrips are facultative predators of small insects such as mites and other thrips, including their eggs, larva, pupa and secretions (Kirk 1995; Mound & Teulon 1995). Predatory species have been observed reducing pest thrips numbers in various cropping systems. High densities of predatory species *Haplothrips victoriensis* (Bagnall) were recorded in strawberry crops, along with low *F. occidentalis* numbers and low damage. Follow up laboratory trials confirmed that *H. victoriensis* was predating *F. occidentalis*. Some polyphagous pest species will predate small arthropods, for example *F. occidentalis* has been observed predating spider mite eggs in cotton crops (Trichilo & Leigh 1986).

Thrips in Australia

There are currently 826 described species of thrips in Australia, 500 are members of the sub-order Tubulifera sub-order, and the remaining 326 members are Terebrantia (ABRS 2012). It is thought that this figure represents approximately 60% of the Thysanoptera taxa in Australia, with many areas of the continent not yet thoroughly investigated, including Tasmania, Western Australia and the tropical north (Mound & Tree 2011). Thrips species differ in their ability to use a plant and can be divided into fungivores, phytophagous, predacious and omnivores. Some are associated with various plant taxa or specific resources such as flowers, leaf tissue and fungi. Some are predators and some are also thought to be important pollinators. In Australia, fungal feeders are all members of the Phlaeothripidae family, feeding on fungi on dead twigs and branches, and in the leaf litter and detritus on the ground (Tree & Walter 2012). Thrips associated with pasture grasses in Southern Australia are European immigrants, such as *Aptinothrips*, *Chirothrips* and *Limothrips* species, while in the north many species are shared with South East Asia. Some species are associated with grasses, Poaceae, such as *Bamboosiella* and *Podothrips*. Some thrips are obligate predators of mites and scale insects such as *Scolothrips* spp. and *Aleurodothrips fascipennies*. Others are facultative predators, such as some species of Aeolothripidae that feed on thrips larvae, mites and eggs, scale insects and whitefly nymphs, as well as feeding on plant tissue. Many thrips are highly anthophilic, associated with flowering plants, using the pollen and nectar (Tsai et al. 1995). Some highly mobile thrips species are thought to be important pollinators of plants such as *Oxythrips australopalmae* (Mound & Tree) in palms *Normanbyia* and *Archontophoenix* in northern Australia (Mound & Tree 2011).

Pest thrips

In Australia, 36 of the described species are classed as pestiferous, all of which are members of the sub-order Terebrantia (Table 2.2). The majority of these species are polyphagous, feeding and breeding across a wide range of plant taxa, and using a range of resources including plant tissues, fruiting bodies and flowers. Very few monophagous species are pests, with only a few examples known, such as *Sciothrips cardamomi* (Ramakrishna), which are a common pest of cardamom (Mound 2005). A thrips species is classified as a pest if the damage caused to the crop sufficiently reduces the yield or quality by an amount unredeemable by the grower (Dent 2000). A crop can sustain a small amount of insect damage, where yield loss is minimal and no control is required. However, all cropping systems have a threshold, a level at which a control needs to be administered to prevent the population from increasing further and causing economic loss. Before the 1970's little time was invested in managing Thysanoptera, as thrips were not considered a threat to plant production (Vierbergen 1995). The increase in plant exchange internationally provided the opportunity for widespread artificial dispersal of many species worldwide and led to the recognition of some species as important agricultural pests (Lewis 1973).

Table 2.2 Pest thrips in Australia.

Pest Species	Host Crop
<i>Anaphothrips obscurus</i> (Müller)	Poaceae
<i>A. sudanensis</i> (Trybom)	Poaceae
<i>Caliothrips fasciatus</i> (Pergande)	Fabaceae (intercepted at quarantine)
<i>Chaetanaphothrips leeuweni</i> (Karny)	Musaceae – <i>Musa</i> sp.
<i>C. orchedii</i> (Moulton)	Orchidaceae & Rutaceae
<i>C. signipennis</i> (Bagnall)	Orchidaceae & Musaceae (<i>Musa</i> sp.)
<i>Dichromothrips corbetti</i> (Priesner)	Orchidaceae
<i>F. occidentalis</i> (Pergande)	Fruit, vegetable & ornamental crops (> 250 species)
<i>F. schultzei</i> (Trybom)	Solanaceae, Fabaceae, Cucurbitaceae, <i>Allium</i> sp., cotton & ornamental crops
<i>F. williamsi</i> (Hood)	<i>Zea mays</i> , <i>Saccharum</i> sp
<i>Heliothrips haemorrhoidalis</i> (Bouché)	Tea, <i>Pinus</i> sp. & ferns
<i>H. errans</i> (Williams)	<i>Dendrobium</i> , <i>Laelia</i> (Orchidaceae),
<i>Hercinothrips bicinctus</i> (Bagnall)	Banana
<i>H. femoralis</i> (Reuter)	Banana, beetroot, celery, eggplant, tomato & pineapple
<i>Leucothrips nigripennis</i> (Reuter)	Ferns – <i>Adiantum</i> sp., <i>Davallia</i> sp., <i>Pteris cretica</i> , <i>P. argyraea</i> & <i>Hypolepsis rugulosa</i>
<i>Limothrips cerealium</i> (Haliday)	Poaceae – <i>Hordeum</i> & <i>Triticum</i>
<i>Megalurothrips usitatus</i> * (Bagnall)	Fabaceae – green beans
<i>Microcephalothrips abdominalis</i> (Crawford DL)	Asteraceae – sunflowers
<i>Neohydatothrips samayunkur</i> (Kudo)	Marigolds
<i>Odontothripsella australis</i> * (Bagnall)	Fabaceae
<i>Parthenothrips dracaenae</i> (Heeger)	Various species, particularly <i>Kentia</i> palm. Recorded on. <i>Ficus</i> sp (Moraceae) <i>Emilia sonchifolia</i> (Asteraceae) & <i>Adiantum formosum</i>
<i>Pezothrips kellyanus</i> (Bagnall)	Rutaceae
<i>Pseudodendrothrips mori</i> (Niwa)	<i>Morus alba</i> trees used for silkworm production
<i>Scirtothrips aurantii</i> (Faure)	Rutaceae & mango
<i>S. dorsalis</i> * (Hood)	Solanaceae, Fabaceae and Cucurbitaceae
<i>Stencchaethrips biformis</i> (Bagnall)	Poaceae - serious pest of rice in Asia, minor pest of sugarcane
<i>T. florum</i> (Schmutz)	Gardenia
<i>T. hawaiiensis</i> * (Morgan)	Plants in the Leguminoase & Convolvulaceae families
<i>T. imaginis</i> * (Bagnall)	Stone and pome fruit
<i>T. nigropilosus</i> (Uzel)	<i>Achillea</i> , <i>Chrysanthemum</i> , <i>Lactuca</i> & <i>Tanacetum</i> sp.
<i>T. novocaledonensis</i> (Bianchi)	Herbs & shrubs
<i>T. palmi</i> (Karny)	Cucurbitaceae, Solanaceae & orchids
<i>T. parvispinus</i> (Karny)	Gardinea
<i>T. simplex</i> (Morison)	Gladiolus
<i>T. tabaci</i> (Lindeman)	<i>Allium</i> sp., cereals & potato

* Native to Australia (Source: Ausveg 2015; Oz Thrips 2016)

Due to the damage caused by this small number of pest species, Thysanoptera have gained notoriety as a pest order amongst horticulturalists. Nine of the top ten economic pest species are members of the family Thripidae, and the three most diverse and advanced genera are *Frankliniella*, *Scirtothrips* and *Thrips* (Lewis 1973; Mound & Teulon 1995; Reitz et al. 2011). In Australia, *F. occidentalis* (Western flower thrips), *F. schultzei* (Tomato thrips), *T. palmi* (Melon thrips) and *T. tabaci* (Onion thrips) are important economic pests of vegetable crops (CSIRO 2015).

Thrips damage

Through a combination of feeding and oviposition, pest thrips cause distortion and stunting, reduce crop yields and damage aesthetic values of fruiting and ornamental crops (Childers & Achor 1995). In vegetables, injury can appear as leaf necrosis, growth deformation, gall formation, and as damage to young leaves, buds, flowers, fruits, bulbs and rhizomes (van Lenteren & Loomans 1998). Concentrated feeding by adults and larvae on leaves results in the formation of silvery patches that turn brown as the cell tissues dry up beneath the epidermis. This reduces photosynthesis and induces premature leaf fall (van Lenteren & Loomans 1998). Feeding injury to floral buds, open flowers or fruit of certain plants can lead to abortion of fruit (Kirk 1995). Kirk (1987) estimated that 2 to 7% of a flower's pollen could be destroyed by a single feeding thrips, reducing pollen viability and crop yield. The most serious of opportunistic thrips are those that are polyphagous, combining leaf and flower feeding. The quality of many fruiting vegetables is also damaged by oviposition of Terebrantia thrips, which elicit a physiological wound response that creates spots on developing fruit that continue to expand as the fruit matures (Nault et al. 2003). These oviposition spots lead to the rejection of export quality produce such as bananas, peas and nectarines (Reitz et al. 2011). Feeding is the primary source of damage, with oviposition the secondary source.

Some species are also vectors of important plant viruses, such as the Tospovirus Tomato Spotted Wilt Virus (TSWV). Globally, tospoviruses are

amongst the most formidable of plant pathogens, causing severe economic losses in a wide range of cultivated vegetable systems (CRCTPP 2007). The three tospoviruses found in Australian crops are tomato spotted wilt virus (TSWV), capsicum chlorosis virus (CaCV) and iris yellow spot virus (IYSV) (CRCTPP 2007). Only first or early second instar larvae thrips feeding on infected plants can acquire the virus. More mature stages of thrips can acquire the virus, but the virus cannot complete the lifecycle within the insect, and therefore cannot be transmitted. A larva can acquire the virus in less than 30 minutes of feeding on an infected plant. Once the larvae acquire the virus, it circulates and multiplies within the insect, which is then transmitted to other plants once the thrips reach maturity, when the adult pierces and sucks the contents of the plants cells. Thrips will remain infected for life, but do not pass the virus onto their offspring through the egg. *Frankliniella occidentalis*, *F. schultzei*, *T. palmi* and *T. tabaci* transmit these viruses (CRCTPP 2007; Funderburk et al. 2011). Thrips spread the virus through primary and secondary infections. Thrips larvae feed on infected plants and acquire the virus (primary) and then when they develop into adults spread the virus by feeding on uninfected plants (secondary) (Funderburk et al. 2011).

Thrips control in vegetable production

Thrips cost growers billions of dollars worldwide in control measures and lost productivity (Ullman et al. 1997). The most effective method of control is to develop integrated pest management (IPM) programs around critical information such as seasonal population trends.

Chemical control

Unlike other management regimes for pests of economic importance, such as the diamondback moth, *Plutella xylostella* (Linnaeus), thrips do not have a widely available array of biological and cultural control techniques. Therefore chemical control is one of the most common tools. Chemical control is effective; however, it can be difficult to apply effectively. A large proportion

of the immature stages escape treatment as the eggs and pupae are concealed during most of their development (van Lenteren & Loomans 1998). First and second instar larvae are usually deep within the developing buds and flowers, and eggs are imbedded in the tissue, protecting these stages from sprays. Many species pupate in the soil and leaf litter protecting them from insecticides.

Many growers apply insecticides to reduce the risk of damage to plants and fruit (Nault et al. 2003). Plants are regularly treated throughout the growing season, with the frequency of applications increasing following the detection of large populations in the crop (Lewis 1997). Often spray decisions are based on the presence of thrips observed in a crop rather than on the relative abundance of pest species known to be responsible for crop injury. In many cases insecticides are used as a preventative measure, applied to ensure damage does not occur, a method that exacerbates insecticide resistance. Some thrips species have readily acquired resistance to insecticides as a result of poor application of insecticides such as repeated sprays. For example, in the United States during the 1970's as the western flower thrips pest status began to rise, successive sprays were used to target and reduce the pest populations in crops. Initial knockdown was successful, however, shortly after the thrips developed resistance to all major classes of insecticides available at the time, including pyrethroids, carbamates, organophosphates and abamectins (Reitz & Funderburk 2012). In Australia, *F. occidentalis* showed resistance to these insecticides shortly after its arrival in 1993 (Gao et al. 2012). Resistance has also been observed in *T. palmi* and *T. tabaci* populations (Cannon et al. 2007). Insecticide resistance has led to limited availability of chemical options available for use by growers in combating pest thrips.

Biological control

Biological control strategies rely on beneficial organisms such as parasites, predators and pathogens to control insect pests. A number of thrips specific hymenopteran parasitoids attack thrips eggs (Mymaridae: *Megaphragma* sp.) and larvae (Eulophidae: *Ceranisus* sp.) (Loomans 2006). Most enemies that attack thrips are generalist predators that occur naturally

within the agro-ecosystem (Ananthakrishnan 1993). Predatory bugs in the genus *Orius* have successfully reduced thrips in field settings. In Japan and Florida, natural populations of *Orius* spp. have been documented colonising capsicum and eggplant fields, suppressing thrips and halting the spread of Tospoviruses (Ramachandran et al. 2001; Reitz et al. 2002; Reitz et al. 2011). While these examples highlight the suppressive capacity of thrips predators, control strategies based solely on biological control agents are uncommon, and convincing field data documenting the significant reduction in thrips pest densities in field grown vegetable crops by biological control agents is scarce (Morse & Hoddle 2006).

In Australia, there are a number of commercially available thrips biological control agents such as the predatory mite *Typhlodromips montdorensis* (Schica), which feeds on a wide range of thrips larvae. This species has proven successful in reducing *F. occidentalis*, *F. schultzei* and *T. tabaci* in protected cropping systems on ornamentals, cucumbers and tomatoes (Steiner et al. 2003). However, in open field production the effectiveness of augmentative biological control agents can be reduced due to the complexity of management and influence of the many other factors in field agro-ecosystem such as broad-spectrum insecticides, low humidity and poor canopy cover. Growers are hesitant to use market available biological control agents in field settings due to the difficulty in providing a suitable environment, the expense of the product and the potential for failure. Release of biological control agents also requires good seasonal pest density knowledge to target pests at key periods (prior to population increase).

Cultural control

Cultural controls are techniques that manipulate and change the environment to disadvantage pest population growth (Morse & Hoddle 2006). This can include the use of reflective mulches and ground cover to disrupt migration and breeding of thrips, reducing the use of broad-spectrum sprays and general hygiene around cropping areas. Ultraviolet reflective mulches suppress thrips populations by disrupting their host-finding abilities (Reitz et

al. 2002). However, the high cost of these materials, and the potential delay in crop maturity, means that reflective mulches are not economically viable for all crops (Reitz et al. 2011). Ground covers have been successful in promoting populations of phytoseiid mites (thrips predators) in citrus groves, and straw mulch has been used to reduce *T. tabaci* in onion crops by making the movement of pro-pupae into the soil more difficult (Hoddle et al. 2002). Sticky traps have been used to reduce thrips in crop, with studies demonstrating a reduction of *T. palmi* in capsicum and eggplant (Kawai 1990), and *Frankliniella intonsa* (Trybom) in strawberry and capsicum as a result (Lim & Mainali 2009; Lim et al 2013). Sampson and Kirk (2013) also demonstrated that blue sticky traps reduce *F. occidentalis* adults in strawberry flowers and reduce bronzing of fruit in semi-protected cropping systems. However, most of this evidence is based on protected or semi-protected systems. The use of sexual-aggregation pheromone lures has been explored in conjunction with sticky traps to disrupt the mating activity of pest thrips. However, more research is needed in field based agro-ecosystems before this can be implemented as an effective control option for thrips (Sampson & Kirk 2013).

Trap cropping is another option for thrips population control in crop. By planting the perimeter of the main crop with a more attractive crop, such as basil, onion, garlic or marigold, the thrips will move toward the trap crop, and the grower can then spray or remove the attractant and the pest species (PAN Germany 2015).

Thrips population dynamics

Understanding the population dynamics of thrips populations provides information on the fluctuation in diversity and abundance of species within and throughout a crop based on the crop type, plant phenology and weather. There are few agro-ecological studies investigating the effect of such factors on thrips species assemblages in vegetables. However, there has been extensive research on the dynamics of key pest species such as *F. occidentalis* and *T. tabaci* in cropping systems such as tomato, capsicum and blueberries. Research on the

interaction between thrips and a vegetable agro-ecosystem are valuable for expanding our understanding of the ecology of Thysanoptera, and are critical for the development of tailored IPM programs. What is also unknown is the diversity of the thrips species assemblage in vegetable agro-ecosystems that are not pests of economic importance. Including an understanding of the dynamics of key pest species within agro-ecosystems that they are not considered to cause major economic damage.

Crop association in vegetables

The complexities of host association between crop and thrips are poorly understood in horticultural agro-ecosystems, particularly the lesser studied species (Hensen et al. 2003). Thrips species differ in their habitat selection, using various crops for feeding, oviposition, shelter from predation or simply subsisting on a plant until a more suitable host becomes available. More than 95% of Terebrantia are associated with green plants (Arèvelo-Rodriguez 2006). While there are many thrips host records, many of these are just lists of species based on where the thrips are found with no solid evidence of the relationship between the species and the crop (Milne et al. 1996a; Mound 2005). In a review of host records for *F. schultzei*, Milne et al. (1996a) found that many of these records were based on places that the thrips had been found, and not in places where they were breeding or feeding, making most of these records arbitrary lists. This also means that the definition of a host plant very is very confusing (Mound 2005). While the majority of economic pest species are polyphagous, some species show a preference for a few specific host plants on which they can feed, reproduce and survive (Mound 2004). Various species of thrips are associated with a number of plant families. For example, *F. occidentalis* and *T. palmi* attack a wide range of crops, whereas, *F. schultzei* attacks a more limited range (Table 2.3). However, there is a large gap in information on what constitutes a true host plant for many thrips species found in vegetable cropping systems (Teulon et al. 1994; Walter & Benfield 1994).

A host plant is a species that provides an environment adequate for reproduction or feeding, ensuring the fitness of the thrips species (Froud et al.

2001; Manners et al. 2010). Plants that provide an environment on which reproduction and feeding occurs and where both adult and larval instars are present in relatively high numbers are generally classed as a primary host (Walter & Benfield 1994). In vegetable production breeding hosts may be one of the most important hosts as it is these crops that promote population growth within a system, followed by feeding by the immobile immature thrips (Northfield et al. 2008). Plants that provide only a subset of these features and are used less regularly, and in relatively low numbers, are secondary or incidental hosts (Walter & Benfield 1994). Thrips will often alight and feed on plants that they cannot reproduce on, using the plant temporarily (temporal host) until a more suitable host is present. For example, whilst *F. occidentalis* is a pest of tomato crops, the plant is a poor reproductive host for this species (Brodbeck et al. 2001; Reitz 2002). Larvae of *T. palmi* feeding on tomato and strawberry plants cannot pupate, and adults feeding on capsicum leaves produce fewer eggs than those feeding on the flowers (Kawai 1990; Tsai et al. 1995). *Frankliniella schultzei* populations perform better when feeding on flower tissues than on leaf tissues of tomato plants (Milne et al. 1996b). The adults of *Thrips* and *Frankliniella* species feed on the flowers of a wide range of plants, including those that are not suitable reproductive hosts, purely feeding on the pollen that provides nutrients for egg production (Tsai et al. 1995). This relationship will influence thrips reproduction, the likelihood of feeding and oviposition damage occurring, and pre-determine the species present in the crop. Understanding these relationships can allow more informed strategies to be employed against pest incursion, and determine if they are required at all.

Table 2.3 Pest-Crop association in Australia.

Species	Main crops affected	Type of injury
<i>F. occidentali</i>	Capsicum, eggplant, tomato, bean, pea, lettuce, celery, potato, parsley, beetroot, spinach, choy sum and bitter melon	Damage to flowers and developing fruit. Tospovirus vector
<i>F. schultzei</i>	Tomato, celery & lettuce	Damage to leaves and immature fruit. Tospovirus vector
<i>M. usitatus</i>	Fabaceae crops – green bean	Flower feeding causing twisting and curling of pods.
<i>T. imaginis</i>	Cucurbit vegetables, lettuce & green bean	Damage to flowers and young fruit.
<i>T. palmi</i>	Cucurbitaceae & Solanceae vegetables	Damage to leaves, growing tips, fruit scarring and fruit drop. Tospovirus vector.
<i>T. tabaci</i>	Garlic, onion, capsicum, celery, pea, Hairy melon, choy sum, bittermelon, Chinese broccoli, long melon, snake bean and cabbage	Damage to leaves. Tospovirus vector

(Source: Ausveg 2015)

Crop phenology

Phenological synchrony between plants and insects sees the diversity and abundance of an insect population fluctuate with the growth of a plant. Species-specific phenological shifts will see individual insect populations increase or decrease dependant on the crop, or ecosystems, will see a change in the diversity of insects within the system. Understanding species and crop phenology relationships can allow the establishment and population diversity within an ecosystem. This can provide insight into the associated timings of species presence and abundance within an assemblage. For example, an assessment of phenology synchrony between the Sinai Baton Blue butterflies, *Pseudophilotes sinaicus* (Nakamura), that feeds exclusively on Sinai Thyme, *Thymus decussatus* B., found flight times were relative to peak flowering times (Thompson & Gilbert 2014). The species-specific phenological shift in bee

activity in apple orchards based on abundance demonstrated that as apple bloom increased, so too did the diversity in bee species present, which resulted in higher rates of pollination (Földesi et al. 2016). Such information provides insight into the movement, establishment and colonisation of insect populations in relation to the phenology of a specific habitat.

Understanding of phenological dependence can also allow for targeted control applications at periods of population growth. For example, in a study of thrips populations in Kenyan French bean crops, *F. occidentalis* and *M. sjostedti* (Trybom) were found to simultaneously inhabit the crop (Kasina et al. 2009). The two species were found to be spatially separated within the crop, with *F. occidentalis* colonising early blooms, whilst *M. sjostedti* inhabited the mature flowers. In a similar study, Nyasina et al. (2013) determined thrips would colonise French bean crops at the two to three leaf stage, with *F. occidentalis* abundance increasing exponentially from budding to podding and flowering stages. Using this information larvacide was applied at pre-budding to target *F. occidentalis* and *M. sjostedti* at pre-flowering to reduce the likelihood of migration to flowers. Timing of control can be critical to ensure maximum success and subsequently decrease the need for further chemical application, which can be achieved in understanding the movement patterns into a crop. As many thrips found in vegetables are anthophilic, therefore increase in populations can coincide with the flowering stage (reproductive phase) of the crop. However, understanding the timing of thrips colonisation at the vegetative phase of the crop is critical to estimate the increase in density as the crop matures, and should therefore not be ignored.

By understanding the change in species diversity and abundance as a result of a response to plant growth, we can begin to understand the relationship between species assemblage diversity and key phenological changes in a crop. Phenological change can be used as a key indicator of insect species diversity and abundance, providing insight into population dynamics of thrips species assemblage within an agro-ecosystem.

Spatial distribution

Spatio-temporal studies of insect populations in vegetables aim to understand the heterogeneity of populations to determine the patterns of distribution and abundance within a crop (Vinatier et al. 2011). The spatial variation of insect populations that exist within agro-ecosystems will fluctuate along a temporal scale, such as season and crop age (van Helden 2010). How different species distribute themselves throughout a crop is a behavioural response of the individual species to the crop and the season and is almost never uniform. In vegetable agro-ecosystems, changing spatial patterns of a species within a crop are likely to reflect the manner in which the insect locates the crop and subsequently redistribute themselves within it (Ferguson et al. 1999). For example, population aggregation toward one area of a crop can be associated with the position of initial immigration. Ferguson et al. (1999) found that wind direction during the period of immigration of the cabbage seed pod weevil, *Ceutorynchus assimilis* (Paykull), was likely to have contributed to large infestations and aggregation in the southern half of an oilseed rape crop. Accurate description and understanding of the relative movements of thrips into crops and subsequent distribution within a crop is a prerequisite for understanding the influence of crop and season on the distribution of thrips species in vegetable agro-ecosystems. This is particularly the case as the spatial variation of populations will change along a temporal scale, such as season and crop age (van Helden 2010). By characterising these patterns, we can begin to understand the growth, in size, of thrips populations across the physical area of an agro-ecosystem.

Seasonal weather cycles

It is fundamentally important to document the seasonal patterns of thrips populations in a cropping system to identify the annual cycles of a species assemblage; identifying the periodic increase and decrease of populations and presence and absence of species (Northfield et al. 2008). To

determine the seasonal change in populations, the impact of weather events and the annual cycles of weather needs to be examined. The annual, seasonal and diurnal changes in rainfall, relative humidity and temperature constitute the weather (Varley et al. 1974). Rainfall, temperature, relative humidity and wind are known to affect the physiology and biology of thrips populations (Ananthakrishnan 1993; Kirk 1997; Varley et al. 1974). A field grown vegetable crop is in a state of constant flux, with the agro-ecosystem changing along with the seasonality of the environment. Vegetable crops augment population increases, by providing habitats for insect population growth that a varied range of species will use dependant on the seasonal weather cycles (Collinge 2000). Variation in the diversity and abundance of thrips will change based on the impact of key weather events and these cycles. From an ecological perspective, examining the relationship between variations in these weather variables (low temperature, high humidity) provide insight into key weather events that act as catalysts for increases in thrips abundance and shifts in the diversity of a species assemblage. High temperatures and low rainfall have been associated with increased thrips populations, while relative low humidity and high rainfall reduce abundance (Hamdy & Salem 1994). At higher temperatures, thrips are more efficient, feeding, developing and reproducing at a greater rate, increasing the intrinsic rate of natural increase in populations (Murai 2000).

Examining the change in seasonal species assemblage in relation to weather events (for example, high rainfall period or low temperatures), can determine the shift in species thrips diversity. In the vegetable-growing region surrounding Bundaberg, southeast Queensland, Walsh et al. (2012) conducted a study to measure the seasonal occurrence of thrips species inhabiting capsicum and chilli crops over a two-year period. Six species were identified in both crops including, *F. occidentalis*, *F. schultzei*, *P. achaetus*, *T. imaginis*, *T. palmi* and *T. tabaci*. *Pseudanaphothrips achaetus* is a native non-pest species, and *T. imaginis* causes no known damage to either chilli or capsicum crops. The remaining species are considered pests, and were found to inhabit separate seasonal windows. *Thrips palmi* was predominant in the cooler months of

autumn and early winter (March to July) and *F. occidentalis*, *F. schultzei* and *T. tabaci* in late winter and spring (August to November) as average daily temperature and rainfall events started to increase.

The greatest contribution of seasonal population studies is the knowledge they provide on the workings of a species assemblage within a crop (Strayer et al. 1986). Examining how a major weather event will likely affect the diversity and abundance of a species assemblage in a crop provides information on the change in dynamics. Investigating the seasonal cycles on species diversity also allows a more in-depth understanding of how species assemblages shift and fluctuate over time. This provides a greater understanding of the relationship of how one or more thrips species populations will shift with the progression of a season in an agro-ecosystem.

Summary

The speed at which thrips can establish themselves within a crop and the propensity of a few key pest species to cause vast damage to a vegetable production systems has seen Thysanoptera labelled as a pest order. This has led to research focused on understanding the population dynamics of pest species to better control, target and minimise the damage caused in vegetable crop production. As a result of this research we have developed an in depth understanding of the ecology and biology of a few key pest species in specific vegetable cropping systems and been able to develop effective targeted IPM programs built around the seasonal timing of specific pests. However, due to the importance of understanding these key pests, there is now a large gap in our understanding of the population dynamics of all other thrips species (pest and non-pest species), which exist within these agro-ecosystem. For many vegetable agro-systems there is no record of any other thrips species that exist within these crops, and no understanding of the population dynamics of these species. Determining the thrips species assemblage in a vegetable agro-ecosystem and examining the interaction between these thrips and the crop,

contributes to our understanding of the Thysanoptera and the relationship of this insect order with the vegetable agro-ecosystem. Understanding the population dynamics of the species that exists within these assemblages can also contribute to the effectiveness of current IPM programs in vegetables.

Chapter Three: General research methodology

Introduction

Field surveys are essential for gathering robust data on the dynamics of insect populations in relation to the environment (Rolečková et al. 2007). Such studies provide data that can be used to further our understanding of the patterns of change of insect populations within various environments. For many vegetable crops, the diversity of thrips species or the species assemblage have not been determined and as a consequence little understanding exists as to how and why these assemblages fluctuate in relation to the crop and environment. Through comprehensive field surveys of thrips, we can identify the species assemblage that occur and begin to understand the factors of casual change in species diversity and abundance in a range of vegetable agro-ecosystems.

This chapter describes the general materials and methods used in this study to conduct field surveys in French bean, lettuce, tomato and zucchini crops.

Rationale for field surveys

The first step to understanding the seasonal composition and abundance of thrips assemblages in vegetable agro-ecosystems was to identify the thrips species that exist within a species assemblage in French bean, lettuce, tomato and zucchini crops. This then allowed for the examination of how a crop, the phenology of the crop, the season, and weather influenced the changes in composition and abundance of the species assemblage. The purpose of this study was to better understand the relationship between thrips species

diversity in various vegetable agro-ecosystems. To achieve this, a series of field surveys were designed to capture as much information on the aforementioned factors as possible. The methods used in this study were based on studies conducted by Kasina et al. (2009), Nyasani et al. (2013) and Walsh et al. (2012).

These three studies assessed the composition and distribution of thrips populations in various field grown vegetables, with the objective of understanding the population dynamics of thrips in agro-ecosystems. Kasina et al. (2009) assessed within-plant distribution and population dynamics of flower thrips infesting French beans in Kenya. The experimental approach involved weekly collections of flower samples and the use of sticky traps to study the change in populations in the crop as affected by the weather, the age of the plant and the progression of the season. Sampling was conducted in two seasonal plantings of six replicate bean plots (3 x 10 m). Season one occurred in the early wet season (January) and the second during the dry season of the same year (July). The survey found that two species of thrips were colonising the crop, *M. sjostedti* and *F. occidentalis*. The former colonised mature flowers, with the latter using the early flowering period. In a similar study, the seasonal abundance of *F. occidentalis* in Kenyan French beans was observed over three growing cycles from January to December 2009 (Nyasani et al. 2013). Results found that *F. occidentalis* density increased as the year progressed, with lower numbers in the early season, and higher numbers later in the year. In the Bundaberg district of South East Queensland, Walsh et al. (2012) recorded six species of thrips in a seasonal abundance survey of thrips in capsicum and chilli crops in two plantings between July 2002 and June 2003. There was a clear definition in the seasonal data with *T. palmi* the most dominant species in the cooler autumnal months (March to July), and *F. occidentalis* the most abundant in spring (August to November).

These three studies used field-based surveys to identify the species of thrips present in relation to the crop; determine the period of species establishment in relation to crop phenology, and understand the fluctuation in species as influenced by the season and weather. The knowledge gained from these studies is essential for establishing the patterns of incursion and

distribution of establishment in a crop. Studies of this nature identify the pest and non-pest thrips species and examine their relationship with the crop, increasing our understanding of the thrips ecology in vegetable agro-ecosystems. This information also allows for preparedness of pest incursion.

The limitation of these surveys, however, was time. With data collected over one or two planting seasons, and only providing a brief insight into the population dynamics of these species. In this study, the aim was to capture more information and provide a robust data set to develop a more comprehensive understanding of the fluctuation in thrips populations. Therefore, this study was conducted multiple plantings that were surveyed over six seasons (summer and autumn).

Project aims

The aim of this project was to study the seasonal composition and abundance of thrips species assemblages in French bean, lettuce, tomato and zucchini crops at the Gatton Research Facility (GRF), Lockyer Valley, South East Queensland.

This was achieved by:

- Identifying the thrips species that comprise the species assemblage in French bean, lettuce, tomato and zucchini crops
- Documenting the period of establishment and decline of thrips populations in each crop
- Monitoring the changes in thrips species temporal abundance between the four vegetable crops, in relation to plant phenology (crop age), season and weather (temperature, relative humidity and rainfall).
- Monitoring the changes in thrips species spatial abundance throughout the experimental area, in relation to plant phenology (crop age), season and weather (temperature and rainfall) for each of the four vegetable crops
- Determining the reproductive suitability of French bean, lettuce, tomato

and zucchini based on the number of progeny produced sentinel field exposed plants and immature thrips collected from the field and reared in the laboratory.

- Assessing the reproductive suitability of French bean, lettuce, tomato and zucchini based on immature relative abundance collected in the field.
- Monitoring the seasonal change in relative abundance of the species assemblage in each vegetable agro-ecosystem.

Research design

When studying insect populations in an agro-ecosystem, a large data set needs to be collected in order to reliably represent the variability of the different species populations within the survey area. In order to fully understand the species composition and population dynamics of thrips in four different field grown vegetables in this study, the experimental area was as large as possible (in land size and time, across multiple seasons) within the bounds of the capability of conducting the survey, the associated costs and availability of land. The purpose was to replicate a field situation (a true representation of a field grown vegetable crop) to account for, and capture, the natural variability of thrips populations.

The design of this study consisted of a series of plantings conducted as factorial design, with crops as main factor and replicates as variable factor. Each experimental planting contained four blocks. Each block consisted of one of the four crops (treatments) with ten replicates per block. One sample was collected per replicate in a repeated measures study over 12 weeks. Here treatment is referred to as crop and the experimental area is referred to as planting. A total of eleven consecutive experimental plantings of this design were conducted over a three-year period to test the repeatability of the responses across different seasonal periods and years. Three plantings took place between December 2011 and March 2012, four between December 2012 and March 2013, and four

between December 2013 and March 2014. These December to March periods were classified as a season. Within each year, each planting was randomised from the previous year planting location.

Each new planting, within each season, was planted successively at four to seven- week intervals (experimental design is attached in Appendix A). Each planting was placed adjacent (directly above) the previous, so that there was no distance between the plantings or blocks. As flyers, thrips are likely not confined to agronomic designs, therefore, this ecological design allowed for the examination of the spatial distribution of thrips throughout each replicate and block. The plantings were staggered to provide a longer monitoring period, which captured data on substantial changes in species present, and their abundance, as affected by the progression of the season, the phenology of the crop and fluctuation in weather.

This design offered robust information on the dynamics of thrips populations in field grown vegetable systems to be gathered in comparison to a smaller trial with a larger weekly sample size. The design also allowed for the hypothesis that crop, season and species affect the seasonal composition and abundance of the species assemblage within the vegetable crop to be tested. The limitation of the design was that although ten replicates provide a mean and variation within each crop treatment, the differences may be due to either the plot or crop due to the non-randomised design. This design does give an indication of likely crop effect, but it cannot be ruled out that those effects are as a result of the site rather than treatment responses (Hulbert 1984; Rolečková et al. 2007). However, as the field survey took place three and four times over the course of three years, and plantings were dissimilar to the previous year location, the likelihood of confounding is reduced.

Experimental field survey area

The experimental study site was situated at Gatton Research Facility (GRF), Lockyer Valley, South East Queensland, Australia (coordinates 27° 32' S, 152° 19' E, elevation 98 m). The Lockyer Valley is one of the major vegetable producing areas, producing around 40% of Queensland vegetables. Important crops include broccoli, lettuce, tomatoes, onions, pumpkins, sweet corn, potatoes and beans (QDAF 2014). With an average rainfall of 791 mm, rainfall is highly variable in the area, making it one of the driest areas in South East Queensland (QDAF 2014). Around 60% of rainfall occurs in the summer months (December to March) with the months of August to September often the driest. The climate within the valley is variable, with temperature extremes ranging from -10°C frosts in winter to > 40°C heatwaves in summer (QDAF 2014). The Lockyer Valley is situated 85 kilometres south-west of Brisbane. It is surrounded by the Great Dividing Range and is at an elevation of 89 meters above sea level (QDAF 2014).

Plantings one to three took place from December 2011 to June 2012 (season one), plantings four to seven from December 2012 to June 2013 (season two), and plantings eight to eleven from December 2013 to June 2014 (season three). Plantings one, four and eight occurred in the month of December; five and nine in January; two, six and ten in February; and three, seven and eleven in March. Initially, plantings were to occur at four-week intervals, with four plantings per season (December to June period). However, due to heavy rainfall periods, this was not possible due to waterlogged soil, which delayed planting by either machine or hand. The design was therefore modified with three plantings in season one between the December to June survey period. Likewise, due to rainfall events in seasons two and three, plantings were staggered at either four, five or six weeks.

Each field planting was a 20 m long x 30 m wide plot and consisted of four blocks (20 m x 7.5 m, five beds per block) (Figure 3.1; the crop treatments are represented as – French bean, black; lettuce,

dark grey; tomato, white and zucchini, light grey). Each block was divided into ten replicates (4 m x 3.75 m) and contained one of the four crop treatments, French bean (*Phaseolus vulgaris*, commercial variety 'Labrador'), lettuce (*Lactuca sativa*, commercial variety 'Rador'), Roma tomato (*Solanum lycopersicum*, indeterminate trial variety courtesy of Syngenta©) and zucchini (*Cucurbita pepo*, commercial variety 'Amanda'). French bean were seeded at 5 cm spacing, two rows per bed (2,400 plants per block). Lettuce seedlings were transplanted at 30 cm spacing, three rows per bed (1000 plants per block). These were sourced as unsprayed (insecticide free) seedlings from Jackwitz Gardens, Lower Tenthill, Queensland. Tomato were raised from seed in the glasshouse before transplanting in the field at 1 m spacing, one row per bed (100 plants per block). At the time of transplanting, tomato and lettuce were approximately five weeks old, which is within the industry standard age for transplanting in the field (five to seven weeks old) (Vavrina 1998). Zucchini were seeded at 55 cm spacing, one row per bed (180 plants per block). At the time of transplanting, tomato and lettuce were approximately five weeks old, which is within the industry standard age for transplanting in the field (five to seven weeks old) (Vavrina 1998). Each new planting was planted adjacent to the previous planting with no separating buffer rows, planted between four and six weeks after the previous planting. Blocks were randomised within plantings at each planting date. By staggering the eleven plantings at intervals, and across three years, the repeatability of the responses could be tested.

No chemical insecticides were used during this study to ensure maximum thrips incursion throughout the seasons. A soft option biopesticide, DiPel® Bt (*Bacillus thuringiensis*), was applied to lettuce in planting one, season one (December 2011 to June 2012), at two weeks post transplanting, to control Lepidoptera larvae. DiPel® Bt does not interfere with Thysanoptera. Prior to planting, the survey site was sprayed with Roundup® to control weeds, and the ground prepared according to standard practices (slow release fertiliser application and over-head irrigation). The area was overhead irrigated

throughout the survey as needed. Regular manual weed removal and Roundup® application occurred to control nutgrass (*Cyperus rotundas* L.), milk thistle (*Silybum marianum* L.), alligator weed (*Alternanthera philoxeroides* G.) sow thistle (*Sonchus oleraceus* L.) and dandelion weed (*Taraxacum officinale* L.)

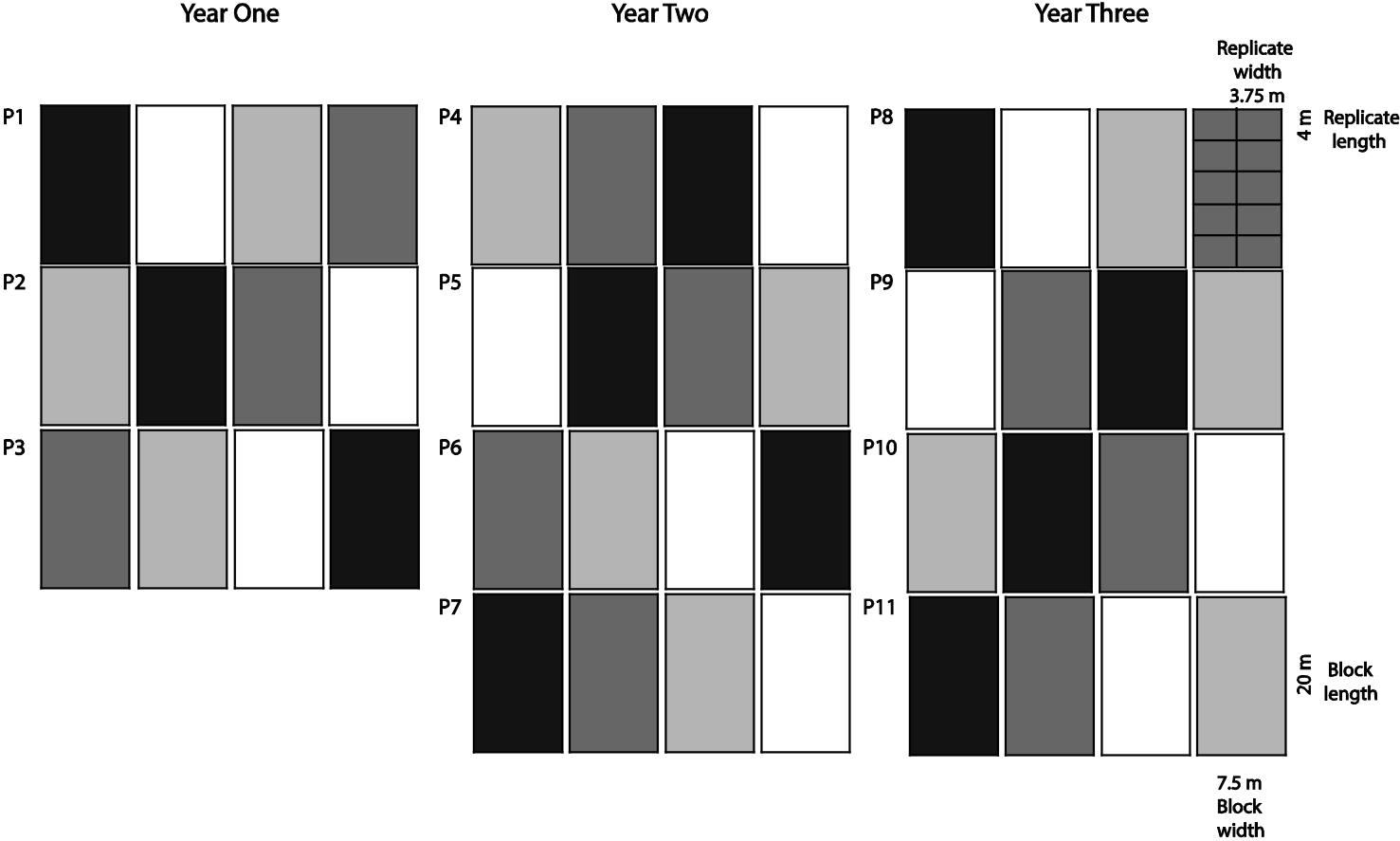


Figure 3.1 Experimental field design layout

Once a planting was no longer being monitored (12 weeks from planting), the crops were cultivated back into the ground. This was to ensure they did not have an effect on thrips species diversity and abundance in the remaining plantings. All crops were established and maintained per standard cultural practices recommended for the survey area.

Survey sampling methods

All vegetable crops were monitored by collecting a flower, growing tip and leaf and stem samples or whole plant sample (crop dependant). Sampling took place from one week after transplanting and seeding until flower production and fruit set or heading had ceased and leaves began to senesce. Insect population distribution within a crop can be clustered, random or regular depending on the sample unit (Begon et al. 1996). To reduce possible confounding by clustering on the plant, a sample unit consisted of one flower, leaf and stem, and growing tip, or a whole lettuce plant. Thrips abundance has been shown to fluctuate within flowers diurnally (Kirk 1985a), therefore samples were collected between 9am and 10 am to reduce any possible variation. For each planting, one sample was collected from each replicate, per block (crop), avoiding the outside and merging rows. Total samples for each crop (from seeding/transplanting to senescence/harvest) differed due to the crop duration, where $n = 110$ for French bean and tomato (eleven weeks), and $n = 100$ for zucchini and lettuce (ten weeks).

Over the sample period of each planting, 100 plants were removed from zucchini and lettuce and 110 plants from French bean. At transplanting or seeding, there were 2000 French bean plants, 1000 lettuce plants, 66 tomato plants and 200 zucchini per block. It was unlikely that removal of French bean, lettuce and zucchini plants would have had any effect on thrips abundance due to the high density of plants still remaining in the block during sampling. Tomato plants require a larger spacing, which meant a lower planting density within the available block area. Therefore, it was decided not to destructively sample growing tip and leaf and stem samples in tomato.

Flower and growing tip samples

One flower and one growing tip sample were collected randomly from each replicate in all flowering crops (French bean, tomato and zucchini), ten flowers in total per block, from budding until senescence. This included one female and one male flower from zucchini (ten male and ten female). Flower samples were stored immediately in 95% ethanol filled vials. The samples were processed by dissecting the flower under a dissecting microscope, and removing the adults and nymphs. Adults were transferred into vials of 95% ethanol using a size 0 paintbrush for later identification. Larvae were counted and stored in 95% ethanol.

Stem and leaf samples

Stem and leaf samples were destructively collected as a whole from French bean, lettuce and zucchini crops. The whole plant was cut at the base of the stem, near the ground, and placed individually into brown paper bags. Samples were stored in paper bags in a cooler box with cold gel packs to ensure temperature remained low while in the field. Lettuce did not flower in the field trials, and whole plant samples were collected as per the stem and leaf method. Whole plant samples were processed by deconstructing the plant – stems, leaves, and fruit - and beating over a black non-stick tray to dislodge adults and nymphs. Thrips were easily visible against the metallic black sheen. Adults were transferred to vials of 95% ethanol using a size 0 paintbrush. Larvae were placed in vials of 95% ethanol for counting. The whole plant sample did not include any flowers that were present on the plant, which were removed in the field, to ensure uniformity in analysing whole plant and flower samples separately. In tomato, intact leaf and stem, and growing tip samples were beaten onto a tray in the field and all thrips collected into 95% ethanol using a size 0 brush (Upton & Mantle 2010).

Thrips identification

All adults specimens were slide mounted according to the method of Mound and Gillespie (1997) and identified to genus and species using the interactive key Oz thrips (Oz Thrips 2016) under a compound microscope. All slides were placed in the Gatton Research Facility insect collection and used for future references. All adult thrips were sexed. Larvae were not identified to species due to the difficulty in identifying the immature stages, however, sub-samples were collected throughout the survey period and reared through to adults for identification (see Chapter 6). Adults and larvae were recorded according to crop, planting, sample date and sample type. Thrips that did not match the key character descriptions were sent for identification to Thysanoptera taxonomist Desley Tree, Biosecurity Queensland, Ecoscience Precinct, Dutton Park. Identification sheets are attached in Appendix B.

Meteorological data

Meteorological data, including rainfall, minimum and maximum temperature were recorded from the Bureau of Meteorology (BOM) weather station 40082 at the University of Queensland, Gatton campus (27° 54' S, 152°34' E, elevation 89 m). The station is situated 1 km south of the field site.

Data analysis

Data collected in this project has been analysed using the statistical programs R (R Core team 2013), Primer version 5 (Clarke & Gorley 2001), IBM SPSS (version 22 2013) and Stata14 (Stata Corp 2015). Details concerning statistical analysis are included in chapters: four – Thrips species assemblages; five – Relative abundance and temporal distribution; six – Reproductive host association; seven – The effect of weather on thrips abundance; eight – Spatial distribution of thrips.

Limitations

In agricultural research, the experimental design typically consists of testing treatments in a replicated trial, followed by data analysis to understand the interaction and outcome. When studying population dynamics in an agro-ecosystem, the limitation of the design is both in space and time, in relation to the scale of the research area and the labour intensiveness of the study. Additionally, materials and running costs are also a limiting factor. Ideally, the design of this trial would have been a randomised block design, four treatments (crop) and ten replicates with a sample size of ten plants per replicate for the duration of the experiment (9 to 12 weeks). Each planting would be repeated four times per year, planted successively at six weeks apart, and repeated over three years. However, this was not feasible due to land size, labour in planting, irrigation logistics, sampling and processing, and the costs involved, which are common problems in large-scale field surveys (Fleischer et al. 1997). Due to the enormous area that such a study would occupy, this was not possible as each planting would be 80 m long x 30 m wide, which would occupy 0.96 ha in land per season. One possibility was to reduce the size of the design. However, smaller plots would mean lower plant numbers, and therefore increased proximity to neighbouring plots. This would have increased the chance that a species collected was transient, and not actually using the crop specifically. Another option was to have a single randomised block design planting of a larger size, each year. However, this would only provide information on the population dynamics of thrips present in each crop over a 12-week period in a single year.

As mentioned, one of the limitations of this study is the smaller plot sizes and lack of randomisation. The smaller plot sizes mean that there is the potential for a site (plot) effect rather than treatment. This is taken into account by increasing the number of plantings, and randomising the plot locations of each planting in each year. For example,

Rivers et al. (2016) studied the effects of arthropod community composition in maize-wheat systems over two seasons in Mexico. They determined that despite the small plot size used (74.5 m x 22 m), and low replication (two replicates), there were obvious, and statistically significant trends observed in predator and herbivore activity densities. This indicates that while we recognise the small plot size, and lack of location replicate randomisation, there is still cause to conclude that there are specific species assemblages that exist within each of the four crops.

Chapter Four: The thrips species assemblage in French bean, lettuce, tomato and zucchini agro-ecosystems

Introduction

A field grown vegetable crop is an agricultural eco-system that contains a multitude of specialised interacting multi-trophic insect, plant and microbe complexes. Each vegetable agro-ecosystem can support a number of insect populations, with a complex of interactions occurring between the species and the crop. Many of the interactions between insect populations and the crop are generally not well understood except when the insect becomes a major agricultural pest (Schellhorn et al. 2010). This is the case for many thrips species, where extensive research has been conducted on the population dynamics of pest species to develop pest control strategies based on the interaction between the pest and the crop; but little else on all other thrips species that dwell in these vegetable crops.

Thysanoptera are opportunistic species that will exploit intermittently occurring environments such as a vegetable crop. Vegetable agro-ecosystems serve as a sink that thrips will move into and use for food and reproduction, or for shelter until a more suitable host becomes available (Northfield et al. 2008). As a result, a variety of species can simultaneously co-occur from planting to harvest. The diversity of thrips present forms a species assemblage, which is a functional community of thrips that co-occur in the same area and interact through trophic and spatial relationships (FAO 1997). The first steps to understanding the dynamics of these populations in these systems, is to establish the species diversity that exists within the crop and determine the species assemblage based on the regularity of species presence and abundance.

In agro-ecology, the approach to studying horticultural and agricultural environments is to focus on the population community (DCS 2014). Therefore, this chapter identifies the thrips species assemblage that exists in four field grown crops: French bean, lettuce, tomato and zucchini. The species within each agro-ecosystem were documented over three years with the objective of understanding the diversity of these assemblages, and determining if these species assemblages differ between the agro-ecosystems.

Thrips in vegetable agro-ecosystems

The life history strategy of thrips is to succeed in a habitat where the optimal conditions for feeding, reproduction and shelter are brief (Funderburk 2001). Vegetable crops provide such an environment, which allows for quick colonisation and establishment of several different thrips species populations. Some species form a close host association with a specific crop, where the plant provides the optimum conditions for feeding or reproduction. This association, between species and habitats, is one of the basic principles of ecology that once understood allows for greater comprehension of the dynamics insect populations (Aarts et al. 2013; Yapp 1922). Many species of thrips can be supported in a vegetable agro-ecosystem at any time. Consequently, documenting the thrips species assemblage is a critical first step toward understanding possible thrips-crop associations.

Identifying the thrips that exist within an agro-ecosystem assemblage can provide insight on thrips-crop interactions, i.e. whether the interaction is a primary host association (feeding or breeding), secondary association (feeding or breeding until a primary host becomes available), or transient (incidental presence in crop). The occurrence of a thrips in a crop does not signify a host association. This is particularly problematic for species that are considered polyphagous, using a wide variety of plants in a diversity of families (Milne et al. 1996a). Thrips will often alight and feed upon plants temporarily until a more suitable host is present. This means that establishing the relationship

between a thrips and a host can be difficult. For example, host records state that *F. schultzei* have been recorded from over 83 plants (Milne et al. 1996a). However, for many of these host records, they simply indicate that *F. schultzei* have been collected from the plant with no regard as to the possible interaction. To attempt to establish if an association between a species and vegetable crop exists, the regularity of their occurrence needs to be determined across a period of time (eg. successive seasons). By determining their regularity in the crop, we can establish if a species exists within the assemblage, and draw further insight into the possible interaction between the species and crop.

French bean

Thirteen species of thrips from seven different genera have been identified from French bean crops across Australia (Table 4.1). Two species, *Desmothrips tenuicornis* (Bagnall) and *Haplothrips gowdeyi* (Franklin) are considered potential beneficial insects. *Desmothrips tenuicornis* are thought to be facultative predators of thrips nymphs and *H. gowdeyi* predators of mite and thrips eggs and nymphs (Minaei & Mound 2008; Pereyra & Mound 2010). *Megalurothrips usitatus* are considered a serious pest of Australian French bean crops, causing scaring and twisting of pods and possible flower abortion (CRCTPP 2007; Duff 2012). There is limited information on the biology and ecology of this species, with much of the literature focusing on pest species *F. occidentalis*, likely due to its global status as an economic pest of many vegetable crops (Funderburk 2009; Northfield et al. 2008; Ssemwogerere et al. 2013). The other seven pest species, are minor bean pests but serious pests of other vegetable crops.

Table 4.1 Thrips recorded on Australian French bean.

Scientific name	Common name	Family
<i>D. tenuicornis</i>		Aeleohipidae
<i>F. occidentalis</i> *	Western flower thrips	Thripidae
<i>F. schultzei</i> *	Tomato thrips	Thripidae
<i>H. gowdeyi</i>	Gold tipped tubular thrip	Phlaeothripidae
<i>Limothrips cerealium</i>	Grain thrips	Thripidae
<i>M. usitatus</i>	Bean blossom thrips	Thripidae
<i>Pseudanaphothrips achaetus</i> (Bagnall)	Hairless flower thrips	Thripidae
<i>Thrips imaginis</i> *	Southern plague thrips	Thripidae
<i>Thrips palmi</i> *	Melon thrips	Thripidae
<i>Thrips parvispinus</i> (Karny)*	Taiwanese thrips	Thripidae
<i>Thrips safrus</i> (Mound & Masumoto)	Northern plague thrips	Thripidae
<i>Thrips tabaci</i> *	Onion thrips	Thripidae
<i>Thrips vulgatissimus</i> (Haliday)	White flower thrips	Thripidae

(Source: Duff 2012)

*Considered a pest of French bean and other vegetable crops

Lettuce

Based on the literature, *F. occidentalis*, *F. schultzei*, *T. imaginis*, *T. palmi* and *T. tabaci* are the most common occurring species in Australian lettuce (McDougall 2003; Natwick et al. 2007; Wilson 1998; Yudin et al. 1988). With the exception of *T. imaginis*, all are species are vectors of tospoviruses, which makes them important crop pest species. Research on thrips in lettuce has largely focused on these species as virus vectors, and there is limited information on any other species that may dwell within these agro-ecosystems. Wilson (1998) recorded *T. australis* (Bagnall), *Chirothrips* sp., *P. achaetus* and *Tenothrips frici* (Uzel) from lettuce crops in Tasmania (Wilson 1998). *Thrips australis* made up 48.2% of thrips mean incidence in one of these crops, followed by *T. tabaci* at 36.8%. However, as stated by Wilson (1998), it is likely that the former was collected incidentally as a transient species as it is highly associated with *Eucalyptus* spp., which were growing within the vicinity of the trial. This highlights the need for careful interpretation of the presence of a

species as belonging to a species assemblage based on its collection from a plant. To establish that a species is a part of an agro-ecosystem assemblage the species would need to be found at various times throughout the year and in several locations in the crop. The presence of a species in a crop does not mean that an association exists between the crop and the thrips but that it has merely been recorded from that crop at that point in time.

Tomato

The pest species diversity of thrips in tomatoes is well known. With extensive research conducted on *F. occidentalis*, *F. schultzei*, *T. palmi* and *T. tabaci*, which commonly occur in tomato crops worldwide (CRCTPP 2007; Funderburk 2009; Kakkar et al. 2012b; Northfield et al. 2008; Ssemwogerere et al. 2013). In Florida, USA, the *Frankliniella* species complex has been identified in tomato crops. The complex is made up of *F. occidentalis*, *F. bispinosa* (Morgan) and *F. tritici* (Fitch) a non-pest species that competes with *F. occidentalis* for resources such as shelter and pollen (Funderburk 2009; Nault et al. 2003; Northfield et al. 2008; Reitz 2002). The benefit in understanding the species complex and/or the species assemblage is understanding the interaction between pest and non-pest species and the crop as well as the interaction between the thrips species present.

Zucchini

The literature on the thrips species diversity in zucchini crops is very limited, likely due to thrips being frequent, but minor, pests of Cucurbit crops. These species include *T. palmi*, *T. tabaci* and *T. imaginis* (CRCTPP 2007; Napier 2009). Most of the literature focuses on *T. palmi* and *T. tabaci* as vectors of tospovirus, due to the high economic importance of Tospovirus damage to crops such as cucumber, melon, pumpkin, squash and zucchini (Napier 2009; Ausveg 2015). This highlights the lack of recognition and identification of all other thrips species that may dwell in these vegetable agro-ecosystems.

Lists of species recorded from an agro-ecosystem are relevant to population studies; however, they reveal little more than that a species has

been recorded from a specific habitat or crop (Brewer et al. 2008). Determining the presence and abundance of a species, the diversity of species and their relationship with the agro-ecosystem in field studies is labour and knowledge intensive. But this information is valuable in determining the species assemblage that exists and understanding the association between the species and the crop (Brewer et al. 2008).

The Thysanoptera are regarded by many as a pest order despite the fact that less than 1% are considered pests (Morse & Hoddle 2006). As a result most, if not all, research on thrips in vegetable agro-ecosystems has a pest focus. Even for well-studied, high-profile pest species *F. occidentalis*, *F. schultzei* and *T. tabaci*, there are still limitations in our understanding of their association with crops in which they are not considered pests. The first step towards understanding the population dynamics of thrips is to establish the species assemblage diversity that exists in vegetable agro-ecosystems.

Materials and Methods

As described in Chapter 3 (General research methodology), samples were collected weekly from each crop, from one-week after planting or transplanting until senescence. This included one sample per replicate. Flower and growing tip samples were collected and placed in 70% ethanol. Stem and leaf and whole lettuce samples were removed in the field (destructive sampling) and collected and placed in individual paper bags, deconstructed in the laboratory and beaten over a tray to dislodge thrips. Thrips were then collected and placed in vials of 95% ethanol. Tomato leaf and stem and growing tip samples were not destructively collected, but beaten over a tray in crop and thrips were collected and placed in 95% ethanol. All thrips were slide mounted and identified, to genus and species, using the Oz Thrips interactive lucid key under a compound microscope. Immature thrips were collected and placed in 95% ethanol and recorded as total abundance counts. Weeds within a 20-meter radius of the experimental area were recorded. Flower samples were collected from these weeds and placed in 70% ethanol and dissected for thrips. Thrips were slide

mounted and identified as per the method above.

Statistical Analysis

To determine the differences in species assemblage abundance for each crop the data was examined using the statistical technique of Multidimensional Scaling Ordination (MDS) and an Analysis of Similarity (ANOSIM) using PRIMER-E. PRIMER-E analyses matrices of species by sample abundance, which makes fewer assumptions than other statistical packages about the form of the data (that it is of a normal distribution, which in this study relates to high zero counts of some species recorded in lower abundance) and uses non-metric ordination and permutation tests to approach analysis. As not all immature thrips were identified, immature thrips counts were not included in this analysis, and are discussed further in Chapter 6.

Data was square root transformed, followed by a Bray-Curtis similarity test to standardise the data between samples (season, planting, crop and replicate) for each species. This test calculated the similarity coefficient between each pair of sample and species collected. The Bray-Curtis similarity coefficient for the similarity between the j th and k th samples S_{jk} is defined as:

$$S_{jk} = 100 \left\{ 1 - \frac{\sum_{i=1}^p |y_{ij} - y_{ik}|}{\sum_{i=1}^p (y_{ij} + y_{ik})} \right\}$$

Here y_{ij} represents the entry in the i th row and j th column of the data matrix, i.e. the relative abundance of the i th species in the j th sample. This prepared the data for MDS analysis.

The MDS analysis determined if the species assemblage for each crop was similar by calculating the relative distance between crop samples that were in the same rank order as to the relative dissimilarities of the samples (as calculated by the Bray-Curtis-coefficients. on the assemblage data). Calculating a stress value within the MDS, determined the dissimilarity between points.

The goodness-of-fit of the regression can be measured by calculating the stress value of the regression:

$$Stress = \sqrt{\frac{\sum_j \sum_k (d_{jk} - \hat{d}_{jk})^2}{\sum_j \sum_k d_{jk}^2}}$$

Where \hat{d}_{jk} is the distance predicted from the fitted regression line corresponding to dissimilarity δ_{jk} . If $d_{jk} = \hat{d}_{jk}$ for all the $n(n-1)/2$ distances in the summation, the stress is zero.

One-way analysis of similarity was applied to determine whether close data points (species samples in each crop) were significantly different from each other. This tested the null hypothesis that there were no differences between species assemblages in each of the crops, calculated as:

$$R = \frac{(\bar{r}_B - \bar{r}_W)}{1/2 M}$$

\bar{r}_W is defined as the average of all rank similarities among replicates *within* groups, and \bar{r}_B is the average of rank similarities arising from pairs of replicates *between* different groups, where $M = n(n-1)/2$ and n is the total number of samples under consideration.

A pairwise comparison of all groups was applied, including a SIMPER test to determine the percentage of the species abundance to the assemblage for each crop, which was blocked by season and planting. This was followed by a logistic regression to assess the probability of finding these species within each agro-ecosystem assemblage. Logistic regression is a generalised linear model where the response variable is abundance (proportion of the species in the assemblage) using a binomial distribution (present or absent) and a logit (natural log of odds ratio) link function, calculated as: $\text{logit}(p(x)) = \log[p(x)/(1-p(x))] = \beta_0 + \beta_1 x$. If $\beta_1 = 0$ then $p(x)$ is constant, that is the probability that presence will

not be dependent on x . $p(x)$ as an increasing function of $\beta_1 > 0$ and a decreasing function of $\beta_1 < 0$. Odds ratios were calculated for thrips species with significantly high abundance levels in each species assemblage to determine the likelihood of presence. The odds ratio is a probability function $p/(1 - p)$. Variation in planting abundance is presented in box and whisker plots, (displayed as P, followed by the planting number 1 to 11), for each crop.

Results

Species recorded

Over 12,000 samples were collected (flower, stem and leaf, growing tip and whole plant) and 6,592 adult thrips mounted for identification.

Table 4.2 Thrips recorded in all crops from Dec 2011 to June 2014.

Sub-order: Terebrantia		
Family	Sub-family	Species
Aeolothripidae:		<i>D. reedi</i> (Mound)
		<i>D. tenuicornis</i>
Thripidae:	Thripinae	<i>Chirothrips frontalis</i> (Williams)*
		<i>F. occidentalis</i> * ^p
		<i>F. schultzei</i> * ^p
		<i>M. usitatus</i> ^p
		<i>Limothrips sp.</i> * ^p
		<i>P. achaetus</i> ^p
		<i>Scirtothrips pilbara</i> (Hoddle & Mound) ^p
		<i>Tenothrips frici</i> *
		<i>T. florum</i> (Schmutz) ^p
		<i>T. imaginis</i> ^p
		<i>T. maculicollis</i> (Hood)
		<i>T. malloti</i> (Preiesner)
		<i>T. palmi</i> * ^p
		<i>T. tabaci</i> * ^p
Sub-order: Tubulifera		
Phlaeothripidae:	Phlaeothripinae	<i>H. gowdeyi</i>

* Introduced species ^p Considered a pest

Seventeen species from nine genera were recorded (Table 4.2); sixteen from the suborder Terebrantia, fourteen from the Thripidae family, subfamily Thripinae and two in the family Aeolothripidae. One species was from the sub-order Tubulifera, family Phlaeothripidae.

Thrips species assemblage in French bean, lettuce, tomato and zucchini

Of the total 17 species recorded, 15 were recorded in zucchini, 13 in French bean, 11 in lettuce and 10 in tomato. The greatest total number of thrips was recorded in zucchini, followed by lettuce, French bean and tomato (Figure 4.1).

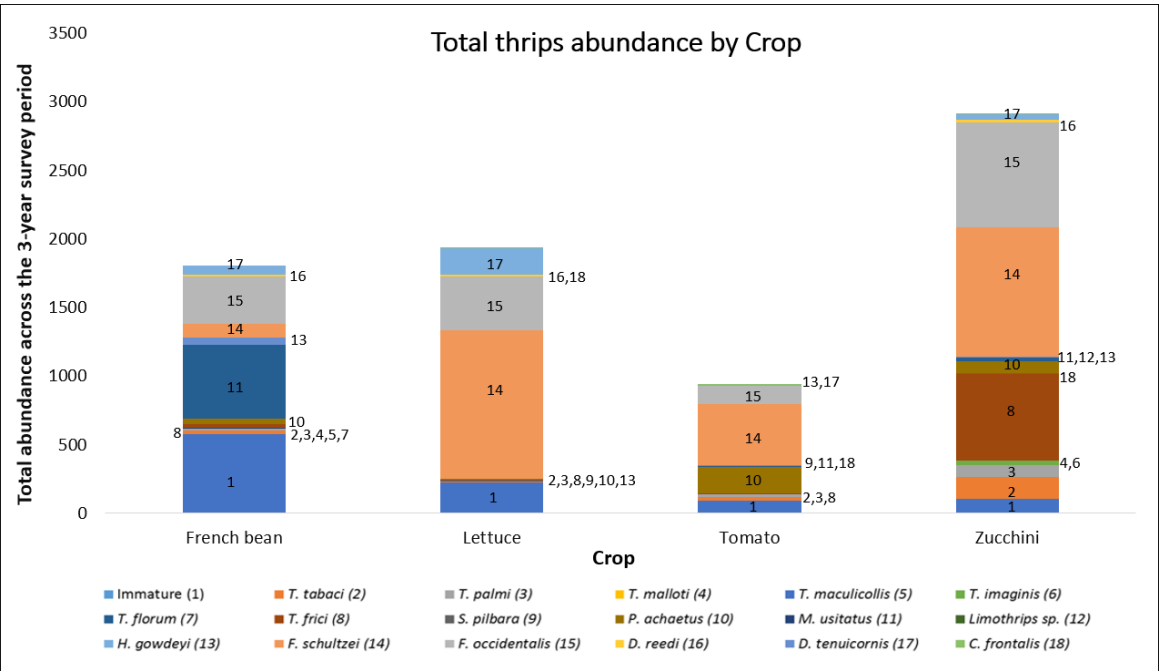


Figure 4.1 Total thrips abundance for each crop.

A 2-dimensional MDS determined that the French bean and zucchini species assemblage were not similar, while lettuce and tomato species assemblages were more similar than not (Figure 4.2). Each point shown represents an individual thrips collected from any of the four crops. An

overlap of points represent assemblages that are similar in species composition. Points that are far apart correspond to different assemblages. The aggregation of points for French bean and zucchini are clearly separated, while lettuce and tomato data points are more closely located, indicating their species assemblage similarity. A stress value of 0.19, signifies good data ordination, which indicates that the interpretation that species assemblages are similar, or dissimilar, is true ($\text{stress} \leq 01$).

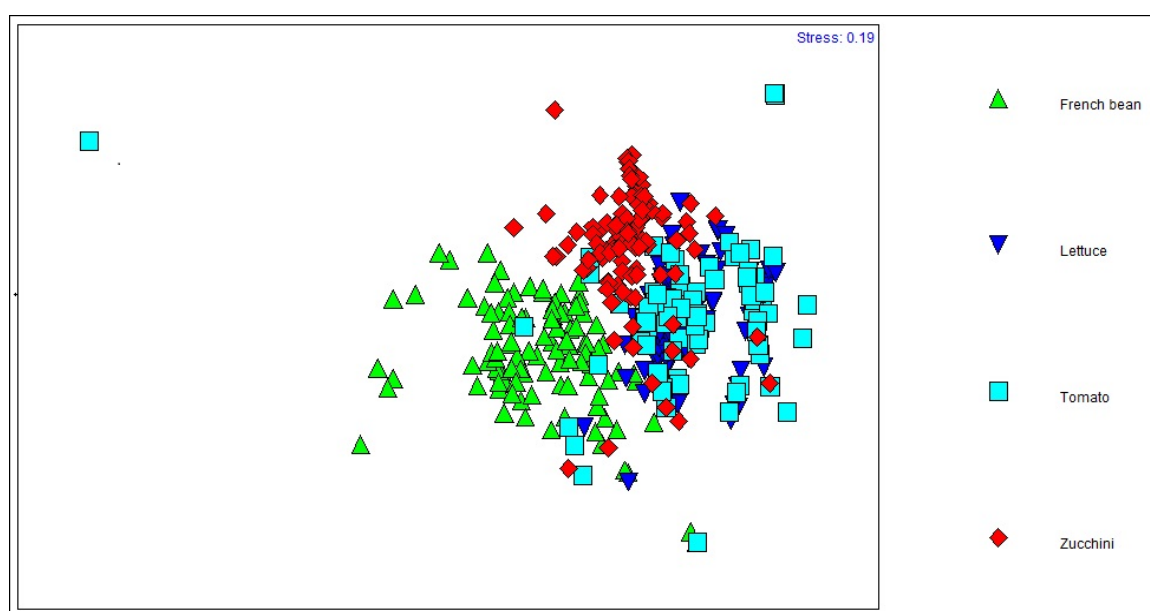


Figure 4.2 MSD Species assemblage in each crop.

Pairwise tests indicate that the French bean species assemblage is significantly different from all other crops, being most dissimilar to lettuce (Table 4.3). Lettuce and zucchini species assemblages are significantly different ($R = 0.520$), as shown in the MSD graphical output. Tomato and zucchini species assemblages were closer to similar than dissimilar at a significance level of 0.1%. The higher the R -value, the greater the dissimilarity between a group on a scale of 0 (indistinguishable) to 1 (distinguishable), and is classed as significantly different at 0.5 level. Based on the ANOSIM results, the null hypothesis that the species assemblages for each crop are the same can be

rejected at the 0.001 level (0.1%). The Global R output at 0.509 indicates that the results are true and not due to chance (an R value of greater than 0.15 will never occur by chance).

SIMPER analysis determined the level of contribution (%) of each thrips species to the crop species assemblage (Figure 4.3). In French bean, *M. usitatus* was the highest contributing species (45.71%), followed by *F. occidentalis* (37.98%), *F. schultzei* (8.99%), *D. tenuicornis* (2.67%) and *P. achaetus* (1.59%). *Frankliniella schultzei* had the greatest contribution in abundance to lettuce (61.78%), followed by *F. occidentalis* (23.92%) and *D. tenuicornis* (14.26%). *Frankliniella schultzei* also contributed the most to the tomato species assemblage (60.13%), followed by *F. occidentalis* (23.24%) and *P. achaetus* (15.56%). In the zucchini species assemblage, *F. occidentalis* contributed 32.80%, followed by *F. schultzei* (30.77%), *T. frici* (20.50%), *P. achaetus* (7.87%) and *T. tabaci* (4.63%). All other species contributions were less than 1.0% to the total species assemblage.

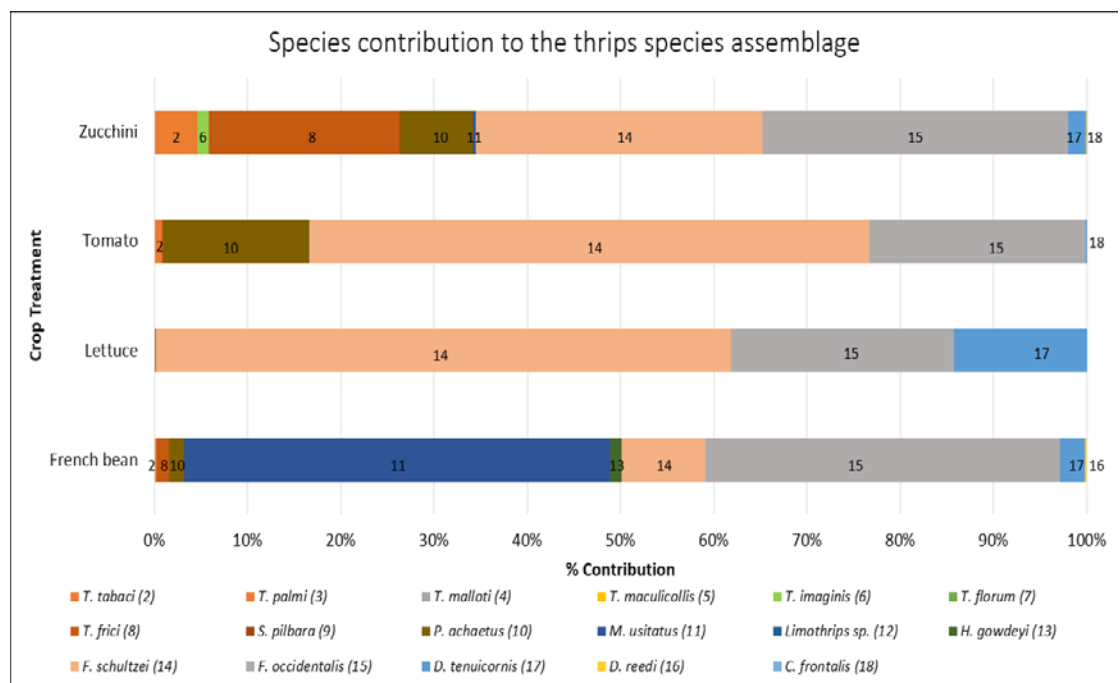


Figure 4.3 Thrips species percentage contribution to each of the crop species assemblages, as calculated by SIMPER tests across all plantings.

Table 4.3 ANOSIM Pairwise test at 0.1 % significance level.

	R statistic
French bean, lettuce	0.708
French bean, tomato	0.554
French bean, zucchini	0.638
lettuce, tomato	0.286
lettuce, zucchini	0.520
tomato, zucchini	0.407

Likelihood of thrips presence in the species assemblage

Data from the French bean agro-ecosystem indicates that there is a high probability of finding *F. occidentalis* and *M. usitatus* present, with the two species being 6.403 and 8.901 times more likely to be present than not (Table 4.4). An odds ratio of one indicates that the presence or absence of a species is equally likely; therefore, in French bean, *F. schultzei* and *T. tabaci* were almost equally likely to be present or absent. *Pseudanaphothrips achaetus* and *T. frici* were also more likely to be present than absent in French bean. In lettuce, *F. schultzei* were 6.403 times more likely to be present than not, followed by *F. occidentalis* and *D. tenuicornis*. This also corresponds to the order of total abundance found in lettuce. In tomato, the probability of finding *F. schultzei* was 370 times greater than not, followed by *F. occidentalis* and *P. achaetus*. *Tenothrips frici* were more abundant in tomato than *F. occidentalis*; however, the lower odds ratio indicates that there were more absence (0) counts across the entire data set compared to *F. occidentalis*. *Thrips palmi* were the least likely species to be present in tomato. In zucchini, the most likely species to be present were *F. schultzei* (749), followed by *F. occidentalis* (244.57) and *T. frici* (182.29). Similar to tomato, *T. frici* were more abundant than *F. occidentalis*; however, the lower odds ratio indicates that there was more absence (0) counts across the entire data set compared with *F. occidentalis*. *Desmothrips reedi* and *M. usitatus* were the least likely to be found within the zucchini species assemblage.

Table 4.4 Odds ratios for estimating the likelihood of thrips species in each crop assemblage (probabilities shown in brackets after the odds ratio).

French bean		Lettuce	
<i>D. reedi</i> (14)*	**	<i>C. frontalis</i> (1)	*
<i>D. tenuicornis</i> (64)	3.373 (0.013)	<i>D. reedi</i> (7)	*
<i>F. occidentalis</i> (342)	6.403 (0.008)	<i>D. tenuicornis</i> (193)	2.635 (0.003)
<i>F. schultzei</i> (105)	1.260 (0.053)	<i>F. occidentalis</i> (397)	3.350 (0.005)
<i>H. gowdeyi</i> (48)	2.725 (0.200)	<i>F. schultzei</i> (1081)	6.403 (0.002)
<i>M. usitatus</i> (542)	8.901 (0.008)	<i>H. gowdeyi</i> (3)	*
<i>P. achaetus</i> (39)	2.725 (0.20)	<i>P. achaetus</i> (7)	*
<i>T. florum</i> (1)	*	<i>S. pilbara</i> (1)	*
<i>T. frici</i> (29)	2.725 (0.020)	<i>T. frici</i> (7)	*
<i>T. malloti</i> (1)	*	<i>T. palmi</i> (3)	*
<i>T. maculicollis</i> (1)	*	<i>T. tabaci</i> (28)	*
<i>T. palmi</i> (12)	*		
<i>T. tabaci</i> (31)	1.334 (0.020)		

Tomato		Zucchini	
<i>C. frontalis</i> (1)	*	<i>C. frontalis</i> (5)	*
<i>D. tenuicornis</i> (7)	*	<i>D. reedi</i> (16)	3.962 (0.05)
<i>F. occidentalis</i> (131)	69.749 (0.0002)	<i>D. tenuicornis</i> (44)	15.95 (0.03)
<i>F. schultzei</i> (446)	370.285(0.0001)	<i>F. occidentalis</i> (770)	244.57(0.0009)
<i>H. gowdeyi</i> (5)	*	<i>F. schultzei</i> (938)	749 (0.0008)
<i>M. usitatus</i> (9)	*	<i>H. gowdeyi</i> (7)	*
<i>P. achaetus</i> (188)	53.999 (0.0002)	<i>Limothrips</i> sp. (3)	*
<i>T. frici</i> (11)	*	<i>M. usitatus</i> (23)	4.367 (0.04)
<i>T. palmi</i> (17)	8.526 (0.004)	<i>P. achaetus</i> (93)	57.74 (0.006)
<i>T. tabaci</i> (28)	13.655 (0.004)	<i>S. pilbara</i> (4)	*
		<i>T. frici</i> (630)	182.296 (0.0008)
		<i>T. imaginis</i> (31)	11.602 (0.04)
		<i>T. malloti</i> (4)	*
		<i>T. palmi</i> (87)	29.72 (0.03)
		<i>T. tabaci</i> (156)	96.72 (0.005)

*The number after the species is the total number collected

**abundance values too low to calculate odds ratio and probabilities

A statistical analysis of the likelihood of finding a species present or absent in any of the four agro-ecosystems was performed (Table 4.5) as there were similarities in the species assemblage diversity across the four agroecosystems (species present in more than one crops assemblage). *Haplothrips gowdeyi* and *M. usitatus* were more likely to be present in French bean, compared to all other crops, at 3.215 and 8.11 respectively. *Desmothrips tenuicornis* was more likely to be found in

lettuce (4.846) than French bean (2.155). In the tomato and zucchini agro-ecosystems, *P. achaetus* was 6.476 and 4.148 times more likely to be present than absent, compared to French bean and lettuce. *Chirothrips frontalis* (3.056) and *D. reedi* (2.333) were more likely to be present than not in zucchini compared to the other crops they were recorded in. *Frankliniella occidentalis* were more likely to be present in zucchini than all other crops. *Frankliniella schultzei* were almost equally likely to be found present, than not, in lettuce (6.021) and zucchini (5.927). *Tenothrips frici* were 20.44 times more likely to be found in zucchini and more likely to be absent from all other crops with ratios < 1. Similarly, *T. palmi* were 12.261 times more likely to be present in zucchini and more likely to be absent in French bean and lettuce. The chance of finding *T. tabaci* present was greatest in zucchini (22.810) followed by French bean (2.159) agro-ecosystems.

Table 4.5 Odds ratios for estimating the likelihood of finding a species in any of the four agro-ecosystems (probabilities shown in brackets after the odds ratio).

Thrips species	Vegetable agro-ecosystem			
	French bean	Lettuce	Tomato	Zucchini
<i>C. frontalis</i>		1.01 (0.09)*	1.02 (0.08)*	3.056 (0.027)*
<i>D. reedi</i>	2.121 (0.045)*	0.588 (0.10)*		2.333 (0.02)*
<i>D. tenuicornis</i>	2.012 (0.023)	4.846 (0.006)	0.121 (0.309)*	1.445 (0.036)
<i>F. occidentalis</i>	2.155 (0.04)	0.523 (0.05)	0.219 (0.21)	3.574 (0.009)
<i>F. schultzei</i>	1.5 (0.53)	6.021 (0.008)	5.927 (0.008)	5.927 (0.008)
<i>H. gowdeyi</i>	3.215 (0.002)	0.03 (0.09)	0.150 (0.03)	0.102 (0.03)
<i>Limothrips sp.*</i>				
<i>M. usitatus</i>	8.11 (0.0003)		0.002 (0.109)	0.014 (0.018)
<i>P. achaetus</i>	3.01 (0.20)	0.15 (0.60)	6.476 (0.03)	4.1480 (0.05)
<i>S. pilbara</i>		0.08 (0.54)		1.24 (0.05)
<i>T. florum*</i>				
<i>T. frici</i>	0.25 (0.20)	0.036 (0.50)	0.271 (0.06)	20.444 (0.009)
<i>T. imaginis*</i>				
<i>T. malloti</i>		0.06 (0.06)		1.89 (0.05)
<i>T. maculicollis*</i>				
<i>T. palmi</i>	0.20 (0.12)	0.13 (0.45)	2.13 (0.06)	12.261 (0.009)
<i>T. tabaci</i>	2.159 (0.05)	0.308 (0.10)	0.440 (0.20)	22.810 (0.007)

*Only present in one crop

Variance in species abundance

Based on box and whisker plots, abundance is highly variable between species in all four agro-ecosystems (Figures 4.4, 4.5, 4.6 and 4.7). There was also high variability within species in each of the eleven plantings, for each of the agro-ecosystems. Plantings with total zero counts were not graphed.

In French bean, there was variance in abundance between species due to the high numbers of *D. tenuicornis*, *F. occidentalis* and *M. usitatus* compared to all other species, which were present in lower numbers (Figure 4.4). With the exception of *F. occidentalis*, *H. gowdeyi* and *M. usitatus*, all others had at least one planting with a median of zero coupled with an upper outlier value. Variability between plantings was apparent for all species, particularly *D. tenuicornis*, *F. occidentalis*, and *M. usitatus*. *Desmothrips reedi*, *T. palmi* and *T. tabaci*, had similar abundance counts with several medians of zero and low variation in abundance (zero and one). In lettuce, there was a variation between species of low abundance (*C. frontalis*, *D. reedi*, *H. gowdeyi*, *P. achaetus*, *T. frici*, *T. palmi* and *T. tabaci*) and more abundant species (*D. tenuicornis*, *F. occidentalis* and *F. schultzei*) (Figure 4.5). Less abundant species had median values of zero in all plantings, with the greatest variation observed between plantings for *F. schultzei*. In the tomato species assemblage variation in *F. occidentalis*, *P. achaetus*, *T. frici*, *T. palmi* and *T. tabaci* abundance was low, even between plantings (Figure 4.6). *Frankliniella schultzei* abundance was highly variable between plantings; and *C. frontalis*, *D. tenuicornis*, *H. gowdeyi* and *M. usitatus* all had median abundance values of zero and consequently showed low variability. Zucchini abundance was highly variable between species due to the large median values of some species compared to those with lower medians (Figure 4.7). There was a large variation in abundance between plantings for *F. occidentalis*, *F. schultzei*, *T. frici* and *T. tabaci*. Each species had median abundance values of zero in all plantings, coupled with upper outliers.

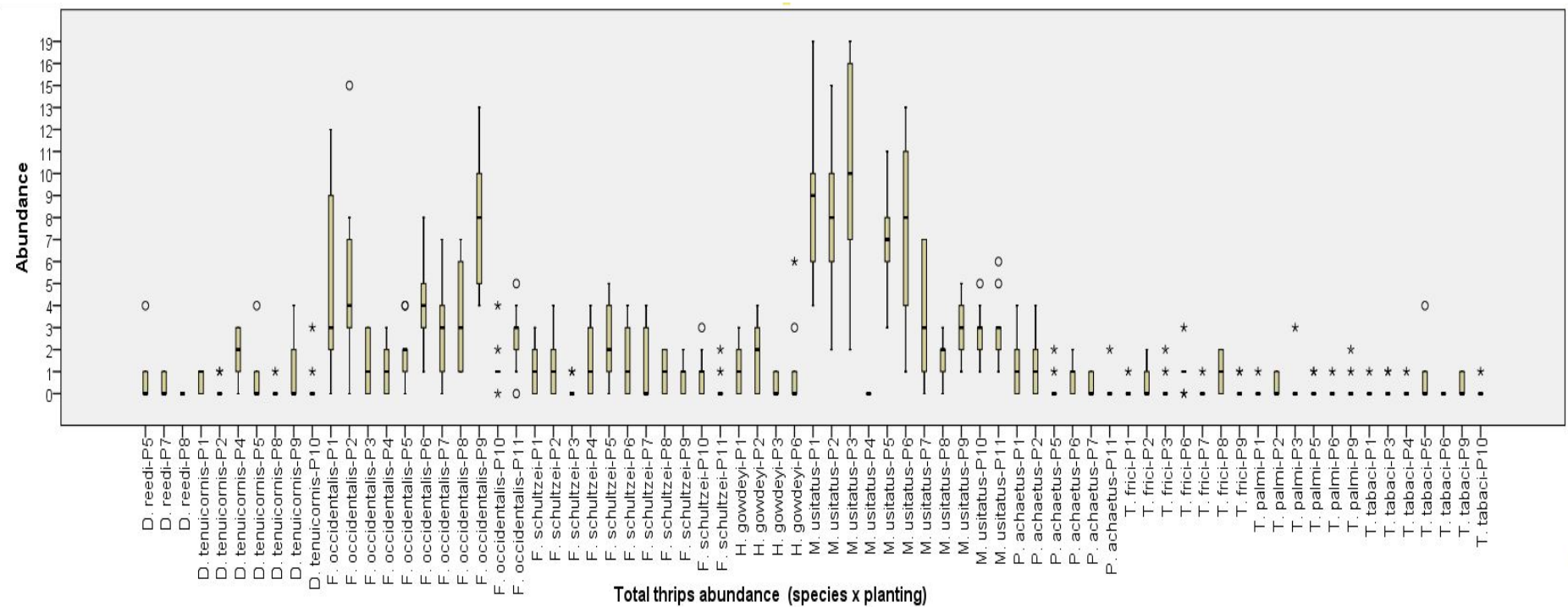


Figure 4.4 Box and whisker plot of the variance in the species abundance in French bean plantings (P).

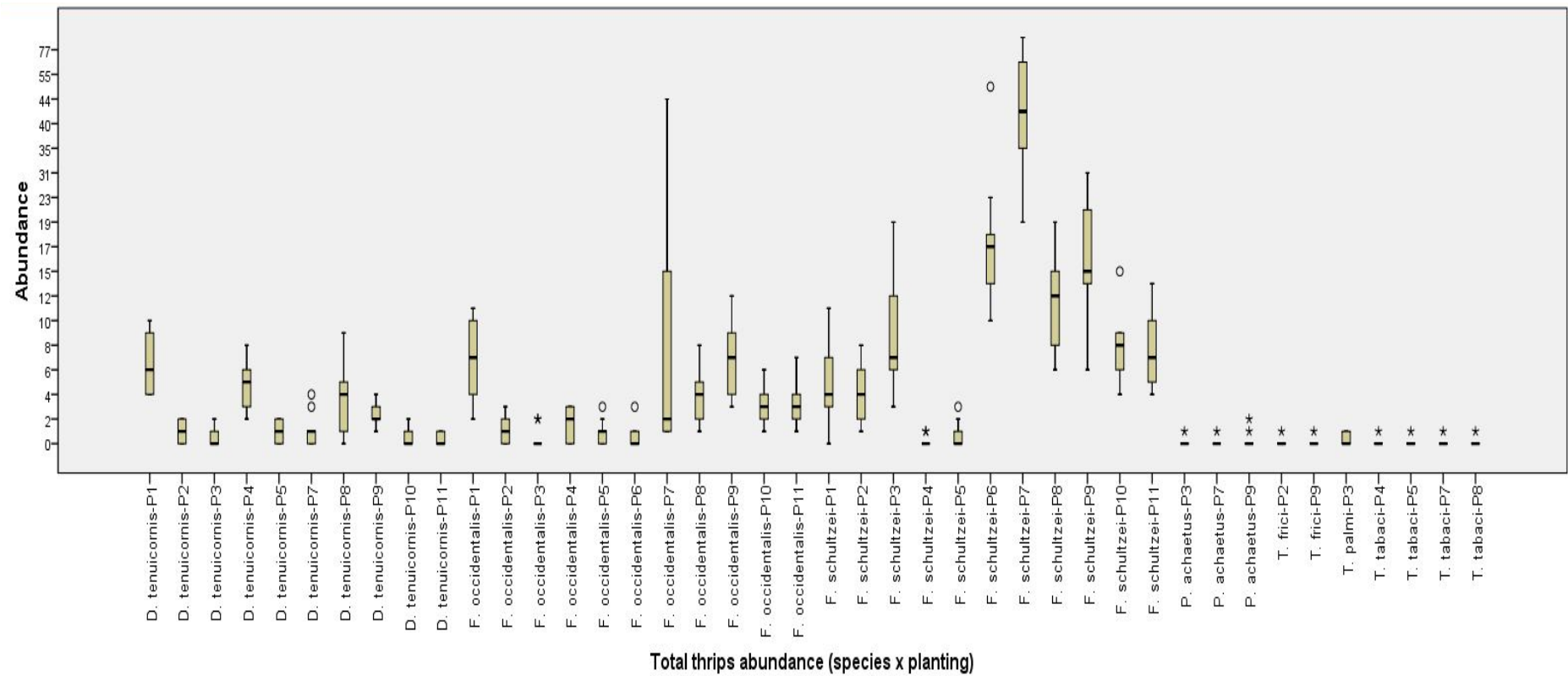


Figure 4.5 Box and whisker plot of the variance in the species abundance in lettuce plantings (P).

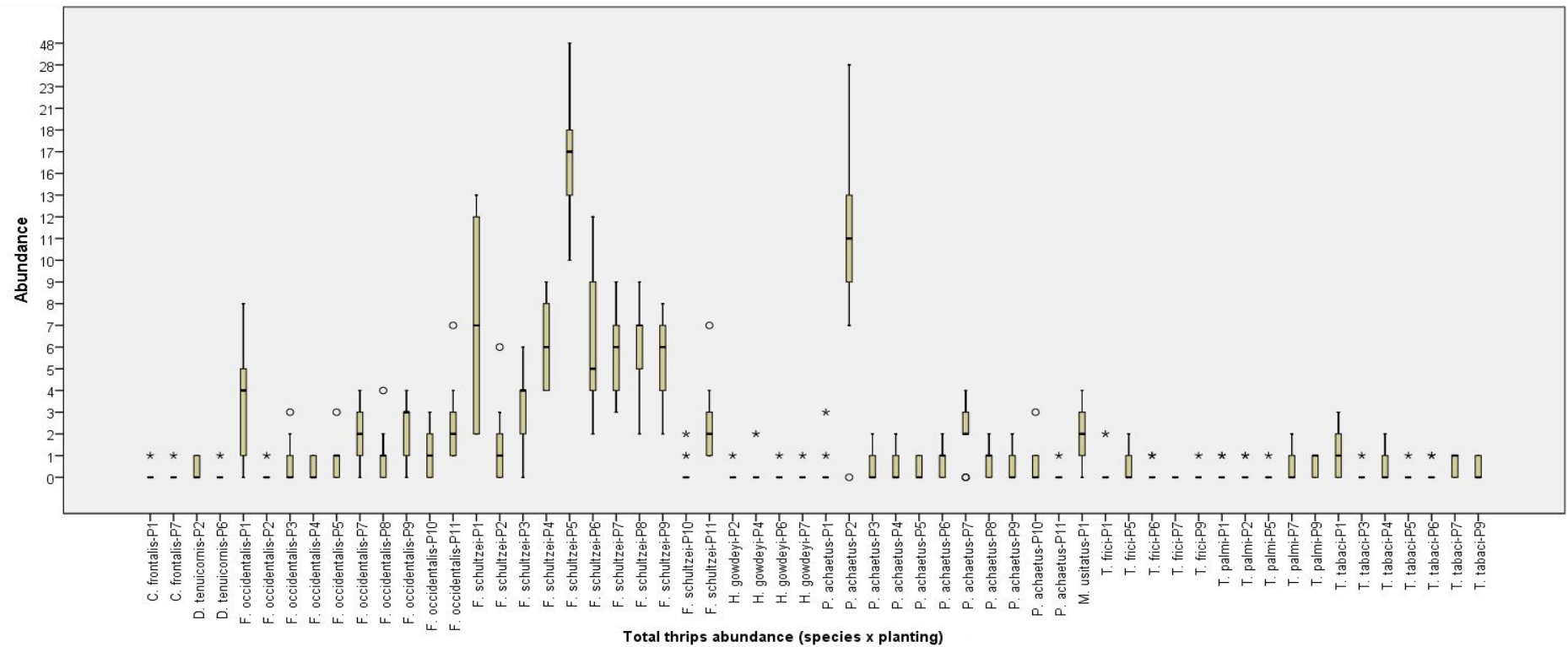


Figure 4.6 Box and whisker plot of the variance in the species abundance in tomato plantings (P).

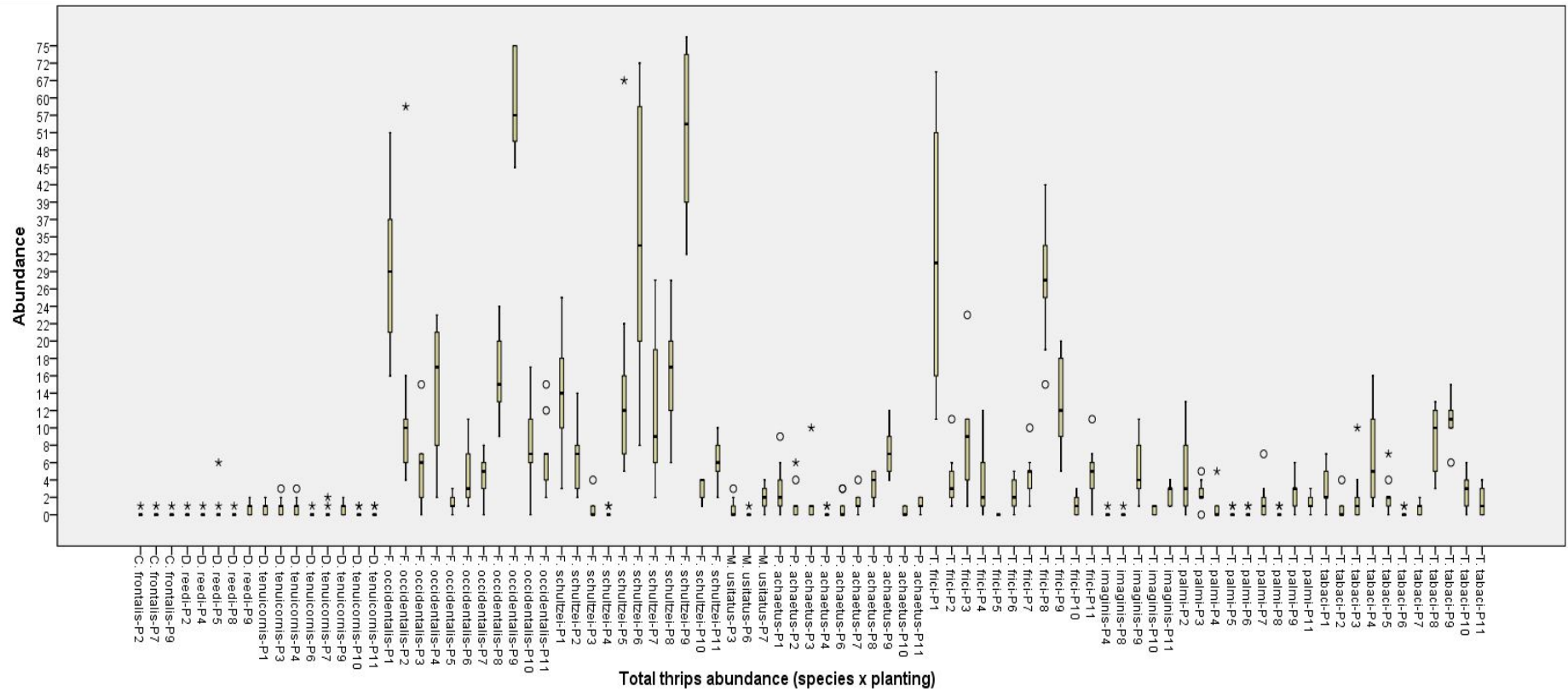


Figure 4.7 Box and whisker plot of the variance in the species abundance in zucchini plantings (P).

Discussion

Species diversity

Thrips species are rarely restricted to only one type of habitat, and as shown in this chapter, the 17 species recorded across four agro-ecosystems are diverse in their abundance within each of the agro-ecosystem species assemblage (Readhead et al. 2016). The high diversity of thrips in these species assemblages highlights the opportunistic nature of Thysanoptera and their ability to succeed in habitats where optimal conditions are brief (Funderburk 2001). Of the seventeen species recorded in this study, seven are introduced. Some species were more commonly occurring compared to other species, which were found in very small numbers throughout the study. Some of these less commonly occurring species included *Chirothrips*, *Desmothrips*, *Scirtothrips*, *Limothrips* and *Haplothrips* species. *Chirothrips frontalis* is a grass dwelling species distributed through South and East Africa, Argentina and Australia, and are found breeding and pupating in florets of Poaceae (Mound & Palmer 1972). In this study, it is likely that *C. frontalis* were only present in lettuce, tomato and zucchini as a transient species. The population was possibly breeding in Poaceae *Lolium perenne* L. (perennial ryegrass), which surrounded the experimental area. The low numbers collected suggests that its association with the crop is likely not for feeding or breeding purposes and therefore it is not a member of the species assemblage that exists in these three agro-ecosystems. This conclusion is consistent with previous literature that notes that host records of some thrips are based on small numbers of a species collected from a plant, with no regard to the regularity of occurrence or insight into the association between the thrips and plant (Milne et al. 1996a).

Like *C. frontalis*, *D. reedi* may have also been collected by chance due to the presence of perennial ryegrass. *Desmothrips reedi* have been collected from the flowers of a wide variety of plants, with no obvious

specificity, although it is thought to be generally associated with Poaceae where it feeds on mites (Oz Thrips 2016). *Desmothrips reedi* are widespread across eastern Australia between Adelaide and Charters Towers (Oz Thrips 2016). The other predatory species within the same genus, *D. tenuicornis*, were found in relatively high numbers in lettuce (Pereyra & Mound 2010). The genus *Desmothrips* is only known from Australia where many species are common in flowers of native plants (Pereyra & Mound 2010). That *D. tenuicornis* were present in lettuce, which does not flower in a commercial planting, suggests that they may be present due to predation of other thrips species. Their potentially predatory behavior toward small arthropods and eggs may have a beneficial impact in reducing populations of small arthropods pests in crop. There is very little information on the biology and ecology of Aeolothripidae thrips, including *D. tenuicornis*, and their predatory ability is an area that could benefit horticultural industries as a naturally occurring biological control agent. Given that they were recovered in reasonable abundance on a regular basis indicates that *D. tenuicornis* exist within the lettuce species assemblage, demonstrating that there is some level of interaction between the crop and the thrips. *Desmothrips tenuicornis* is widespread east of the Great Dividing Range across eastern Australia, including Lord Howe Island (Oz Thrips 2016).

One *Limothrips* sp. was recovered from zucchini. This introduced pest is associated with cereal and grass crops (Oz Thrips 2016) and was also likely recovered by chance. In Europe, *Limothrips* sp. are known as ‘thunderflies’ due to their habit of swarming en masse, indicating the ease with which they disperse and seek out suitable hosts (Thrips of California 2012). This high dispersal ability of the *Limothrips* sp. is consistent with it being a transient collected in zucchini, and not a member of the species assemblage. *Scirtothrips pilbara* were recovered from zucchini in very low numbers and one specimen was also collected from lettuce. *Scirtothrips pilbara* are known only from Australia (Western Australia, Northern Territory and Queensland). This species is thought to feed and breed on young phyllodes of various *Acacia* sp. (Hoddle &

Mound 2003). It is therefore likely that the very few specimens recovered were transient thrips.

Of the four native species within the *Thrips* genus found in this study *T. maculicollis* and *T. malloti* are not considered pests. Both species are native to Queensland and *T. malloti* is also found in New Caledonia (Mound & Masumoto 2005). They are associated with a wide range of flowering plants, which may explain their absence from lettuce and their recovery in low numbers from French bean and zucchini. These species have not previously been recorded from these crops. However, the irregularity in which they were recovered, and at such small densities, suggests that their presence was merely transient, not as a member of the species assemblage. The remaining two native *Thrips* species are considered polyphagous pests. *Thrips florum* feeds and breeds on various plants, and is commonly found in Queensland and the Northern Territory. In Hawaii, it is a pest of ornamental flowers, particularly Gardenia; however, in Australia it is only considered a minor pest (Hollingsworth 2003). *Thrips imaginis* is distributed across Southern Australia, including Tasmania, and as far north as Brisbane (Mound 1997). It has been recorded in very small numbers from Fiji and New Zealand and has established populations in New Caledonia (Mound 1983; Mound & Kibby 1998). *Thrips imaginis* are a pest of a wide range of plant species, including French bean, where it feeds and breeds in flowers. In this study, *T. imaginis* were only recorded in small numbers from zucchini, and only from the plantings in the final year of the study, suggesting environmental factors may have affected their presence in this study.

That there was only one Tubulifera, *H. gowdeyi*, recorded in this study is not unusual as the most commonly recorded species on vegetables are those from the sub-order Terebrantia. Terebrantia species are largely phytophagous, feeding and breeding in flowers and on leaves. Amongst Phlaeothripidae, flower living is not common, with the exception of the genus *Haplothrips*. Many species in this genus are associated with flowers of Asteraceae, Poaceae and Cyperaceae (Mound & Minaei 2007). *Haplothrips gowdeyi* are widely distributed across tropical and sub-tropical countries and are thought to originate from tropical Africa where the only male specimens have been

recorded (Palmer et al. 1989). *Haplothrips gowdeyi* were recovered in largest numbers from French bean in this study. This species is known to feed and breed in flowers, with no apparent host association (Thrips of California 2012). This suggests that of the three flowering crops in this study, French bean was the most suitable for *H. gowdeyi* at the time (providing shelter, food or both). Despite their recovery from French bean, they do not appear to be a true member of the species assemblage due to their irregularity in recovery.

The native *M. usitatus* were one of the more commonly occurring species collected from French bean. They are found across the northern areas of Australia, from Western Australia to Queensland and northern New South Wales. More recently they have become a serious pest of Fabaceae crops in China (Tang et al. 2015). *Megalurothrips usitatus* feed and breed in the flowers of Fabaceae plants, which would account for the high recovery in French bean. While they are considered a serious pest of Australian French bean crops, there is still much that is not known about the biology and ecology of this species (CRCTPP 2007). Most of the literature is focused on *M. usitatus* in China and Taiwan, with no literature from Australia despite its serious pest nature. Considering that Duff (2012) determined that one adult per flower can cause extensive damage to bean pods, the lack of understanding of the association between this species and French bean in Australian crops highlights the need for further research. Based on the high concentration of their abundance in French bean and their regular recovery, *M. usitatus* are a dominant species within the assemblage in this crop. This warrants further investigation to determine the level of association as either a feeding or breeding host for *M. usitatus*.

Pseudanaphothrips achaetus are distributed across all states and territories of Australia (Oz Thrips 2016). Highly polyphagous, this native thrips feeds and breeds in flowers of a range of plants. It has been associated with stone fruit in Australia, New Zealand and California; however, it is not considered an important pest (Milne et al. 1997). In vegetable crops, it has been given a pest status largely by association with thrips that are considered pests such as *F. occidentalis*, *F. schultzei* and *T. tabaci* (pers. comm. Duff 2016). The

high abundance and regularity of occurrence indicates that tomato provides the necessary requirements to support *P. achaetus* within the species assemblage and that there is an association between the species and crop.

Tenothrips frici are an introduced species found feeding and breeding in Asteraceae weeds, in particular Hieraceum, *Sonchus oleraceus* L. (sow thistle) and *Taraxacum officinale* L. (dandelion) (Hoddle et al. 2008). Both weed species were regularly found and removed, around all plantings in this study.

Tenothrips frici were found in very high numbers in zucchini, which suggest that there is a possible association between this crop and the species.

Tenothrips frici have been recorded in Cucurbitaceae crops previously, but are not considered a pest and it is possible that *T. frici* were feeding in zucchini and breeding on the sow thistle and dandelion.

Frankliniella occidentalis and *F. schultzei* were the most abundant species recovered across this study. Originally from western USA, *F. occidentalis* has spread worldwide across temperate regions (Kirk & Terry 2003). It is a serious pest of an extensive range of horticultural, broad acre, ornamental and tree crops, although they have been recorded feeding on leaf mites (Kirk & Terry 2003). Similarly, *F. schultzei* feed and breed in flowers and leaves of a wide range of plants and also consume eggs of spider mites (Silva et al. 2013). *Frankliniella schultzei* were a dominant species within the lettuce, tomato and zucchini species assemblages; however, were less abundant in French beans, indicating that the crop is unsuitable for feeding or breeding.

Like *F. occidentalis* and *F. schultzei*, *T. palmi* and *T. tabaci* are considered serious horticultural pests. *Thrips palmi* originates from the Asian tropics, and is present in Queensland and the Northern Territory. It is commonly found on Cucurbitaceae and Solanaceae plants (Mound & Masumoto 2005) and was recovered in highest abundance from and zucchini in this study. Widespread across Australia, *T. tabaci* have a close association with Allium crops and are commonly found on potato. They are considered polyphagous, however, are found only in low numbers on native Australian plant species (Mound & Masumoto 2005). Males are known in eastern Mediterranean countries and

New Zealand, however, not in Australia. Based on their collection, both thrips species are considered central species in the zucchini species assemblage.

Species assemblages

In this study, we have determined that a thrips species assemblage exists in each of the four agro-ecosystems. Each vegetable agro-ecosystem species assemblage is unique in its diversity and abundance. While there are similarities between the assemblages, in that some species are present in two or more crops, the differences lie in the variation of abundance and the presence or absence of other species.

Based on their abundance and regularity of recovery, the French bean species assemblage consists of *M. usitatus*, *F. occidentalis*, *D. tenuicornis*, *P. achaetus*, *T. frici*, *F. schultzei* and *T. tabaci*. *Megalurothrips usitatus* and *F. occidentalis* were the two dominant species within the assemblage. Of the seven species within the assemblage, *T. frici* and *P. achaetus* are not considered pests of this crop, while *D. tenuicornis* is potentially a beneficial predator. This is also the first published record of *T. frici* from French bean crops in Australia. Of the fifteen species of thrips collected from French bean, *F. schultzei* and *T. tabaci* were recovered on a regular basis. However, based on their low abundance, these two species appear to have a very low association with the crop. Both species are found in much higher regular abundance from the other three agro-ecosystems, indicating that French bean is a poor reproductive and/or feeding host for these two species.

Comparing the species within each agro-ecosystem assemblage, *M. usitatus* is the key species that differentiates the French bean species assemblage from all others. It is absent from lettuce and found in very low numbers in all other agro-ecosystems. In this study, *M. usitatus* appears to be monophagous toward Fabaceae rather than polyphagous across all families (Asteraceae, Cucurbitaceae and Solanaceae). There is likely a strong feeding or reproductive association between this species and French bean, which appears to be a main host crop for *M. usitatus*. *Haplothrips gowdeyi* were collected in

relatively high numbers from French bean, and have been recorded from this crop in the past (Duff 2012). Their predatory nature would be a valuable addition to naturally occurring beneficial insects in crop. However, the fact that they were only collected in high abundance in one year indicates that their presence in crop was likely as a secondary or transient event.

Most of the thrips species recorded in this study are highly anthophilic. Therefore, low species diversity in the lettuce agro-ecosystem is not unusual, as it did not flower during this study. The species assemblage in lettuce consists of *F. occidentalis*, *F. schultzei* and *D. tenuicornis*. While these three species are considered anthophilic, the nutritional quality of a plant is an important factor affecting the host selection of thrips (Brodbeck et al. 2001). Lettuce is known to have good nutritional content, providing high concentrations of amino acids, which are converted to proteins and sustain rapid growth of immature thrips (Brodbeck et al. 2001). Based on this information and the high abundance of adults collected in crop, it is possible that these two species are reproducing in the crop (determination of immature presence is needed to investigate this theory, discussed in Chapter 6). The absence of flowers, and the potential reproductive association between *Frankliniella* and lettuce, present the potential hypothesis that *D. tenuicornis* may be present in the lettuce agro-ecosystem as a result of predation on immature *Frankliniella* sp. (see Appendix C). Many species in the Aeolothripidae family appear to be facultative predators of other small arthropods (Oz Thrips 2016). For example, Hoddle (2003) found that Aeolothripidae *Franklinothrips orizabensis* (Johansen & Crawford) will attack first and second instar *Scirtothrips perseae* (Nakhaea) in controlled avocado leaf arena assessments. However, despite *Desmothrips* species being considered facultative predators (Pereyra & Mound 2010) literature is very limited on the predation capacity of *D. tenuicornis* species, and this theory warrants further investigation before conclusions can be drawn (see Appendix C). Of the 250 host plants that *F. occidentalis* have been recorded from, and the 83 from which *F. schultzei* have been recorded, there is no evidence to suggest that they use these plants as breeding hosts. This too is a topic that is investigated further in this project (discussed in Chapter 6).

While abundance was low in tomato, the number of species within the tomato agro-ecosystem assemblage was greater than lettuce, highlighting that the presence of flowers as important for many of the species found in this study. *Frankliniella occidentalis*, *F. schultzei* and *P. achaetus* were the dominant species in the tomato species assemblage, followed by *T. palmi* and *T. tabaci*. Tomato is considered a poor reproductive host for thrips, particularly *F. occidentalis* (Brodbeck et al. 2001; Reitz 2002). Therefore, it is likely that any association that exists between these species and tomato is a feeding interaction rather than reproductive. Of the five species, only *P. achaetus* is not considered a pest of tomato. Across all agro-ecosystems, *P. achaetus* was found in greatest numbers in tomato, which likely meets the nutritional or reproductive requirements for this species.

The zucchini species assemblage is characterised by nine thrips species. Similar to lettuce and tomato, *F. occidentalis* and *F. schultzei* were two of the most dominant species in the assemblage, demonstrating their polyphagy across a wide range of crops. *Tenothrips frici* was also a dominant species in the assemblage. While *T. frici* does not exist within the tomato assemblage, its occurrence in zucchini and its presence in the French bean assemblage, indicates that pollen is an important nutritional requirement for this species. Some thrips species require pollen to complete development and optimise egg production, which may explain the high diversity in this crop and the higher number of species within the assemblage, including *D. tenuicornis*, *P. achaetus*, *T. imaginis*, *T. palmi* and *T. tabaci* (Kirk 1984). That *F. schultzei* were present in high abundance in both lettuce and zucchini, suggests that pollen may not be as important for them to complete their life cycle compared to other flower-dwelling species. As demonstrated by Milne et al. (1996b), *F. schultzei* fecundity and development time was no different on a pollen diet as compared to a non-pollen diet. That *D. tenuicornis* was present in relatively large numbers across French bean, lettuce and zucchini indicates the breadth of its use of flowering and non-flowering plants, and highlighting its facultative nature.

The common species between the four agro-ecosystem species assemblages is the presence of the *F. occidentalis* and *F. schultzei*, which were

found co-occurring in all crops. This co-occurrence has been recorded in many cropping systems across the globe, including tomato and French bean (Funderburk 2009; Kakkar et al. 2012b; Ssemwogerere et al. 2013).

Variation in species abundance

A vegetable agro-ecosystem is a constantly changing multi-trophic system. The species assemblages that exist within these systems fluctuate with biological (births, deaths and predation), physiological (phenological stage) and environmental changes of the habitat. Based on the results of this study, there is a large variation in the presence and abundance of each species.

Understanding the cause of these changes in relation to season, weather and crop phenology allows a greater comprehension of the interaction between the agro-ecosystems and the assemblages, and the possible association between the crop and thrips. For example, Navas et al. (1991) established that a *Frankliniella* species complex exists in south-eastern Florida tomato crops, consisting of *F. occidentalis*, *F. fusca* (Hinds) and *F. tritici*. Further investigation determined that population abundance varied with the season, with highest densities in May during the warmer months and tapering off as the weather cooled from October. Crop phenology has a large impact on presence and variation in thrips populations, with species using a plant at specific phenological stages in the crops growth. *Frankliniella occidentalis* prefer lower canopy leaves and early flowers of bean plants in Kenya during the warmer months and *M. sjostedi* prefer the middle canopy leaves and more mature flowers of the same crop as the temperatures cool (Kasina et al. 2009).

Establishing the species assemblage increases our understanding of the population dynamics of thrips in vegetable agro-ecosystems. Determining the species diversity and the thrips species assemblage, however, only tells us the species that are likely associated with the crop. It does not tell us the strength of the association (primary or secondary), the type of association (feeding, breeding) or how the assemblage fluctuates in relation to crop type or the phenological stage of the crop (investigated further in Chapters 5 and 8). Suppositions can be made as to the possible associations, but to understand the

relationship between an insect population and an agro-ecosystem, the system as a whole needs to be assessed. No conclusion can be drawn or assumed about the dynamics of a population without looking at the other environmental factors that play a role influencing the change in abundance of populations and how that in effect changes the assemblage makeup of an agro-ecosystem (investigated further in Chapter 7).

Conclusion

A total seventeen thrips species were recorded across the survey period, seven of which are introduced species, and eleven that are a pest of various horticultural crops. The zucchini agro-ecosystem supported the highest number of species, 15 in total, followed by French bean (13), lettuce (11) and tomato (10). The lettuce and tomato assemblages were more similar in their species composition, whilst the French bean and zucchini assemblages were vastly different. Key species in each assemblage included *D. tenuicornis*, *F. occidentalis* and *M. usitatus* in French bean; *D. tenuicornis*, *F. occidentalis* and *F. schultzei* in lettuce; *F. occidentalis*, *F. schultzei* and *P. achaetus* in tomato and *F. occidentalis*, *F. schultzei*, *T. frici* and *T. tabaci* in zucchini. The two *Frankliniella* species were the most abundant species recorded across the survey period., in comparison to all other thrips species recorded. Defining the composition of a thrips species assemblages is the first step towards understanding the relationship between the insect and the agro-ecosystems. This is explored further in the following chapters.

Chapter Five: Relative abundance and temporal distribution of *Frankliniella occidentalis* and *Frankliniella schultzei* on French bean, lettuce, tomato and zucchini in relation to crop age

Co-author statement for Publication

Healey, MA, Senior, LJ, Senior, PH, Brown & J, Duff 2016, ' Relative abundance and temporal distribution of *Frankliniella occidentalis* (Pergande) and *Frankliniella schultzei* (Trybom) on French bean, lettuce, tomato and zucchini in relation to crop age', *Journal of Asia Pacific Entomology*, 20 (3), 859-865.

M.A. Healey, Field design, trial setup, data collection, analyses and manuscript write-up (Contribution -100%);

L.J. Senior, P.H. Brown & J. Duff Field design, trial setup and proof-reading (Contribution-30%)

This paper has not been submitted for an award by another research degree candidate either at CQUniversity or elsewhere.

I declare that the publication above meets the requirements to be included in the thesis as outline in the Research Higher Degree Theses Policy and Procedure

Madaline Healey:

Date: 5/07/2017

Introduction

Pest thrips are becoming increasingly difficult to control, therefore new approaches to management are required. Pest thrips infestation in horticultural plants reduces product quality, and economic loss can be attributed directly to injury from feeding or oviposition and indirectly to transmission of plant diseases such as tospoviruses (Ullman et al. 1997). Thrips have an inherent opportunistic nature that allows them to exploit a variety of vegetable crops (Morse & Hoddle 2006). A crop can support a number of pest and non-pest species at any one time, with population densities fluctuating with the phenological stage of the crop. However, of the more than 5500 described thrips species, less than 1% are considered serious economic pests (Morse & Hoddle 2006).

With limited commercial availability of biological agents and soft chemical options (those that provide effective control of a pest with reduced impact on beneficial species, such as narrow-spectrum chemicals), broad-spectrum chemical insecticides are the main tool used by vegetable growers to control pest thrips. Many vegetable growers apply insecticides at regular intervals across the life of the crop, increasing in frequency following the detection of large thrips populations (Nault et al. 2003). However, once a large population has been detected, insecticide application is often ineffective as feeding damage and reproduction has already occurred. Oviposition by species from the Terebrantia suborder into the plant tissue means that eggs are protected from foliar sprays. Moreover, thrips typically occupy interstitial spaces, such as flowers and leaf clusters, protecting adult and larval stages from foliar sprays (Parrella 1995). Indiscriminate use and repeat application of pesticides in the carbamate, organophosphate, organochlorine and pyrethroid chemical groups has also led to insecticide resistance in some species including *F. occidentalis* and *F. schultzei* (Immaraju et al. 1992), reducing the number of effective insecticides available. For optimum control, insecticides should be

applied to coincide with periods prior to population increase, thus decreasing the need for further chemical application.

The most serious opportunistic thrips pests are those that are polyphagous (Milne & Walter 2000). Both *F. occidentalis* and *F. schultzei* are polyphagous species that are considered pests of a wide range of vegetable crops (Reitz 2009; Vierbergen & Mantel 1991). These two *Frankliniella* species are often found co-occurring in Fabaceae, Solanaceae and Cucurbitaceae crops (Kakkar et al. 2012ab; Nyasani et al. 2012; Nyasani et al. 2013; Walsh et al. 2012). However, there is limited information comparing their abundance in other vegetable crops, particularly in relation to their temporal distribution between vegetable agro-ecosystems across the life of the crop. Phenological synchrony between plants and insects means that population diversity and abundance fluctuates with plant growth. Understanding these fluctuations in relation to crop age would enable vegetable growers to determine which species is likely to be most prevalent and when they are likely to increase in abundance. This would allow for insecticides to be applied at critical periods prior to population increase.

This study compared adult *F. occidentalis* and *F. schultzei* abundance in four different vegetable crops, three fruiting (French bean, tomato and zucchini) and one non-fruiting (lettuce) in the Lockyer Valley, South East Queensland, Australia. We tested the hypothesis that abundance and temporal distribution of both *Frankliniella* species was the same across all four crops and at all stages of the crop from one week after planting to senescence or harvest. The aims of this study were to: establish if there was a difference in species abundance, establish if the two species were spatially separated within the plant (flower, leaves and stem and growing tip), and determine if the distribution of each species was temporally separated by the age of the crop between four field grown vegetable crops.

Materials and methods

This study was undertaken to determine the distribution of abundance of *F. occidentalis* and *F. schultzei* in four vegetable crops. Each experimental unit was conducted as a factorial design, consisting of four blocks with four crop treatments and ten replicates per block. Samples were collected weekly from one week after planting until senescence in lettuce and zucchini, and until harvest (flowering and fruit set had ceased) in French bean and tomato. A total of eleven consecutive experimental unit plantings of this design were conducted over a three-year period to test the repeatability of the responses across different seasonal periods and years.

As described in Chapter 3 (General research methodology), samples were collected weekly from each crop, from one week after planting or transplanting until senescence. This included one sample per replicate. Flower and growing tip samples were collected into 70% ethanol. Stem and leaf and whole lettuce samples were removed in the field (destructive sampling) and collected into individual paper bags, deconstructed in the laboratory and beaten over a tray to dislodge thrips. Thrips were then collected into vials of 95% ethanol. Tomato leaf and stem and growing tip samples were not destructively collected, but beaten over a tray in crop and thrips collected into 95% ethanol. All thrips were slide mounted and identified, to genus and species, using the Oz Thrips (2016) interactive lucid key under a compound microscope. Immature thrips were collected into 95% ethanol and recorded as total abundance counts. Weeds within a 20-meter radius of the experimental area were recorded. Flower samples were collected from these weeds into 70% ethanol and dissected for thrips. Thrips were slide mounted and identified as per the method above.

The total abundance of *F. occidentalis* and *F. schultzei* from each sample type, corresponding to the sample date, planting number, crop treatment and replicate were recorded. Immature thrips totals were not included in the analysis (see Chapter 6).

Statistical analysis

The data was analysed using the statistical software package IBM SPSS (version 22, 2013). Data was checked for normality and homogeneity of variance using Shapiro-Wilk ($p > 0.05$) and Levene tests followed by a square root transformation $(X + 0.5)^{1/2}$ to normalise the data. A square root transformation was used as it could be applied to count data with zero values. Results presented are back-transformed mean \pm 1 standard error.

To examine thrips abundance, data (sample types pooled) was analysed using a three-way analysis of variance (ANOVA) with crop treatment, thrips species and planting number as factors. A Tukey Honest Significant Difference (HSD) at the 95% confidence interval (CI) determined the mean difference between the two species for each crop treatment, and for differences between the crop treatments for each species. To determine if there was a difference in thrips abundance within the plant (sample type), a two-way ANOVA was performed for each crop treatment, with sample type and species as factors (data pooled by planting) and abundance the variable. Comparison between crops could not occur due to the difference in sample types for each crop treatment. Species was used as a factor to determine any difference between the two *Frankliniella* in relation to their abundance (population densities) in each crop treatment and the sample type. A Tukey HSD at the 95% CI determined the mean difference between sample types. Lettuce was not included in the analysis as it consisted of only one sample type.

To determine temporal distribution of each species within each crop treatment, data was analysed using a three-way ANOVA, with planting number, crop treatment and crop age (weeks from the time of planting) as factors and abundance the variable. Due to the low number of either *F. occidentalis* or *F. schultzei* in some crop treatments, comparison of abundance between the two species could not occur,

therefore the two species were analysed individually in relation to crop age. Data was further subjected to two-way repeated measures ANOVA, to determine the effect of crop age (nine levels), at each weekly sample point on the abundance of each species. Weeks one and eleven were not included in the analyses to standardise time for all four crop treatments. Interaction between crop and crop age was used to determine whether there was a temporal pattern of abundance of each species across the life of the crop treatments. Pairwise comparison of means determined which crop age had significantly more thrips, compared across crop treatments. Pearson correlation coefficient was calculated to determine the strength of the relationship between thrips abundance and crop age for each crop treatment.

Results

Thrips abundance in crop

There was a significant effect of crop treatment, $F_{(3,792)} = 16.92$, $p < 0.001$, planting, $F_{(10,792)} = 16.04$, $p < 0.001$ and species, $F_{(1,792)} = 11.36$, $p < 0.001$, on thrips abundance. There was a significant three-way interaction between planting, crop treatment and species, $F_{(30,792)} = 10.65$, $p < 0.001$, including a statistically significant two-way interaction between species and crop for *F. occidentalis* $F_{(3,792)} = 2.311$, $p < 0.001$ and *F. schultzei* $F_{(3,792)} = 3.98$, $p < 0.001$. Pairwise comparison between species means within each crop determined that *F. occidentalis* were more abundant in French bean than *F. schultzei*, whereas in lettuce and tomato, *F. schultzei* were more abundant compared to *F. occidentalis* (Figure 5.1). There was no difference in abundance of the two species in zucchini (Figure 5.1). Pairwise comparison of species means within and between crop treatments determined that *F. occidentalis* abundance was significantly higher in zucchini, and *F. schultzei* was significantly higher in lettuce and zucchini, compared to all other crop combinations, but were not significantly different from each other (Figure 5.1). For each species,

means with a letter in common are not significantly different ($p > 0.05$)
Of a total 6,611 adult thrips, 1,640 were *F. occidentalis* and 2,590 were *F. schultzei* adults.

Thrips abundance within plant

There was no difference between species abundance by sample type, $F(2, 27) = 28.92, p = 0.092$, however sample type had a significant effect on total thrips abundance (*F. occidentalis* and *F. schultzei*) in French bean, $F(2, 27) = 13.32, p < 0.001$, and tomato, $F(2, 27) = 37.29, p < 0.001$, with significantly more thrips in flowers, followed by leaf and stem and growing tip samples (Table 5. 1). Sample type also had a significant effect on thrips abundance in zucchini, $F(2, 36) = 23.60, p < 0.001$, with significantly more in female flowers compared to male flowers (Table 5.1). Mean (back-transformed mean \pm standard error) number of adult thrips (*F. occidentalis* and *F. schultzei*) in each sample type, sampled in each crop, across all plantings are presented in table 5.1. Mean thrips abundance, in each planting, on lettuce (leaf samples only) were 171.9 (± 12.45).

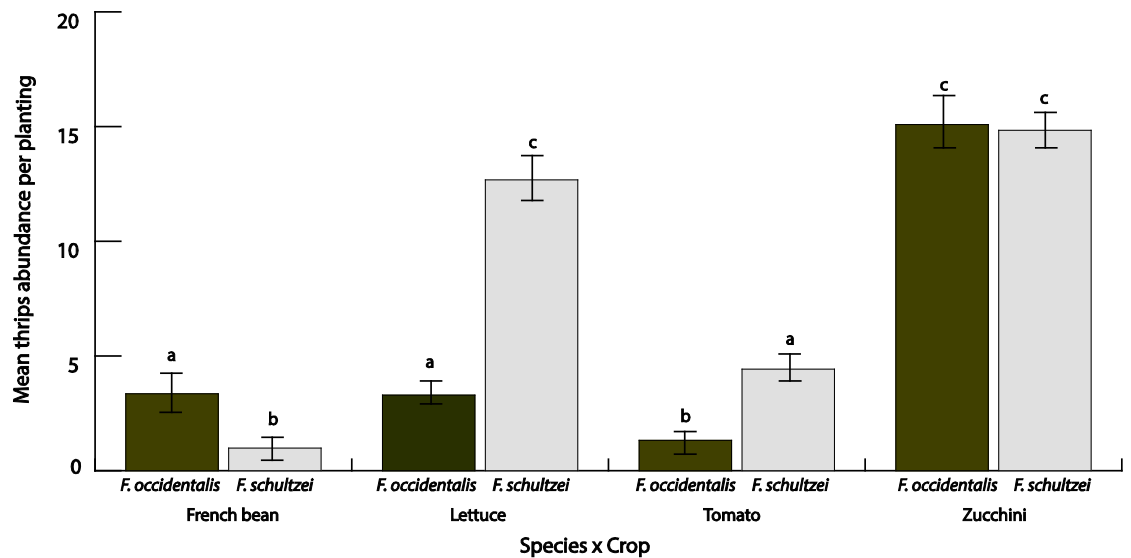


Figure 5.1 Mean (back-transformed mean \pm 1 standard error) number of *F. occidentalis* and *F. schultzei* sampled in each crop, across all plantings.

Table 5.1. Mean number of adult thrips in each sample type within each crop.

Mean number of total adult thrips (<i>F. occidentalis</i> and <i>F. schultzei</i>)				
Sample Type**	French bean	Lettuce	Tomato	Zucchini
Flower	78.0 (± 3.1) a	NA	24.1 (± 2.2) a	NA
Leaf and Stem	24.1 (± 2.3) b	NA	21.0 (± 1.3) b	16.2 (± 2.1) c
Growing Tip	8.0 (± 0.7) c	NA	19.1 (± 0.5) c	19.1 (± 1.7) c
Female Flower	NA	NA	NA	223.0 (± 11.2) a
Male Flower	NA	NA	NA	124.0 (± 8.9) b

** For each crop, sample type means with a letter in common are not significantly different, between the sample types ($p > 0.05$)

Temporal distribution

Crop age had a significant effect on *F. occidentalis* abundance $F(8, 3564) = 13.398, p < 0.001$, including a significant three-way interaction between planting, crop treatment and crop age, $F(240, 3564) = 14.032, p < 0.001$. There was a significant two-way interaction between crop and crop age on *F. occidentalis* abundance in French bean, $F(3, 3564) = 1.367, p$

= 0.015, lettuce, $F(3, 3564) = 4.192, p < 0.001$ and zucchini. $F(3, 3564) = 1.864, p < 0.001$, but not in tomato, $F(3, 3564) = 0.427, p = 1.00$. There was also a significant effect of crop age on *F. schultzei* abundance, $F(8, 3564) = 12.732, p < 0.001$, including a significant three-way interaction between planting, crop treatment and crop age $F(240, 3564) = 14.13, p < 0.001$.

There was a statistically significant two-way interaction between crop treatment and crop age for *F. schultzei* abundance in lettuce, $F(3, 3564) = 2.535, p < 0.001$, tomato $F(3, 3564) = 2.018, p < 0.0001$ and zucchini $F(3, 3564) = 3.108, p < 0.001$, but not in French bean, $F(3, 3564) = 0.060, p = 1.10$. There was no significant interaction between planting and crop age for *F. occidentalis* $F(80, 3564) = 0.060, p = 1.100$, and *F. schultzei* $F(80, 3564) = 0.427, p = 1.00$.

Frankliniella occidentalis mean abundance was significantly higher in zucchini than other crop treatments between weeks three and six after planting, followed by a shift to French bean between weeks eight and ten (Figure 5.2; for each crop age, means with a letter in common are not significantly different ($p > 0.05$)). *Frankliniella occidentalis* was generally lowest in lettuce and tomato at all crop ages. *Frankliniella schultzei* mean abundance was significantly higher in lettuce in weeks two and three and between weeks eight and ten, with significantly higher abundance between weeks four and six in zucchini (Figure 5.3; for each crop age, means with a letter in common are not significantly different ($p > 0.05$)). *Frankliniella schultzei* was generally significantly lower in French bean, compared to all other crops ($p < 0.05$).

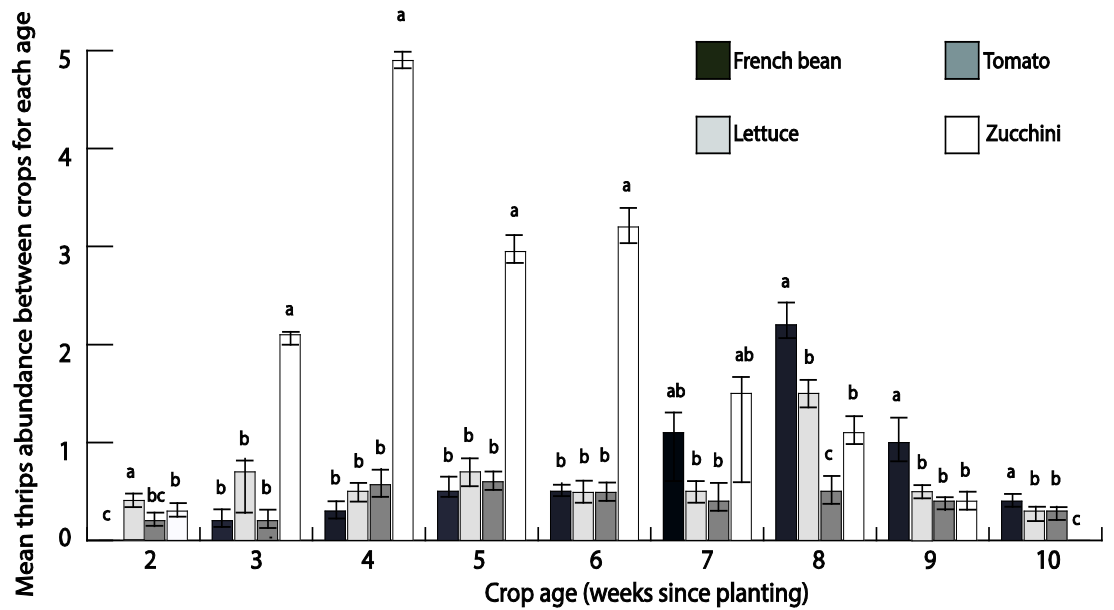


Figure 5.2 Mean (back-transformed mean \pm 1 standard error) number of *F. occidentalis* at each crop age, sampled in each crop, across all plantings.

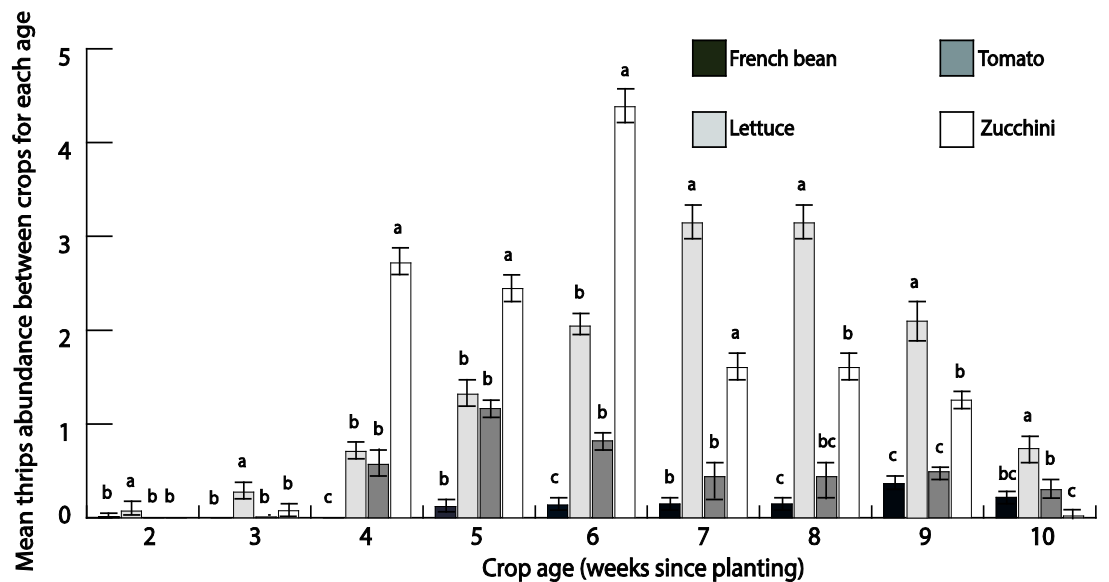


Figure 5.3 Mean (back-transformed mean \pm 1 standard error) number of *F. schultzei* at each crop age, sampled in each crop, across all plantings.

Pearson correlation coefficient determined that *F. occidentalis* abundance in French bean, lettuce and tomato was positively correlated with increasing crop age, abundance increasing over time within the crop, and was negatively correlated with crop age in zucchini, abundance decreasing over time (Table 5.2). Correlation of *F. schultzei* abundance in all four crops was positively correlated with crop age (Table 5.2).

Table 5.2 Pearson Correlations coefficient for the relationship between *F. schultzei* and *F. occidentalis* abundance and increasing crop age (weeks since planting)

<i>F. occidentalis</i>			<i>F. schultzei</i>		
Crop	<i>r</i>	Sig. (2-tail)	Crop	<i>r</i>	Sig. (2-tail)
French bean	0.781	< 0.001	French bean	0.011	< 0.001
Lettuce	0.432	< 0.001	Lettuce	0.458	0.002
Tomato	0.201	0.020	Tomato	0.021	< 0.001
Zucchini	-0.630	< 0.001	Zucchini	0.566	< 0.001

*value of *r*: -1.0 to -0.5 or 1.0 to 0.5 strong; -0.5 to -0.3 or 0.3 to 0.5 moderate; -0.3 to -0.1 or 0.1 to 0.3 weak; -0.1 to 0.1 no relationship

Discussion

Abundance in crop

Of the 17 thrips species recovered, *F. occidentalis* and *F. schultzei* were the two most abundant species collected from the four crops across the three-year trial period. Both species were recorded in high abundance in zucchini, which indicates that this crop likely provides the optimum conditions for feeding, breeding, shelter, or a combination of the three, and that there may be no competition for resources between the two species in this crop. That *F. schultzei* abundance was equally abundant in lettuce (a non-flowering crop) and zucchini (a flowering crop) shows the breadth of this species' potential host range. Pollen is an important nutritional requirement for reproduction and development for

many flower thrips (Kirk 1985b). *Frankliniella occidentalis* has been shown to have higher fecundity and larval development on a diet inclusive of pollen (Trichilo & Leigh 1986), whilst *F. schultzei* has been reported to perform equally as well with or without pollen on *Malvaviscus arboreus* Cav. Therefore, pollen may not be as important for *F. schultzei* success as *F. occidentalis* (Milne et al. 1996b), explaining the difference in their relative abundance in lettuce.

Abundance of both species was low in tomato and French bean compared to lettuce and zucchini. While there is potential that the sample method may have had an effect on abundance (tomato was not destructively sampled), the likelihood of this is low due to the thoroughness of in field scouting and beating of tomato plants in combination with flower collection. In tomato *F. schultzei* was more abundant than *F. occidentalis*, which is consistent with findings from other studies (Jiménez Jiménez et al. 2006; Kakkar et al. 2012b; Monteiro et al. 2001; Sakurai 2004). In French bean, *F. occidentalis* was more abundant than *F. schultzei*, which contrasted with findings by Nyasani et al. (2012) in Kenya, but was consistent with an Australian study by Duff (2012). Insect population dynamics are highly site specific, with a species regarded as a pest in a crop in one part of the world often noted as causing little to no damage in the same crop elsewhere (Hill 1987). This highlights the need for further research into the relationship between thrips and agro-ecosystems to be performed in a wide range of regions if management strategies based on ecological knowledge are to be developed for pest thrips species.

Thrips abundance within the plant

Frankliniella occidentalis and *F. schultzei* displayed similar patterns of spatial distribution within each crop, with higher abundance recorded in flowers compared to leaf plus stem and growing tip samples. This is not surprising as both species are flower dwelling thrips (Chellemi et al. 1994; Milne et al. 1996a), and indicates that flower-sampling is a

sound method of assessing thrips numbers in French bean, tomato and zucchini. Thrips were less abundant in zucchini male flowers compared to female flowers. This was unexpected as male flowers have a higher pollen content and more nectar than female flowers. It is possible that female zucchini flowers provide more than just the nutritional needs of the thrips. Rosenheim et al. (1990) found more *F. occidentalis* adults in female cucumber flowers compared to male, and suggested that thrips may have been feeding on the developing fruit. Very few thrips were recovered from the growing tips of any crop.

Temporal distribution

In vegetable agro-ecosystems, an increase in thrips abundance is associated with the phenology of the crop, where density increases as the crop matures (Shelton 1995). This phenomenon was apparent in this study, where population establishment and increased abundance coincided with successive periods of the crop's phenology: budding, flowering and fruiting, and head formation in lettuce. This was followed by a decline with senescence and abscission of leaves, when the suitability and nutritional quality of the plant was no longer optimal for thrips feeding or reproduction (Nyasani et al. 2012; Nyasani et al. 2013; Palomo et al. 2015).

Population establishment can be defined as the crop age at which thrips numbers began to build, followed by an increase in abundance thereafter. Thrips established themselves earliest in lettuce, at two weeks after transplanting, followed by zucchini and tomato in the third week, and at three to four weeks after seeding in French bean. The difference in these periods of establishment reflects the structural differences between the crops. Thrips seek out protection in narrow crevices such as leaf folds, under bracts, in buds, within leaf bases and along leaf veins (Morse & Hoddle 2006). Therefore, at two weeks, lettuce provided the most suitable environment, with four to five densely arranged leaves present at this crop stage compared to French bean and zucchini, which

were direct seeded, and were still developing leaves. In the flowering crops, French bean, tomato and zucchini, establishment occurred during the pre-flowering period. This was followed by an increase in abundance at week four in tomato and zucchini, and week four to five in French bean, corresponding with the findings of Kasina et al. (2009) and Ssemwogere et al. (2013). Nyasani et al. (2013) found that *F. occidentalis* colonised French bean at the two to three leaf stage and population establishment occurred at pre-budding (three to five weeks after seeding).

A clear crop effect, relating to the physiology of the plant growth stage (budding, flowering, senescing) was demonstrated by the temporal segregation of the two species across the life of the crop treatments. *Frankliniella occidentalis* was temporally separated by crop age between the zucchini (weeks three to six) and French bean (weeks eight to ten) flowering periods. Similarly, *F. schultzei*, displayed a temporal segregation, by crop age, between the zucchini flowering period (weeks four to six) and the later stages of the lettuce crop (weeks eight to ten). This suggests that both *F. occidentalis* and *F. schultzei* established populations in zucchini flowers before moving into French bean and lettuce, respectively, as the zucchini crop approached senescence and flower numbers declined. Rhainds & Shipp (2003) determined that female *F. occidentalis* were more likely to disperse from a senescent than a healthy chrysanthemum inflorescence, and inversely more likely to colonise a healthy inflorescence.

Conclusion

To improve the control of thrips, it is necessary to understand fluctuations in populations as this knowledge allows growers to anticipate periods of high abundance and apply controls accordingly. Crop treatment had a strong effect on species, with *F. occidentalis* more abundant in French bean than *F. schultzei*, whereas in lettuce and tomato,

F. schultzei were more abundant compared to *F. occidentalis*. Both species were equally abundant in zucchini. In all flowering crops, total adult thrips abundance was greater in flower samples compared to all other sample types (within each crop). This was reflected in their temporal distribution, which was related to the physiological growth stage of the crop, with *F. occidentalis* moving into French bean and zucchini, and *F. schultzei* into tomato and zucchini, just prior to flowering. *Frankliniella occidentalis* abundance was greatest in zucchini between three and six weeks, followed by a shift to French bean. Similarly, *F. schultzei* abundance was greatest in lettuce between the early and later stages of the crop, with higher abundance in zucchini between weeks four and six. Knowledge of the relative abundance and temporal distribution of key thrips species in vegetable agro-ecosystems can be used to optimise field monitoring and the implementation of control strategies according to the species and the age of the crop.

Chapter Six: Reproductive host association between thrips and hosts: French bean, lettuce, tomato and zucchini

Introduction

Host plant records for many thrips species are ambiguous. Traditionally, literature on thrips host association classified a plant host to be any plant from which an adult thrips had been collected (Froud et al. 2001). A plant may therefore be classified as a host based solely on the presence of a thrips, with no information concerning the feeding or reproductive relationship that would confirm a specific host association (Mound 2005). This deficiency was highlighted by Milne et al. (1996a) when investigating the polyphagous nature of *Frankliniella schultzei*. A review of the literature found that 83 plants across 35 families had been recorded as feeding hosts for *F. schultzei*. However, many of these records merely indicated that *F. schultzei* had been collected from the plant with no evidence to suggest that feeding was taking place. To highlight the problem with defining host association based solely on presence of the species, Milne et al. (1996a) noted a study where *Thrips imaginis* was collected from washing hung on a clothes line (Lloyd 1973), meaning that bed linen could be defined as a host despite it being unlikely that *T. imaginis* would be involved in feeding or reproduction on bed linen.

A truer definition of a host plant is that it provides an adequate environment for reproduction or feeding to occur (Froud et al. 2001; Manners et al. 2010). To further describe the relationship, the level of host association can be classified as primary, secondary or temporal. Primary hosts are those that provide optimum conditions for population fitness and survival, where a species is regularly found feeding, or breeding, in high numbers. Plants that provide only a subset of these features and are used less regularly are considered secondary hosts (Walter & Benfield 1994). The classification of a temporal host is used to define the association where thrips will alight and feed

upon plants on which they cannot reproduce, utilising the plant temporarily until a more suitable host is located.

Feeding hosts typically provide all nutritional requirements for an insect to complete their lifecycle. Some plants are more nutritionally adequate for a particular species compared to another. For instance, pollen is considered a nutritional component of the diet of many flower thrips, required for egg laying and lifecycle completion (Milne et al. 1996b). Reproductive hosts provide all nutritional requirements for breeding to occur and are important for insect population growth in a crop. These host plants promote reproduction, and therefore subsequently support relatively high numbers of both adult and immobile feeding larval instars (Mound & Marullo 1996; Northfield et al. 2008; Walter & Benfield 1994). For a plant to be classified as a reproductive host, both immature and female thrips need to be recovered in high relative abundance, over a period of time (crop life) and on a regular basis (successive seasons) (Mound & Marullo 1996; Walter & Benfield 1994). Many papers have reported a reproductive association between thrips and a plant based on the recovery of both adults and immatures from a crop (Groves et al. 2002; Johnson et al. 1995; Kasina et al. 2009; Toapanta et al. 1996; Workman et al. 2007). However, very few of these papers have identified the larval thrips to species. This classification based on immature and adult collections alone is especially problematic in vegetable agro-ecosystems, which can support a wide number of thrips species throughout the life of the crop (as shown in this study), and therefore clarifying which of the species present has a reproductive association with that plant may not be possible (Paini et al. 2007).

Seventeen thrips species were collected and recorded across the four vegetable agro-ecosystems in this study (See Chapter 4 - Thrips species assemblage). The key species within each assemblage were determined as *Desmothrips tenuicornis*, *F. occidentalis*, *F. schultzei*, *Haplothrips gowdeyi*, *Megalurothrips usitatus*, *Pseudanaphothrips achaetus*, *Tenothrips frici* and *T. tabaci* in French bean; *D. tenuicornis*, *F. occidentalis* and *F. schultzei* in lettuce; *F. occidentalis*, *F. schultzei*, *P. achaetus*, *T. palmi* and *T. tabaci* in tomato; *D. tenuicornis*, *F. occidentalis*, *F. schultzei*, *M. usitatus*, *P. achaetus*, *T. frici*, *T. palmi*

and *T. tabaci* in zucchini. These assemblages were determined based on adult samples. This does not necessarily mean that a primary reproductive or feeding host association exists between these species and the crop.

Of the seventeen species collected, host associations have been determined for five species across the four crops in this study. Feeding and breeding host associations have been described for *F. occidentalis* in French bean (Nderitu et al. 2008; Olson et al. 2006; Zhang et al. 2007) and tomato (Funderburk 2009; Zhang et al. 2007) and *M. usitatus* in French bean (Tang et al. 2015). Feeding associations have been reported for *T. palmi* on French bean (Hollinger 1992), tomato (Kawai 1990) and lettuce (McRitchie 1986), *T. tabaci* in tomato (Ssemwogerere et al. 2013) and *F. schultzei* in tomato (Ssemwogerere et al. 2013) and French bean (Nyasani et al. 2012). Understanding the reproductive host association is not only important for a greater comprehension of thrips biology and ecology, but is critical for understanding what is driving rapid population increases in an agro-ecosystems. However, records for reproductive hosts are still limited for many thrips due to the length of time needed to determine the association (regularity over successive seasons or years) and the difficulty in identifying immature thrips to species. Understanding the suitability of a plant for thrips reproduction provides key information on the population dynamics of thrips in agro-ecosystems, as a reproductive host promotes an increase in the population. Establishing if a reproductive host association exists between a thrips species and a crop is important in differentiating between increases in thrips density as a result of migrations into the crop for feeding, and increases due to reproduction in the crop. In this chapter, we explore the suitability of French bean, lettuce, tomato and zucchini as reproductive hosts, including identifying the species that have a reproductive host association with one or more of the four vegetable crops.

Materials and methods

Field surveys

As described in the General research methodology (Chapter 3), the field survey was conducted as eleven plantings over the course of a three-year period. Each planting consisted of four blocks, four crop treatments and ten replicates per block. One plant sample (flower, growing tip, leaf and stem or whole plant) was collected from each replicate per crop, weekly over the life of the crop. Flower and growing tip samples were collected into 95% ethanol. Stem and leaf and whole lettuce samples were removed in the field (destructive sampling) and collected into individual paper bags, deconstructed in the laboratory and beaten over a tray to dislodge thrips. Thrips were then collected into vials of 70% ethanol. Tomato leaf and stem and growing tip samples were not destructively collected, but beaten over a tray in crop and thrips collected into 95% ethanol. All adult thrips were slide mounted and identified to genus and species, using the Oz Thrips (2016) interactive lucid key under a compound microscope and sexed.

For many taxa of thrips, it is impossible to morphologically identify immature stages due to the lack of taxonomic keys (Kumar et al. 2013). Therefore, immature thrips were recorded as total abundance counts corresponding to the crop, planting and sample date and stored in 95% ethanol. Sub-samples of immature thrips taken from weekly field samples, were reared through to the adult stage, identified to genus and species using the Oz Thrips Lucid key (2016) and sexed. Sub-sampling took place on two or three occasions, from each crop, in each of the eleven plantings at weeks three or four; six or seven and/or week ten, after planting or seeding (see Appendix D for sub-sample dates). Immature thrips were removed from only five of the ten replicate samples (one sample per replicate). Each sample consisted of one flower, leaf and stem and growing tip. The five replicate samples were pooled, and reared on Lebanese cucumbers as per the adapted method of De Graff & Wood (2009) in Manners et al. (2013). These sub-samples of identified

immature thrips were used to determine whether reproduction by a species occurred in the crop.

Lebanese cucumbers were cleaned in a 60:40 bleach: water solution, followed by a detergent and water mix, rinsed and left to air dry. Cucumbers were cleaned to ensure any chemical insecticide residue present was removed and to remove fungal inoculum. Rearing cages were constructed from a plastic storage container (30 cm wide x 15 cm long x 20 cm high). The lid of each container had a 10 cm x 15 cm section removed and 90 µm mesh glued on the top to provide air circulation and reduce humidity and condensation build-up. Each cage contained a thin layer of vermiculite on the bottom of the container, covered with paper towel, which provided a pupation medium. A plastic dish (3 cm in diameter x 0.5 cm high) filled with bee pollen and a second identical dish holding a 3 cm dental wick dipped in a honey water solution provided a food source for adult thrips. One or two sterilised cucumbers were placed in a cage on an upturned plastic tray (10 cm wide x 6 cm long x 2 cm high). The bottom section of the container had been cut away and replaced with 90 µm mesh on which the cucumbers rested. The cucumbers were placed on these stages to ensure good air circulation. Immature thrips were transferred onto a cucumber using a fine brush, placed into individual cages, and labelled according to the sample (crop, planting and date). Cages were checked daily and adults collected into 95% ethanol, slide mounted and identified. Cucumbers were replaced as they became soft.

Rearing took place in an insect rearing room, at a temperature of $24^{\circ}\text{C} \pm 3^{\circ}\text{C}$. The room was naturally lit by large windows, with light and dark hours approximately 11:13 (light:dark) in March, and 10:14 (light:dark) in October.

Sentinel planting

Insect free French bean and lettuce plants were exposed in the field for seven days. Any adult thrips present on the field-exposed plants were removed and the plants were isolated under laboratory conditions to monitor for the emergence of immature thrips (those which had developed from eggs laid in

the field thus demonstrating a reproductive association). The methodology used in this experiment was adapted from Karban & Strauss (1994). Based on the total number of immatures collected from the field, French bean and lettuce were used for the sentinel experiments – they both supported large numbers within the crop (see Chapter 4).

French bean (commercial variety 'Labrador') and lettuce (commercial variety 'Rador') seedlings were grown from seed inside 90 µm mesh cages (40 cm wide x 40 cm long x 100 cm high), to ensure exclusion of thrips, within a glasshouse at GRF. Seeds were planted into propagation trays (29.5 cm wide x 35 cm long x 5 cm high) filled with pre-moistened sterile potting medium (Yates Seed Raising Mix). Approximately 30 lettuce seeds and 20 French bean seeds were planted into ten trays, at around 1 cm deep. Trays were placed inside the mesh cages (four trays per cage) and watered every second day using a hand spray bottle to keep the soil moist. Seedlings began to emerge around one week after seeding, and were thinned, leaving approximately 100 seedlings of each. Three weeks after emergence, seedlings were transplanted into individual plastic pots (11.2 cm diameter top, 1 L volume) filled with potting mix (Yates General Purpose Potting Mix) and fertilised with seaweed extract fertiliser (Seasol Powerfeed for Vegies). Potted seedlings were around six weeks old when placed in the field. French bean seedlings were at pre-inflorescence emergence (code 042) and lettuce at head development (20% of the expected head size reached) (code 42) according to the Biologische Bundesanstalt für Land und Forstwirtschaft (BBCH) scale for French beans and leafy vegetables forming heads (Meier 2001). Growing the seedlings free from insects meant that observation of an immature thrips on the sentinel seedling once collected from the field indicated that reproduction had occurred.

There were four treatments, consisting of caged and uncaged lettuce, and caged and uncaged French bean. Uncaged treatments were exposed to thrips landing on the plants and possible oviposition. Caged treatments acted as controls, excluding thrips from landing on the plants in the field. Caged seedlings were covered by a clear plastic cylinder (11 cm diameter x 30 cm high), which was placed over the top of the seedling and secured by being

pushed down 5 cm into the potting mix. Each cylinder had a 3 cm diameter hole in the side, covered with 90 μ m mesh, to allow air circulation while excluding thrips.

Each replicate block was 120 cm wide x 240 cm long, divided into four treatments (60 cm wide x 120 cm high). In each treatment, ten holes were dug at 30 cm intervals, arranged in a five by two layout. Potted plants, caged and uncaged, were placed in the holes, with the base of the plant flush with the ground. Placement in the ground reduced transpiration to avoid plant desiccation and simulated regular field conditions. Pots were labelled by replicate, treatment and plant number (1 to 10) and watered daily. There were four replicates located in different areas around the GRF farm station (see Appendix E for trial layout and location). A total of eighty lettuce and eighty French bean seedlings were placed in the field. Each replicate contained twenty lettuce and twenty French bean seedlings.

Plants were removed from the field after seven days and placed back into the mesh cages inside the glasshouse, arranged by replicate and treatment (ten plants from one replicate of a treatment in one cage). A clear plastic cylinder (as per the caged treatment) was placed on the uncaged treatments at the time of removal from the field to prevent contamination en route to the glasshouse. After movement to the glasshouse, all plants from all treatments were inspected for thrips. All adult thrips were removed with a fine brush into a vial filled with 95% ethanol. Thrips were collected into individual vials and labelled according to replicate, treatment and plant number. Thrips were slide mounted and identified according to the interactive key Oz Thrips (2016). No immature thrips were present on any of the plants on removal from the field.

The clear plastic cylinders remained on all treatments after removal from the field and placement into the mesh cage to ensure any emerging thrips did not leave the plant on reaching adulthood. Plants were checked daily, immature numbers counted on emergence and adults collected into 95% ethanol and labelled accordingly.

The sentinel experiment was conducted on four occasions: 2nd October 2012, 5th March 2013, 4th October 2013 and the 1st March 2014. These dates correspond to the date the potted plants were placed in the field. Each experiment was analysed separately.

Statistical analysis

Data was checked for normality and homogeneity of variance using Shapiro-Wilk ($p > 0.05$) and Levene tests before being square root transformed $(X + 0.5)^{1/2}$ to normalise the data.

Field surveys

To determine if there was a significant difference in immature abundance amongst French bean, lettuce, tomato and zucchini, data was subjected to a two-way ANOVA, with planting (1 to 11) and crop as factors. Sample types (flower, leaf and stem, and growing tip) were pooled to standardise the data across the four crops (lettuce was sampled as a whole plant). Data was further subjected to a Tukey HSD at the 95% CI to determine the mean difference in immature abundance between crops for each planting (no comparison between the crops across the plantings).

A Pearson chi-square test for association was conducted between crop and species for the abundance of immatures reared to adult from each crop (referred to as sub-sampled immatures), followed by a Cramer V symmetric measure to test the strength of the association (maximum ranges between -1 and +1). Data was further analysed by cross tabulation in a 4 x 4 contingency table of observed frequencies to determine that the observed field emerged adult abundance was not by chance.

The percentage of female and male adult thrips was calculated for the dominant species across the four crops (*D. tenuicornis*, *F. occidentalis*, *F. schultzei*, *M. usitatus* and *P. achaetus*) (as determined in Chapter 4).

Sentinel experiments

A two-way ANOVA was performed on each of the four sentinel experiments to determine if there was a significant effect of crop or thrips species on total number of thrips reared through to adult stages (referred to as sentinel emerged) or interaction between these factors. This was followed by pairwise comparison of each sentinel emerged species mean within and between treatments (French bean and lettuce) at a 95% CI. Caged treatments were excluded from the analysis due to the data consisting only of zeros.

Results

Field surveys

Crop ($F_{(3,396)} = 37.172, p < 0.001$) and planting ($F_{(10,396)} = 12.243, p < 0.001$) had a significant effect on immature abundance and there was a statistically significant interaction between the two factors ($F_{(3,396)} = 10.385, p < 0.001$), indicating that mean abundance in the four crops was not consistent amongst plantings.

Based on a Tukey HSD, there were generally significantly more immatures in French bean compared to other crops in plantings 1 to 8, but in the later plantings (year three) there were more in lettuce (Figure 6.1, for each planting, crop means with a letter in common are not significantly different, $p > 0.05$). Based on the effect of crop, French bean ($F_{(3,396)} = 7.355, p < 0.001$), lettuce ($F_{(3,396)} = 8.899, p < 0.001$) and zucchini ($F_{(3,396)} = 12.726, p < 0.001$) had a significant effect on the number of immatures present ($p < 0.001$), however there was no effect of tomato ($F_{(3,396)} = 0.610, p = 0.805$).

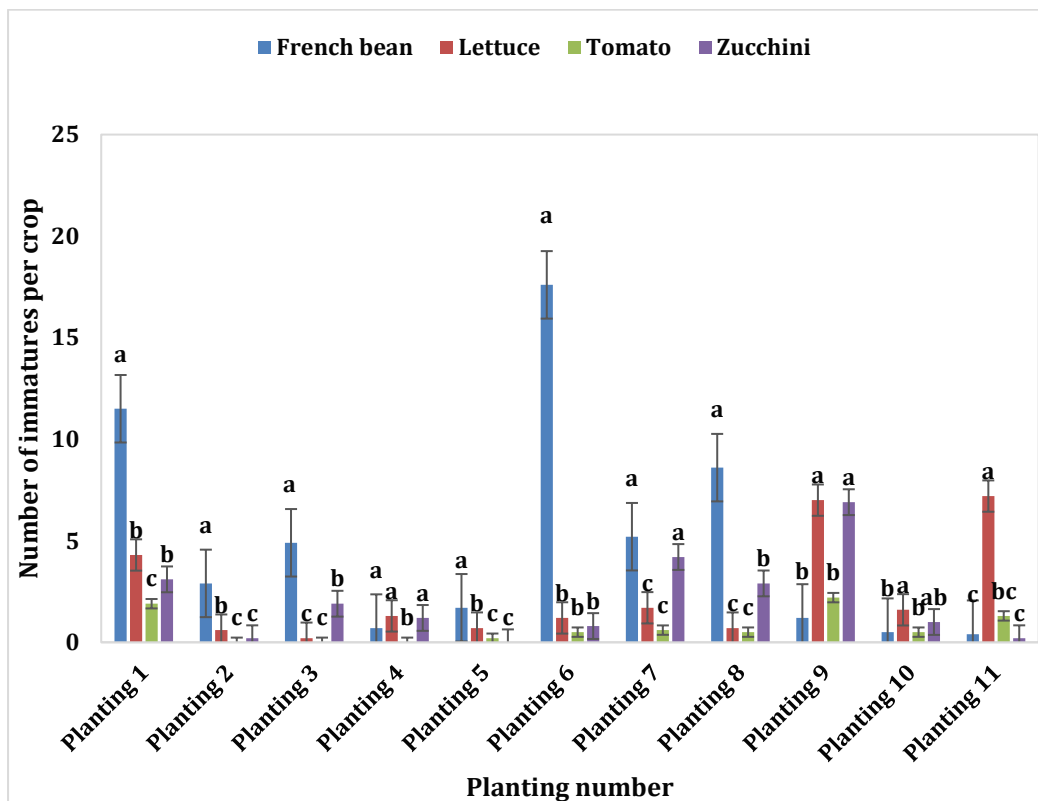


Figure 6.1 Mean (± 1 standard error) number of immature thrips collected from each crop in each planting.

The immature thrips collected from the field and reared through to adults (sub-sampled immatures) were identified as *F. occidentalis*, *F. schultzei*, *M. usitatus* and *T. tabaci*. Based on the Pearson chi-square test, there was a significant association between crop and species $X^2 (9) = 549.07, p < 0.001$, which was considered strong, $V = 0.840, p < 0.001$, by Cramer's V test. The cross tabulation of observed and expected frequencies of emerged adults in each crop show that the frequency of *M. usitatus* and *T. tabaci* in French bean, *F. occidentalis* and *F. schultzei* in lettuce and tomato, and *F. occidentalis*, *F. schultzei* and *T. tabaci* in zucchini, could not have been observed by chance alone (the observed counts were higher than the expected) (Table 6.1).

Table 6.1 Cross tabulation and observed count and expected frequencies of sub-sampled immature collected and reared from each crop

		Species				
Crop		<i>F. occidentalis</i>	<i>F. schultzei</i>	<i>M. usitatus</i>	<i>T. tabaci</i>	Total
French bean	Observed Count	58	4	210	54	326
	Expected	83.5	90	113.2	39.3	326
	% of contribution	9.6	0.7	34.7	8.9	53.9
Lettuce	Observed Count	68	129	0	4	201
	Expected	51.5	55.5	69.8	24.3	201
	% of contribution	11.2	21.3	0	0.7	33.2
Tomato	Observed Count	6	15	0	0	21
	Expected	5.4	5.8	7.3	5.5	21
	% of contribution	1	2.5	0	0	3.5
Zucchini	Observed Count	23	19	0	15	57
	Expected	14.6	15.7	19.8	6.9	57
	% of contribution	3.8	3.1	0	2.5	9.4
Total	Observed Count	155	167	210	73	605
	Expected	155	167	210	73	605
	% of contribution	25.6	27.6	34.7	12.1	100

The percentage of female and male adult thrips showed there were fewer adult males present in proportion to adult females in all crops (Table 6.2).

Table 6.2 Percentage of female and male adult thrips collected throughout the field survey, corresponding to crop and year.

		Species									
Year	Crop	<i>D. tenuicornis</i>		<i>F. occidentalis</i>		<i>F. schultzei</i>		<i>M. usitatus</i>		<i>P. achaetus</i>	
		♀	♂	♀	♂	♀	♂	♀	♂	♀	♂
1	French bean	100	0	57.65	42.35	93.95	6.05	91.20	8.8	100	0
2		100	0	63.15	36.85	82.05	17.95	93.40	6.60	100	0
3		68.5	31.5	100	0	72.10	27.90	100	0	100	0
1	Lettuce	93.65	6.35	96.95	3.05	60.70	39.30	0	0	0	0
2		100	0	92.40	7.60	91.75	8.25	0	0	0	0
3		68.45	31.55	96.35	3.65	96.65	3.35	0	0	0	0
1	Tomato	0	0	81.95	18.05	89	11	0	0	87.70	12.30
2		0	0	87	13	95.65	14.35	0	0	91.65	8.35
3		0	0	94.10	5.90	99.30	0.70	0	0	93.55	6.45
1	Zucchini	100	0	64.30	35.70	63	37	100	0	100	0
2		100	0	96.70	3.30	93.70	6.30	100	0	93.55	6.45
3		100	0	92.95	7.05	92.90	7.10	100	0	89.45	10.55

Sentinel experiments

On removal of the sentinel plants from the field, six species of adult thrips were recovered: *F. occidentalis*, *F. schultzei*, *H. gowdeyi*, *M. usitatus*, *T. palmi* and *T. tabaci* (Table 6.3). All specimens were adult females. All six adult species were collected from French bean sentinel plants, and only *F. occidentalis* and *F. schultzei* were collected as adults from lettuce. *Haplothrips gowdeyi* were only present on French bean in October 2012, and *T. palmi* on French bean in October 2012 and 2013.

Table 6.3 Total adults removed from uncaged sentinel plants upon removal from the field.

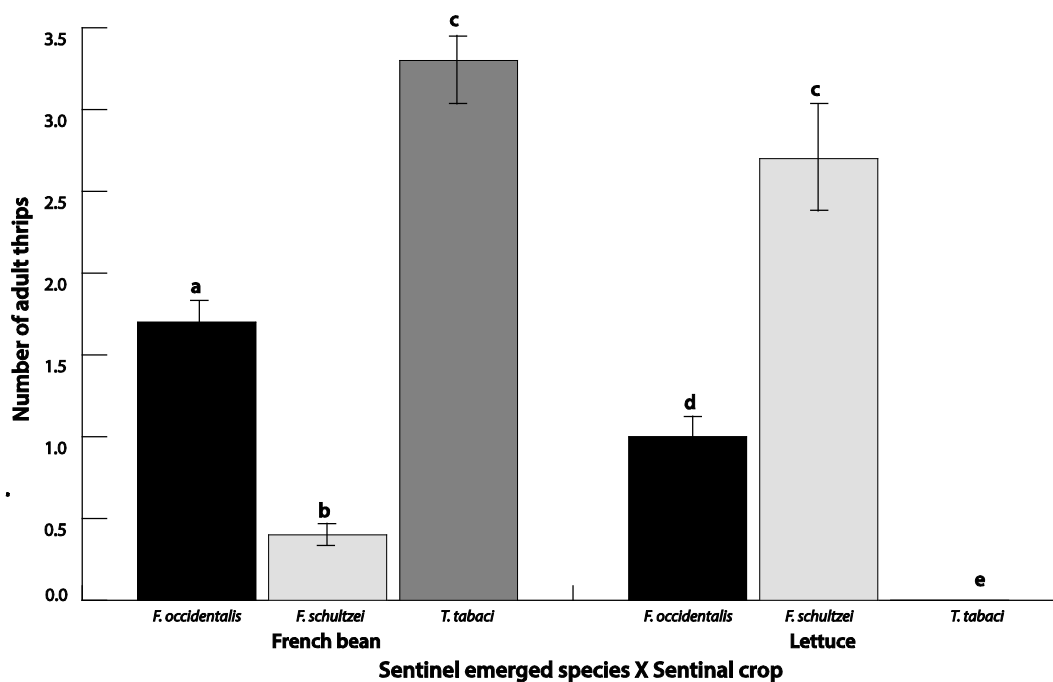
	<i>F. occidentalis</i>	<i>F. schultzei</i>	<i>H. gowdeyi</i>	<i>M. usitatus</i>	<i>T. palmi</i>	<i>T. tabaci</i>
French bean	16	3	12	8	4	5
Lettuce	20	28	0	0	0	0

No immature thrips were present at the time of removal from the field on any of the caged or uncaged sentinel plants in all four experiments. Therefore, any thrips that emerged on the sentinel plants were from eggs laid on the plants in the field, indicating that reproduction had occurred. Both *Frankliniella* species were collected as sentinel emerged adults from sentinel French bean and lettuce in all four experiments. *Thrips tabaci* were only recovered as sentinel emerged adults on sentinel French bean in the October 2012 and 2013 experiments; while *M. usitatus* were collected as sentinel emerged adults on French bean plants in the March 2013 and 2014 experiments. On lettuce, *T. tabaci* was collected as sentinel emerged adults in the October 2013 experiment. No *H. gowdeyi* or *T. palmi* were recorded as sentinel emerged adults in either crop.

Crop and species had a significant effect on sentinel emerged abundance, but not in all four sentinel experiments (Table 6.4), however there was an interaction effect between the two factors in all experiments. Pairwise comparisons for the October 2012 experiment determined significantly more *F. occidentalis* and *T. tabaci* emerged on French bean compared to lettuce, and more *F. schultzei* on lettuce compared to French bean (Figure 6.2, means with different letters are significantly different, $p < 0.05$). A similar result was observed in October 2013 (Figure 6.3, means with different letters are significantly different, $p < 0.05$). In the March 2013 and 2014 experiments, there were significantly more *F. occidentalis* and *M. usitatus* in French bean compared to lettuce, and significantly more *F. schultzei* in lettuce than French bean (Figure 6.4 and 6.5, means with different letters are significantly different, $p < 0.05$).

Table 6.4 Results of two-way ANOVA for each sentinel trial.

	Factor	df	<i>F</i>	Sig.
October 2012	Crop	1,234	27.22	< 0.001
	Species	2,234	2.73	0.067
	Crop x Species	2,234	222.27	< 0.001
March 2013	Crop	1,234	24.92	< 0.001
	Species	2,234	5.74	0.004
	Crop x Species	2,234	262.78	< 0.001
October 2013	Crop	1,234	3.20	0.075
	Species	2,234	9.03	< 0.001
	Crop x Species	2,234	264.06	< 0.001
March 2014	Crop	1,234	23.54	< 0.001
	Species	2,234	8.96	0.126
	Crop x Species	2,234	151.78	< 0.001

**Figure 6.2** Mean numbers (± 1 standard error) of sentinel emerged thrips in French bean and lettuce in October 2012.

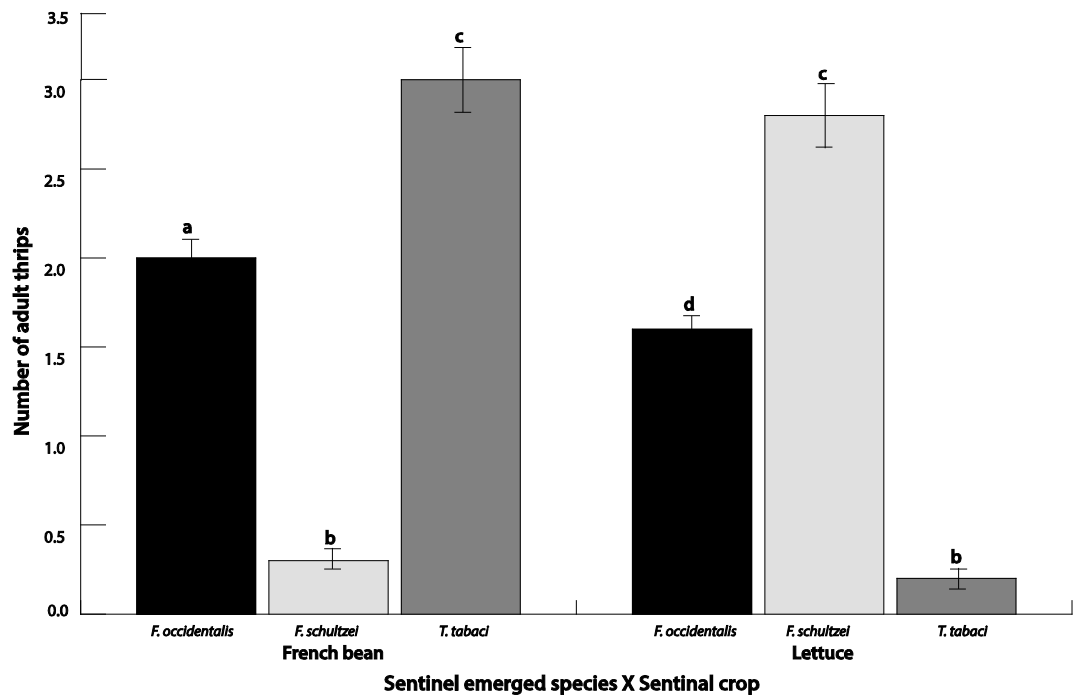


Figure 6.3 Mean numbers (± 1 standard error) of sentinel emerged thrips in French bean and lettuce in October 2013.

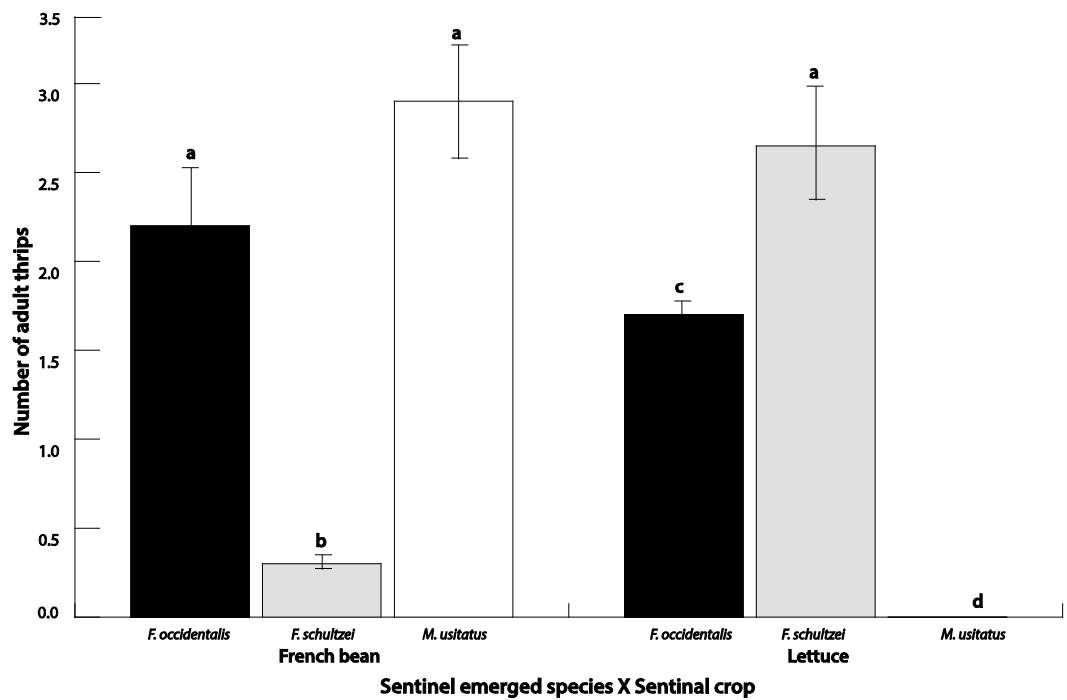


Figure 6.4 Mean numbers (± 1 standard error) of sentinel emerged thrips in French bean and lettuce in March 2013.

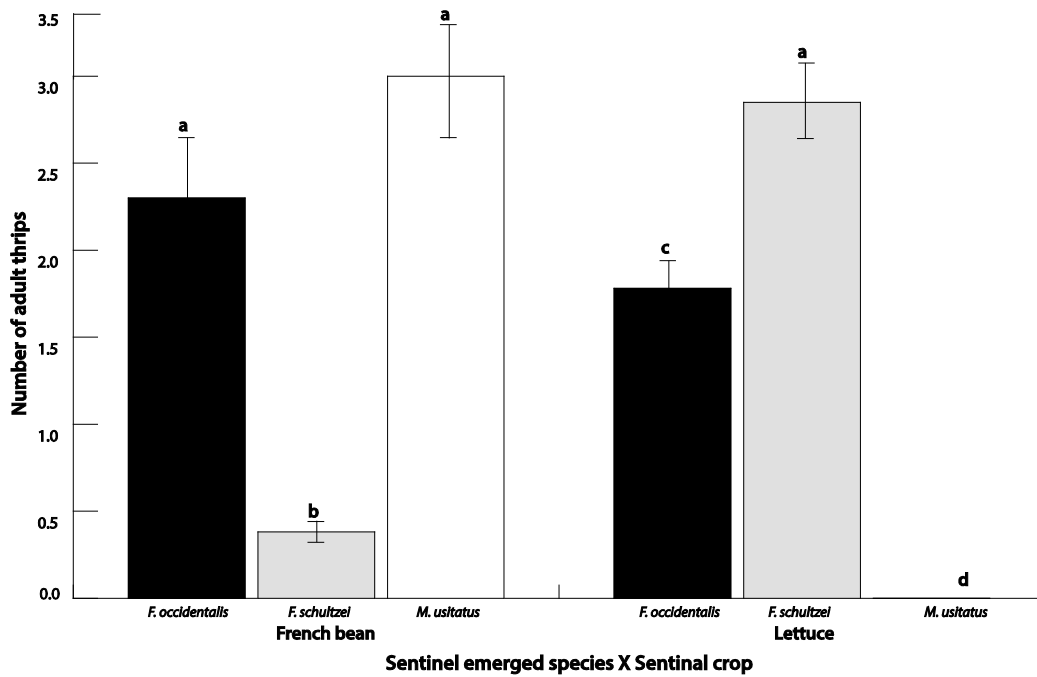


Figure 6.5 Mean numbers (± 1 standard error) of sentinel emerged thrips in French bean and lettuce in March 2014.

Discussion

The problem with host association classification is that often there is no strong evidence of reproduction occurring, and no identification of the immature stages, with an assumption that immatures present are the same species as the adults. For example, Workman et al. (2007) stated that lettuce was a poor reproductive host for *T. tabaci* in comparison to onion crops in the Pukekohe area, South Auckland, New Zealand, based on the low recovery of immature thrips in lettuce compared to onion. While the low immature abundance does indicate a low rate of thrips reproduction, classification as a poor reproductive host for *T. tabaci* cannot be drawn conclusively from a low abundance of unidentified immature thrips alone. Of particularly relevance in that study was the report that adult *F. occidentalis* and *F. intosa* (Trybom) were also collected from the same lettuce crops along with *T. tabaci*. Therefore, in this study, conclusions are drawn from the relative abundance of

immatures collected in the field surveys, identification of sub-sampled immatures reared through to the adult life stage and from the sentinel emerged species in four sentinel experiments, to determine the existence of reproductive association.

Frankliniella occidentalis and *F. schultzei* have both previously been reported reproducing on French bean (Kakkar et al. 2012a; Seal et al. 2014; Zhang et al 2007) and tomato (Funderburk 2009; Zhang et al. 2007). The reproductive association of *M. usitatus* (Chang 1987; Tang et al. 2015) and *T. tabaci* (Alston & Drost 2008) with French bean has also been determined. However, these are the first published reports of a reproductive host association between *F. occidentalis*, *F. schultzei* and *T. tabaci* and lettuce and zucchini. Very few studies have investigated the reproductive association between a crop and a thrips species. For example, Palomo et al. (2015) estimated that based on the high relative abundance of *F. occidentalis* in zucchini crops in Mexico, and the weather conditions, which were optimal for *F. occidentalis* reproduction, it is likely that this species could complete at least one generation in the crop. However, with no evidence of reproduction this was simply a hypothesis. Identifying if an association exists and then the level of association is fundamental for understanding the population dynamics of thrips and the management of infestations in crop.

French bean, lettuce, tomato and zucchini displayed a reproductive association with at least two thrips species. However, the strength of these associations as primary or secondary reproductive hosts varied between the species and the vegetable crop. French bean are considered a reproductive host for a wide range of thrips species, including *F. occidentalis*, *F. schultzei* and *M. usitatus*, and French bean pods are often used as a rearing medium for culturing thrips colonies (De Graff 2009; Murai & Loomans 2001; Steiner & Goodwin 1998), which is a reflection of their suitability as a reproductive host. This is evident in this study, with the field surveys generally indicating a higher immature abundance in French bean compared to all other crops in many of the

plantings. French bean also supported a large and diverse adult population, which is likely a reflection of their suitability as a reproductive host; and would subsequently lead to increased abundance in crop.

A high number of immature *M. usitatus* and *T. tabaci* immatures were recovered from the field sub-samples and sentinel French bean plants, which suggests a primary host association. While a low abundance of *F. schultzei* immatures were collected from sub-samples and sentinel French bean plants, indicating a secondary association. *Thrips tabaci* are considered to have a broad host range (Alston & Drost 2008). The results in this study support Alston & Drost (2008) who suggested that this species has a strong reproductive association with French bean. In this study, *T. tabaci* displayed a seasonal difference in reproduction on sentinel French bean, with the species only present on sentinel plants in October, when temperatures are increasing. This suggests that the presence and population growth of *T. tabaci* may be dependent on warmer conditions (see Chapter 7).

The results from the sentinel experiments and sub-sampled immatures indicate that there is a strong reproductive association between *M. usitatus* and French bean, particularly as they were not found reproducing on any of the other three crops. The absence of *M. usitatus* from sentinel French bean plants in October in both years, suggests that population growth is influenced by cooler autumn conditions (see Chapter 7 and 8). *Megalurothrips usitatus* are associated with Fabaceae crops (Chang 1987; Oz Thrips 2016; Tang et al. 2015). The results in this study are in accordance with those found by Tang et al. (2015), who determined that population growth of this species was greatest on French bean compared to other Fabaceae crops such as pea, cow pea and lima bean. *Megalurothrips usitatus* appears to be monophagous in its association with French bean, based on the results from the sub-sampled immatures, the sentinel experiments and the low numbers of adults collected from all other crops in the field survey (see Chapter 4).

Monophagous species tend to develop a cyclic relationship with their host plant in response to the phenology of the crop in relation to flowering periods, which can result in low vagility (Mound & Teulon 1995).

The results from the sub-sampled immatures and sentinel experiments determined that *F. occidentalis* can reproduce on all four crops in this study. Based on the results from the immature sub-samples, French bean, tomato and zucchini are only secondary reproductive hosts. However, the results from French bean sub-sampling contradict the findings of the sentinel experiments, which indicate that both French bean and lettuce are primary reproductive hosts for *F. occidentalis*. This is also reflected in the high abundance of adults collected from French bean and lettuce (see Chapter 4), which suggests that the large numbers of adults in these crops is a result of their ability to reproduce in the crop and sustain high adult populations (Duff 2012; Kasina et al. 2009; Nderitu et al. 2008; Nyasani et al. 2012; Nysanai et al. 2013). Despite the contradictory results, the findings from the sentinel experiments are similar to the findings of Zhang et al. (2007). These authors determined that French bean was a suitable host for *F. occidentalis* based on development time and immature survivorship. Based on the high abundance of adults found in French bean (see Chapter 4), coupled with the sentinel results, French bean is likely a primary reproductive host for *F. occidentalis*. However, further data needs to be collected to explore the contradictory results from the sub-sampling of immatures and sentinel plantings before French bean can be classified as a primary host. *Frankliniella occidentalis* were also present on French bean sentinel plants in all four experiments, indicating that their reproductive association with these crops is not likely as dependant on the weather conditions as *M. usitatus* or *T. tabaci*.

Haplothrips gowdeyi and *T. palmi* were collected from sentinel French bean plants only as adults, with no evidence of reproduction occurring. It is likely that these species were present on French bean

sentinel plants as transient species, using the plant for shelter (temporal host) or feeding on the plant tissue. *Haplothrips gowdeyi* have been previously collected from French bean (Duff 2012). The *Haplothrips* genus includes more than 230 species worldwide, many of which feed mostly on flowers, particularly those from the families Asteraceae, Poaceae and Cyperaceae (Mound & Minaei 2007; Mound & Zapater 2003). Similarly, the low numbers of *T. palmi* adults recovered in both the sentinel and field studies indicate no reproductive association with French bean. *Thrips palmi* have been recorded on 117 species of plant across 34 families, and are considered a pest of French beans, feeding on leaf and fruit tissue (Miyazaki & Kudo 1988; Seal et al. 2013). Therefore, it is likely that French bean is a secondary feeding host for *T. palmi* adults. Like reproductive host association, much of the feeding hosts are also largely based on inference from field observations. Therefore, further field and laboratory trials would be required to establish the true nature and level of any possible associations.

Based on the results from the field sub-sampled immatures and the sentinel experiments, lettuce is a primary reproductive host for *F. occidentalis* and *F. schultzei* and a secondary reproductive host for *T. tabaci*. Adult sampling in lettuce found *F. schultzei* were most abundant, followed by a high abundance of *F. occidentalis* collected and only a small number of *T. tabaci* found in crop (see Chapter 4). Significantly more *F. schultzei* emerged on sentinel lettuce compared to French bean, and significantly more on lettuce compared to *F. occidentalis* and *T. tabaci*. This indicates that the high abundance of *F. schultzei* recovered from the lettuce agro-ecosystems is likely a direct result of their ability to reproduce in high numbers on this particular crop. Both *F. occidentalis* and *F. schultzei* were recovered from lettuce in all four sentinel experiments, supporting the theory that the reproductive association of these species with lettuce may be less affected by changes in the environmental conditions than that of *M. usitatus* and *T. tabaci*. A literature search failed to find any studies on the reproductive host

association of these three species with lettuce, and all information has only been based on observations of adults and unidentified immatures. Therefore, this research contributes greatly to the understanding of the biology and ecology of this species in lettuce agro-ecosystems.

Tomato is considered a poor reproductive host for thrips, particularly *F. occidentalis* (Brodbeck et al. 2001; Reitz et al. 2002; Zhang et al. 2007). This is reflected in the results of this study, in which this crop consistently supported the lowest immature abundance compared to all crops in all plantings, including low recovery of immature *F. occidentalis* and *F. schultzei* from the field collected sub-samples. Reproductive hosts are known to have a direct effect on increasing population densities. Therefore, the low abundance of adult thrips collected from the tomato plantings may be a direct result of the poor reproductive relationship between tomato and thrips.

Based on the findings in this study, *F. occidentalis*, *F. schultzei* and *T. tabaci* can use zucchini as a reproductive host, however the results indicate that the crop is only a secondary host. Zucchini supported significantly fewer immature thrips in crop compared to French bean and lettuce across the majority of the plantings; but supported a very high abundance of adult thrips, suggesting that the crop was supporting an adult population that had migrated into the crop to feed. The suitability of a plant as a reproductive host is dependent on a range of factors, including the anatomy and physiology of the plant. For example, the presence of trichomes on eggplant have been known to reduce population density of aphids and thrips (Leite et al. 2006). Zucchini trichomes may reduce the suitability of the plant tissue for thrips oviposition and therefore reduce immature abundance in the crops. However, this is based merely on an observation. To validate this hypothesis, further experiments would need to take place in the field and the laboratory to establish if the physiology of the crop affects reproduction and determine the feeding association between the crop and thrips.

For some of the species found in relatively high abundance as adults (see Chapter 4), such as *D. tenuicornis* in lettuce, *P. achaetus* in tomato, *T. frici* and *T. palmi* in zucchini, no adults were reared from the immature subsets. This suggests that they are not using any of the four crops as reproductive hosts, but were only using the crops for feeding or shelter. *Tenothrips frici* has a known association with *S. oleraceus* and *T. officinale*, two weeds found bordering the experimental area at various times through the three-year period. Collections of flowers from both plants were found to have adult *T. frici* in the florets, however no immatures were collected. Based on the findings here, it is likely that *T. frici* were moving into the crop to feed on zucchini and not using it as a reproductive host; but if the weeds were supporting reproduction of the thrips it was not evident in this study.

In general, there were more immatures supported in French bean compared to all other crops, except for plantings nine, ten and eleven in the third year (2013 to 2014). In planting nine there were more immatures in zucchini and lettuce, and significantly more in lettuce in planting ten and eleven. The variation in this final year suggests a possible environmental effect. Year three received the least rainfall and was the warmest compared to year one and two (see Chapter 7 & 8), which may have been more suitable conditions for zucchini and lettuce growth compared to French bean.

A higher proportion of the sampled adults were female. Field populations of most thrips species are bisexual, but generally there are a greater proportion of females present compared to males (Vasiliu-Oromulu 2002). Thrips are haplodiploid, with females reproducing parthenogenetically and sexually (Lewis 1973). For some species, males are rare or unknown, and reproduction is partly or wholly thelytoky parthenogenesis, with eggs developing without being fertilised (Chapman 1998). Most unfertilised eggs contain only X chromosomes (females XX, homogametic) as Y chromosomes must come from males (males XY, heterogametic), therefore will only give rise to female

offspring (Chapman 1998). The higher incidence of female thrips in this study suggests that for most of the time, thrips are reproducing parthenogenetically. However, the incidence of male *D. tenuicornis*, *F. occidentalis*, *F. schultzei*, *M. usitatus* and *P. achaetus* suggests that sexual reproduction is taking place, increasing the genetic diversity of the populations.

Conclusion

Overall, French bean supported significantly more immatures in the field survey compared to all other crop treatments, followed by lettuce. French bean, lettuce and zucchini treatments had an effect on immature abundance in the field, however tomato did not. *Frankliniella occidentalis*, *F. schultzei*, *M. usitatus* and *T. tabaci* were reared from sentinel exposed plants. There were significantly more *F. occidentalis*, *M. usitatus* and *T. tabaci* reared on French bean than lettuce and significantly more *F. schultzei* on lettuce than French bean. Therefore, it can be concluded based on the findings of the field surveys and sentinel experiments that a reproductive host association exists between these crops and the respective thrips species. A reproductive host association between a species and a crop will influence the population dynamics of thrips in a vegetable agro-ecosystem, as it is these reproductive hosts that increase the rate of reproduction and thus increase the population density. This knowledge will increase our capacity to monitor and control key pest species in field grown vegetable agro-ecosystems.

Chapter Seven: Effect of rainfall, temperature and relative humidity on thrips population dynamics in French bean, lettuce, tomato and zucchini

Introduction

The study of population dynamics involves a complexity of factors and interactions occurring between an insect population, host plants and the environment (Cammell & Knight 1992). The dynamics of these populations are dependent on climatic factors such as rainfall, temperature and relative humidity that not only influence thrips abundance but have an impact on the variety of species that dwell within an agro-ecosystem (Kirk 1997). For thrips populations in vegetable agro-ecosystems, several studies have determined the seasonal distribution of key pest species such as *F. occidentalis* (Kasina et al. 2009; Stacey & Fellowes 2002), *T. palmi* (Tsai et al. 1995; Yadav & Chang 2014) and *T. tabaci* (Jamieson et al. 2012; Liu 2004; Merene 2014), in response to changes in weather. For vegetable production, this has allowed for the prediction of pest population outbreaks in relation to the seasonal conditions – information that is critical for implementing pre-emptive control strategies to manage and reduce pest impact. There is, however, a lack of information on the relationship between weather conditions and species population dynamics in many other vegetable agro-ecosystems, such as French bean, lettuce, tomato and zucchini, including the association of all other species that exist in these assemblages, something that this study aims to inform.

Weather

Any changes in rainfall, temperature or relative humidity are not neutral for insect assemblages, and the impact may be reflected in the relative

abundance, activity and reproduction of the insect within a vegetable agro-ecosystem (Jaworski & Hilszczański 2013). As a result, the variety of thrips species supported within a crop fluctuates with the progression of a season and changes with fluctuations in weather conditions. Increased mortality and reduced abundance can occur as a result of dramatic changes in conditions, such as heavy precipitation, heat waves, frost or snow (Henson 1968; Jones 1979). Conversely, periods of warm and favourable weather conditions can cause rapid increases in population abundance, and changes in temperature and humidity can trigger population outbreaks by stimulating the mass movement of thrips seeking preferable conditions (Cammell & Knight 1992). Relatively warm temperatures and low rainfall have been associated with an increase in thrips, while high humidity and rainfall have been recorded to reduce thrips populations in vegetables (Hamdy & Salem 1994). Temperature, rainfall and relative humidity do not act in isolation and interactions with other weather variables need to be considered when investigating seasonal population dynamics (Harrington et al. 2001). Plants also respond to seasonal changes in temperature, rainfall and relative humidity, which is reflected in the growth of the plant. Seasonal distribution patterns are also likely to be dependent on the plant morphology and physiology. Change in climatic factors can influence insects indirectly by affecting the physiology and nutrient metabolism of the plant (Ayres & Lombardero 2000; Jaworski & Hilszczański 2013). Therefore, optimum conditions for plant growth may also provide thrips with an optimum environment for feeding or breeding to occur, increasing thrips abundance in the crop as a result (Rathcke & Lacey 1985).

Temperature

Temperature influences the intrinsic rate of natural increase of thrips populations (Murai 2000), by directly affecting insect survival, development and reproduction. As such, temperature regulates the presence and abundance of insect populations within an agro-ecosystem (Cammell & Knight 1992; Deka et al. 2009; Harrington et al. 2001; Stacey & Fellowes 2002). As poikilothermic organisms, insects' body temperature is approximately the same as their

surrounding environment and temperature, therefore, regulates individual thrips development rates, with the relationship dependant on each species' requirements (Deka et al. 2009). Many species develop quicker when average temperatures increase, and slower when temperatures decrease.

In temperate zones, cooler weather can delay thrips reproduction, with the cycle resuming with the arrival of warmer spring months (Bale et al. 2002; Sites & Chambers 1990). *For example, the egg to adult development period of T. palmi can be completed in as little as 9.6 days at 31°C and increases to 35.7 days as the temperature declines to 16°C* (Yadav & Chang 2013). In relation to fecundity and male and female longevity, the optimum development temperature for *T. palmi* is 25°C (Capinera 2008; Yadav & Chang 2013). Therefore, *T. palmi* are often more abundant in warmer months compared to cooler periods. While insects have optimum development temperatures, upper and lower temperature thresholds can also impact on their development. For *F. occidentalis*, the upper threshold is 35°C and the lower 7.9°C; outside of these temperature thresholds, the insect cannot complete its lifecycle (McDonald et al. 1998). Changes in both mean temperature and the extent and frequency of extremes can, therefore, have major impacts on insect populations (Harrington et al. 2001).

Insects will also change their activities, such as dispersal and feeding, according to the temperature of the environment (Bale et al. 2002). Warm temperatures at the thermal optimum of a species cause the insects' metabolism to accelerate and, therefore, their activity also increases (Jaworski & Hilszczański 2013). This can increase the migration of thrips, and movement within a crop, due to the temperature threshold at which a species can take flight to disperse, and increase their foraging and feeding activities (Cammell & Knight 1992; Harding 1961; Scaven & Rafferty 2013). Plants also respond to increasing temperatures in temperate regions by growing at a faster rate, although growth rate does decline if the temperature exceeds the optimum threshold (Scaven & Rafferty 2013). A faster growth rate leads to greater plant biomass as well as accelerated progress through phenological stages, including flowering. These changes can result in insect population growth through greater

food resources, increased movement and reproduction under optimum temperatures (Scaven & Rafferty 2013).

Rainfall

Thrips survival is significantly affected by rainfall intensity (Norris et al. 2002; Patterson et al. 1999). An increase in rainfall can cause an immediate decline in adult thrips numbers remaining on the plant, through run off and drowning. Thrips that shelter from the rain on the underside of leaves and in crevices or in the flowers are less likely to be affected by rainfall than those that are on exposed parts of the plant. However, these protected thrips may subsequently be affected by runoff. Overhead irrigation is often used as a means of thrips control in protected cropping and field grown vegetable systems (Passlow 1957). However, rainfall can also have a positive association with thrips abundance. Following rainfall, the crop canopy can become lush with new growth, particularly if moderate temperatures prevail, leading to an increase in thrips abundance due to favourable crop conditions (Cammell & Knight 1992).

Relative humidity

Unlike temperature, humidity is much more variable. This variability makes it more difficult to determine direct trends between insect population behaviour and relative humidity (Jaworski & Hilszczański 2013). Optimum conditions for many insects lie between 60 to 80% relative humidity with a gradual lengthening of the development period as relative humidity declines when coupled with low temperatures (Cammell & Knight 1992). Thrips are known to be highly susceptible to dry microclimates, and perform best (vigour, longevity and reproduction) at 70 to 90% RH (Kirk 1997). Like other climatic factors, the relationship between relative humidity and thrips is variable dependant on species. For example Patel et al. (2009) found that a decrease in relative humidity (between 20 to 40%) resulted in an increase in *S. dorsalis* populations in chilli crops. Often the combined effects of relative humidity and temperature have an impact on insect populations. For example, Shipp and Gillespie (1993) studied the effect of temperature and relative humidity on

various life stages of *F. occidentalis*. Larval stages were most sensitive to low relative humidity, with low survival rates of first instar larva at all relative humidity levels when temperatures were $\geq 25^{\circ}\text{C}$, and high survival rate of second instars at relative humidity $> 90\%$. Female adults were only sensitive to low relative humidity at temperatures $> 25^{\circ}\text{C}$ and pupae, in the soil, were insensitive to both relative humidity and temperatures between 15°C and 30°C .

Seasonal distribution

Because of thrips' dependency on climatic factors, such as rainfall, temperature and relative humidity for lifecycle development, feeding and movement, the presence and relative abundance of a species may vary on a seasonal scale. For example, in the vegetable growing area of Bundaberg, South East Queensland, there are two annual capsicum and chilli growing seasons, each of which supports a thrips species assemblage. The autumn cropping season is dominated by cooler temperatures, supporting a species assemblage of *F. occidentalis*, *P. achaetus*, *T. tabaci*, *T. imaginis* and dominated by *T. palmi* (Walsh et al. 2012). The spring growing season is characterised by warm temperatures, and higher rainfall and relative humidity, supporting a similar species assemblage to the autumn period but dominated by *F. occidentalis*, and relatively low numbers of *T. palmi*, *P. achaetus* and *F. schultzei*. In an ecological field survey of native flowering plant species adjacent to tomato crops in northern Florida, Chellemi et al. (1994) found that *Frankliniella* species and their relative abundance were temporally distributed by month. *Frankliniella tritici* was most abundant in March, May and August; *F. bispinosa* (Morgan) in June and July; and *F. occidentalis* in February and April.

Weather variables do not act in isolation to influence the fluctuation in population density, and it is important to consider interactions with all other variables (Harrington et al. 2001). To develop a sound understanding of the dynamics of thrips assemblages in vegetable agro-ecosystems the responses of

thrips populations to climatic factors needs to be monitored over a period of several years (Cammell & Knight 1992). Therefore, in this study, the influence of rainfall, relative humidity and temperature on the abundance of thrips within each crop species assemblage is investigated over a three-year period.

Materials and methods

As described in the General research methodology (Chapter 3), the field survey was conducted as eleven plantings over the course of a three-year period. Each planting consisted of four blocks, four crop treatments and ten replicates per block. One plant sample (flower, growing tip, leaf and stem or whole plant) was collected from each replicate per crop, weekly, over the life of the crop. Flower and growing tip samples were collected into 95% ethanol. Stem and leaf and whole lettuce samples were removed in the field (destructive sampling) and collected into individual paper bags, deconstructed in the laboratory and beaten over a tray to dislodge thrips. Thrips were then collected into vials of 95% ethanol. Tomato leaf and stem and growing tip samples were not destructively collected, but beaten over a tray in crop and thrips collected into 95% ethanol. All adult thrips were slide mounted and identified to genus and species, using the Oz Thrips (2016) interactive lucid key, under a compound microscope. Immatures were not included in this analyse, and are discussed in Chapter 6.

Average rainfall, temperature and relative humidity were recorded from the BoM weather station at the University of Gatton campus, as described in Chapter 3.

Statistical analysis

Data was checked for normality and homogeneity of variance using Shapiro-Wilk ($p > 0.05$) and Levene tests before analyse, followed by square-root transformation $(X + 0.5)^{1/2}$ to normalise the data .

To determine the effect of weather on species abundance in each agro-

ecosystem, the data was subjected to a binomial logistic regression. Due to the high zero count for abundance data, logistic regression overcomes the restrictive assumptions of linear regression, such as linearity, normality, equal variance and that the error term variance is normally distributed. The logistic regression determined the effect of crop age, temperature, total rainfall and relative humidity on the maximum likelihood estimates that thrips would be present within the vegetable agro-ecosystem. The dependant variable, thrips abundance, is dichotomous, being present (1) or absent (0). The logistic regression generates the coefficients (and its standard errors and significance levels) of a formula to predict the logit transformation and the probability of presence of each species:

$$\text{logit}(p) = b_0 + b_1X_1 + b_2X_2 + b_3X_3 + \dots + b_kX_k$$

where p is the probability of the presence of the species, b_{0-k} are the regression coefficients and X_{1-k} the independent variables. A Hosmer and Lemeshow goodness of fit test for the logistic regression was applied and the data divided into approximately ten groups defined by increasing order of estimated risk (Hosmer et al. 2013; Laerd Statistics 2015). The observed and expected numbers of cases in each group were calculated by a Chi-squared test:

$$\chi_{HL} = \sum_{g=1}^n \frac{(O_g - E_g)^2}{E_g(1 - E_g/n_g)}$$

Each weather variable was calculated as an average accumulated total, averaged over the number of days from the previous sample date to the current sample date. The linearity of the variables, with respect to the logit of the dependant variable, was assessed via the Box-Tidwell (1962) procedure. A Bonferroni correction was applied using all ten terms in the resulting model to determine the level of statistical significance as accepted when $p < 0.005$, to assess the linearity of all independent variables in relation to the logit of the dependant variable. A binomial logistic regression was calculated for each agro-ecosystem (French bean, lettuce, tomato and zucchini). Individual species, within each agro-ecosystem species assemblage, were not included in the

analysis as the data was already subjected to a regression analysis in Chapter 4.

Pearson correlation coefficients were calculated for each species to measure the degree of association between presence and rainfall, temperature and relative humidity. Data was square-root transformed to ensure normality and assessed for normal distribution via Shapiro Wilks test ($p > 0.05$). Pearson correlation coefficients are considered weak between 0.1 and 0.3 (or between -0.1 and -0.3 in the case of negative correlation), moderate between 0.4 and 0.5, (or between -0.4 and -0.5 in the case of negative correlation), and anything greater than 0.5, or -0.5, was considered strongly correlated (Laerd Statistics 2015). Pearson correlation coefficient is the common approach for analysing the relationship between population size and climate variables (Stenseth et al. 2002). Only species that had a significant abundance in the species assemblages (as determined in Chapter 4) were included in the analysis.

To understand the relationship between season and thrips species assemblage, data was subjected to a three-way ANOVA. Factors were the year of planting (year), planting number (planting) and species. Each crop was analysed separately. Pairwise comparison at the 95% confidence interval (CI) was calculated to determine the mean difference in total thrips abundance between plantings. Seasonal distribution of the species assemblage in each crop and in each year (2011 to 2012, 2012 to 2013, and 2013 to 2014) was summarised in graphs. Daily total rainfall (mm), minimum and maximum temperature (°C) and relative humidity % were calculated as mean values between sample dates and graphed between the first sample date (December) and the last (June) according to the year.

Results

Weather

In year one (December 2011 to June 2012) (Figures 7.1, 7.4, 7.7 & 7.10; average minimum and maximum temperature (°C), relative humidity, and total rainfall (mm) are displayed between sample dates for

each figure) the lowest temperatures were recorded in May and the highest in January, the latter of which also received the most rainfall. Relative humidity was highly variable across the survey period. January had the highest single rainfall event, with 68 mm recorded on the 28th. Total rainfall for year one was 385 mm. Year one was significantly cooler overall compared to year two and three (see Chapter 8, Figure 8.6).

In year two (December 2012 to June 2013) (Figures 7.2, 7.5, 7.8 & 7.11; average minimum and maximum temperature (°C), relative humidity, and total rainfall (mm) are displayed between sample dates for each figure) the lowest and highest temperatures were recorded in May and January, respectively, with relative humidity variable across the survey periods. Year two received the highest total rainfall of all years (670.8 mm).

Year three (December 2013 to June 2014) (Figures 7.3, 7.6, 7.9 & 7.12; average minimum and maximum temperature (°C), relative humidity, and total rainfall (mm) are displayed between sample dates for each figure) received the lowest total rainfall of the three years (359.5 mm). May and June were the coolest months, while December and January were the warmest months. Like the previous years, relative humidity was variable across all months.

Seasonal abundance

For French bean, total thrips abundance in year one was 528, year two 780 and year three 380 (Figures 7.1, 7.2 & 7.3). In year one, *D. tenuicornis* were present only in February, however, individuals were recorded from all months in year two and three, except December. *Frankliniella occidentalis* were collected in all months across the entire survey period, with relative abundance increasing from February. *Megalurothrips usitatus* were present from February to May in year one and three, and between March and June in year two. *Frankliniella schultzei* were present between December and April in year one, and

February and June in the following years. *Haplothrips gowdeyi* were collected in French bean from February in year one and January in year two, until May and were absent in year three. *Pseudanaphothrips achaetus* were not present in year three, and were collected in low numbers between February and March in year one, and April and June in year two. *Tenothrips frici* were present in low numbers between January and May in year one and two, and only in April in the third year. *Thrips tabaci* and *T. palmi* presence were variable across the three years.

Low numbers of thrips were found in all lettuce plantings from December onwards, with numbers increasing from January. Year one recorded 346 total thrips, year two 969 and year three 346 (Figure 7.4, 7.5 & 7.6). *Desmothrips tenuicornis* were collected between January and May/June, with the highest abundance in January and February. *Frankliniella occidentalis* and *F. schultzei* were present from December to June.

In tomato, 300 total thrips were recorded in year one, 589 in year two and 264 in year three (Figures 7.7, 7.8 & 7.9). *Frankliniella occidentalis*, *F. schultzei* and *T. palmi* presence and abundance were highly variable throughout the survey period. *Pseudanaphothrips achaetus* were most abundant in January in year one, and collected in low numbers from the following years. *Tenothrips frici* were present in very low numbers in April in year one and two. *Thrips tabaci* abundance was low, except for December and January in year one.

Zucchini plantings in year one recorded 1337 total thrips, 1586 year two and 2728 year three (Figures 7.10, 7.11 & 7.12). *Desmothrips tenuicornis*, *F. occidentalis*, *F. schultzei* and *T. frici* were present from January to May. *Pseudanaphothrips achaetus* presence and abundance in zucchini were highly variable between years, with high numbers recorded in January in year one, June in year two and February in year three. *Thrips palmi* presence was variable, while *M. usitatus* were present in low abundance in May. *Thrips tabaci* were present from January

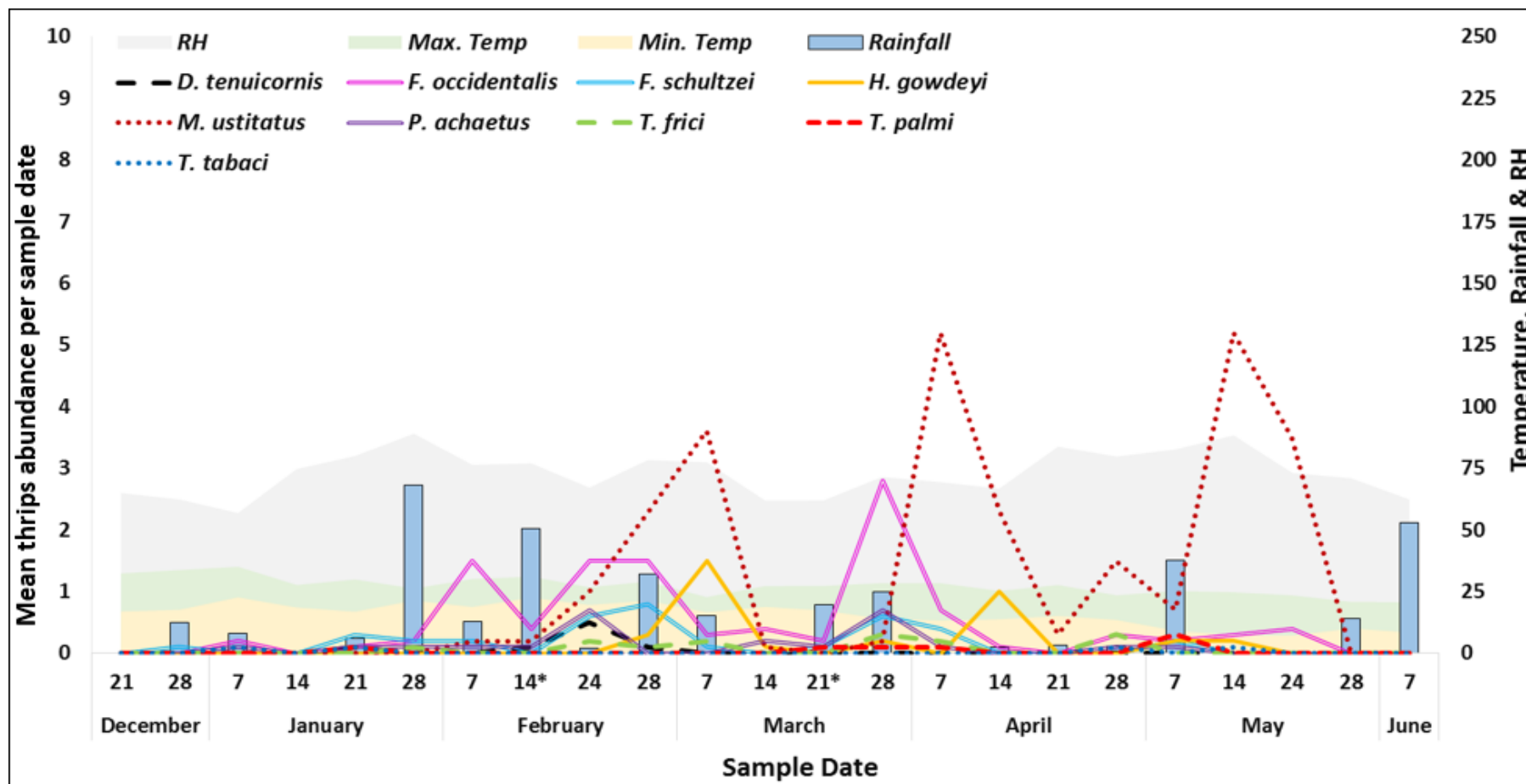


Figure 7.1 Weekly mean species abundance by sample date in year one (December 2011 to June 2012) in French bean (* denotes a planting).

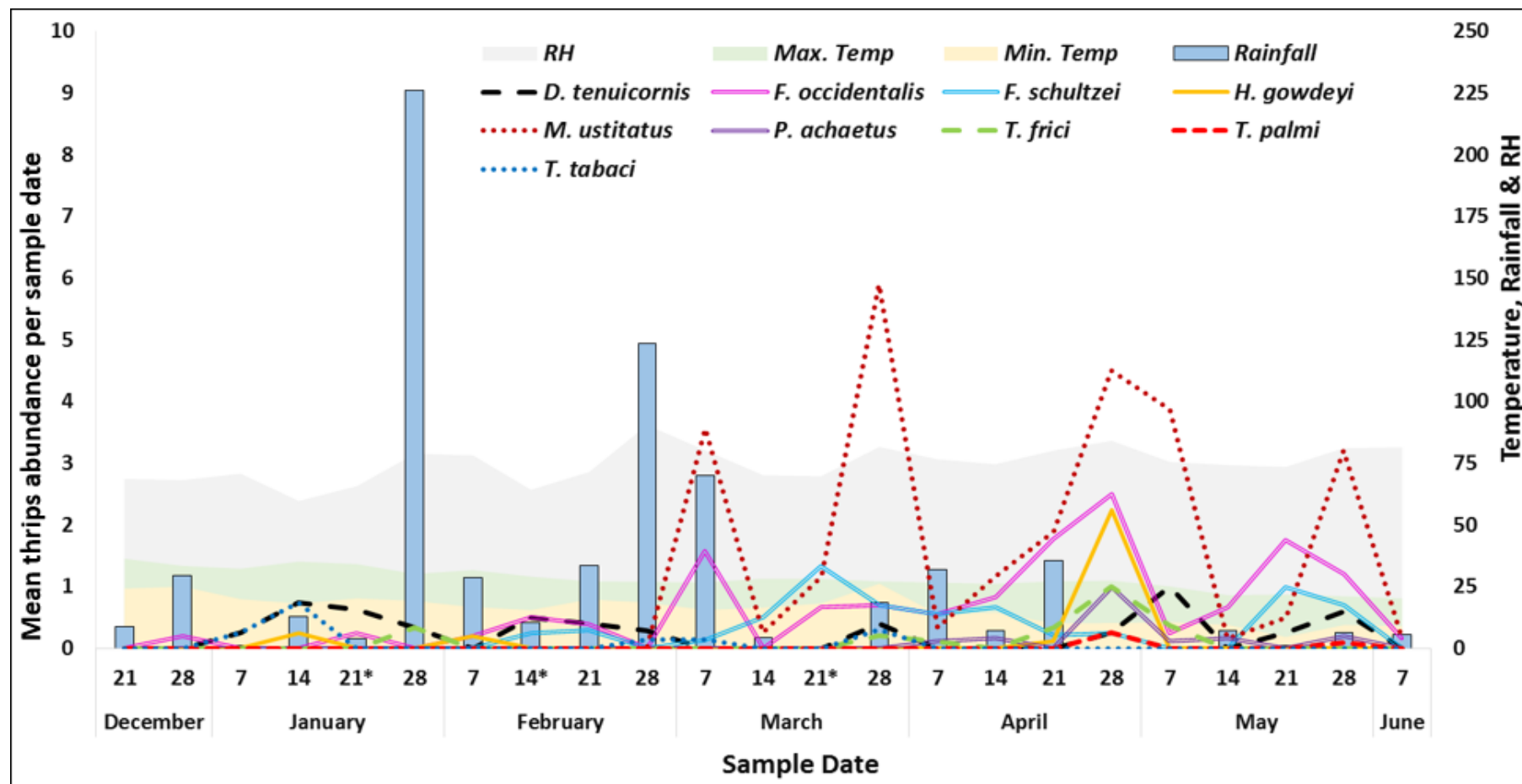


Figure 7.2 Weekly mean species abundance by sample date in year two (December 2012 to June 2013) in French bean (* denotes a planting).

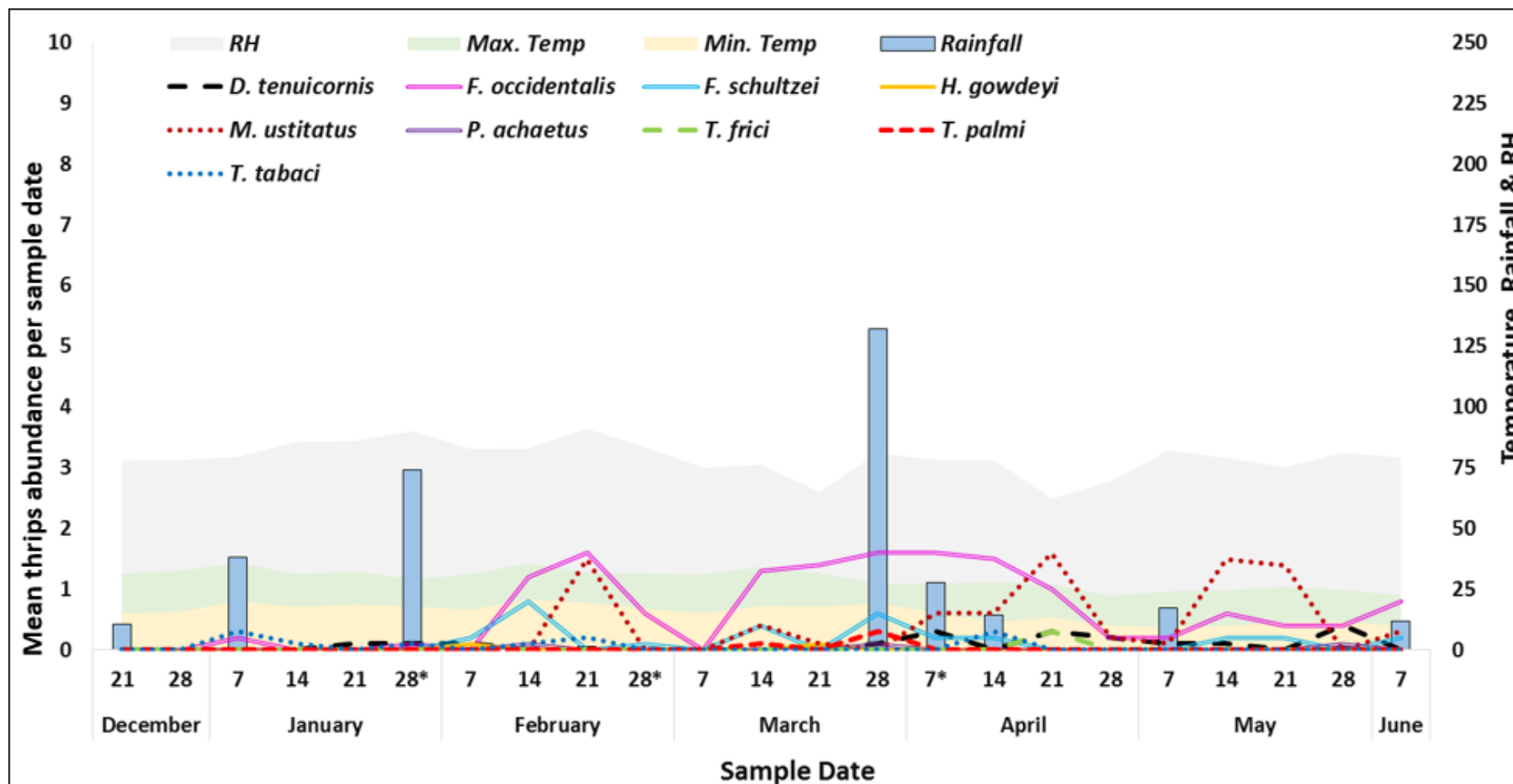


Figure 7.3 Weekly mean species abundance by sample date in year three (December 2013 to June 2014) in French bean (* denotes a planting).

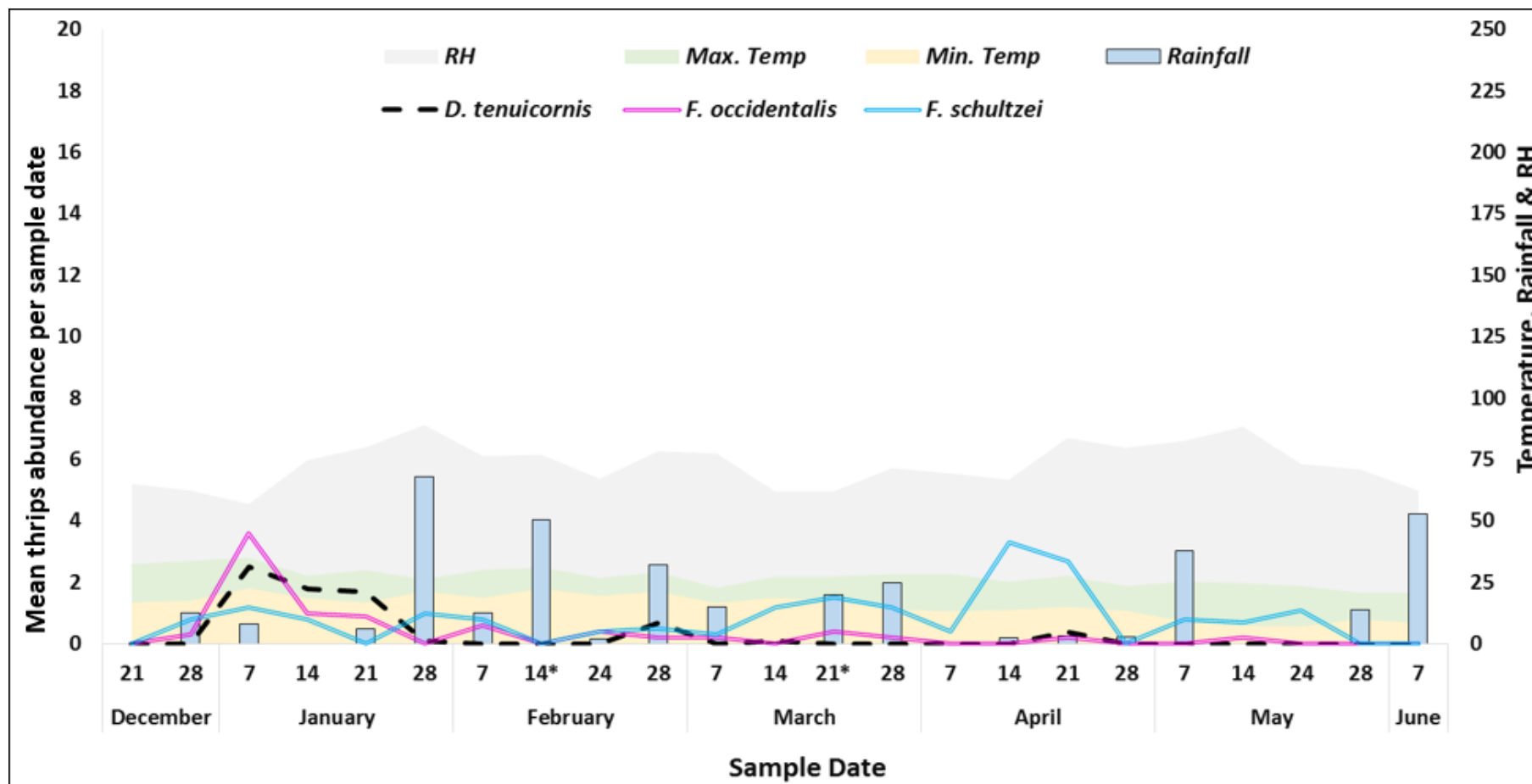


Figure 7.4 Weekly mean species abundance by sample date in year one (December 2011 to June 2012) in lettuce (* denotes a planting).

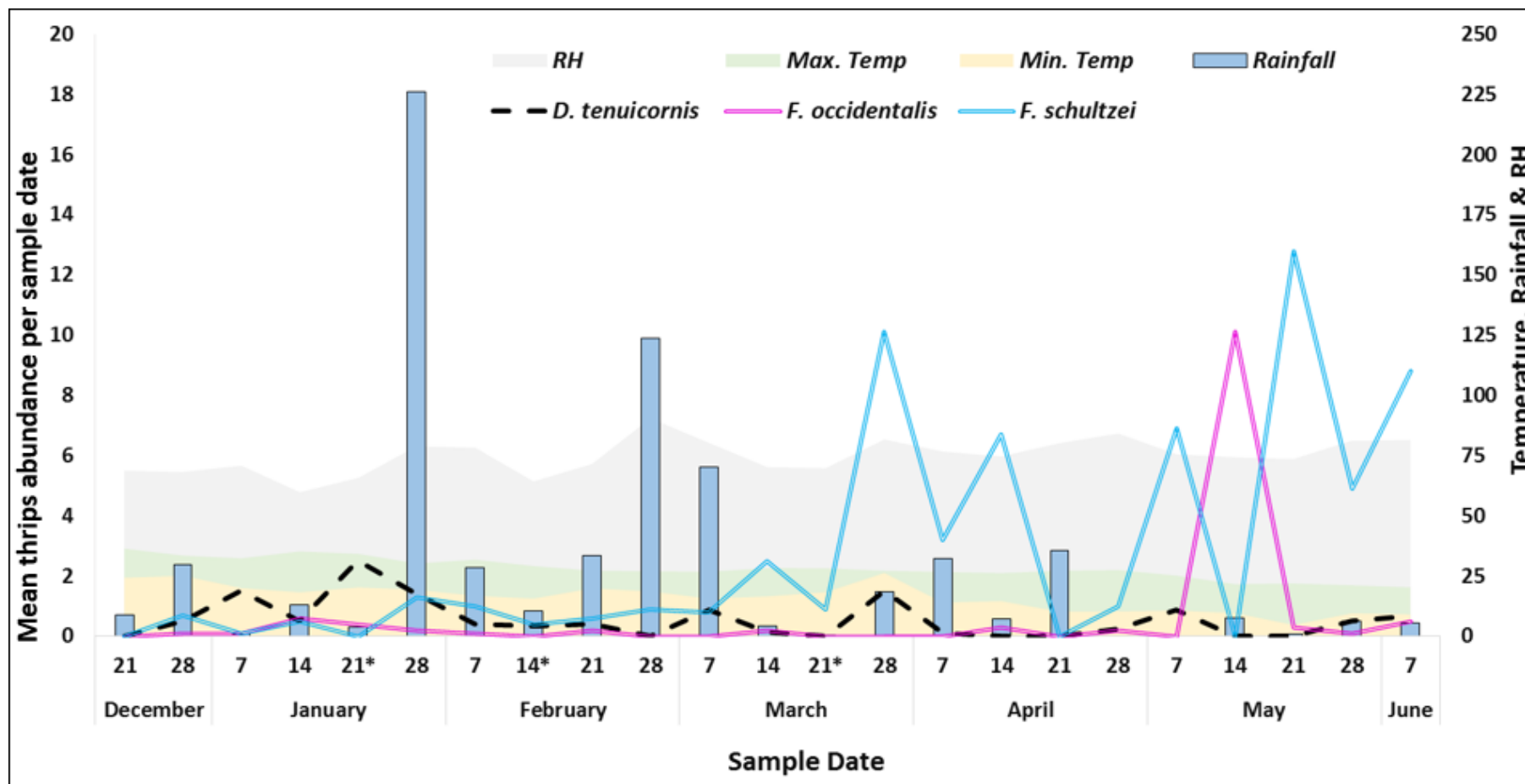


Figure 7.5 Weekly mean species abundance by sample date in year two (December 2012 to June 2013) in lettuce (* denotes a planting).

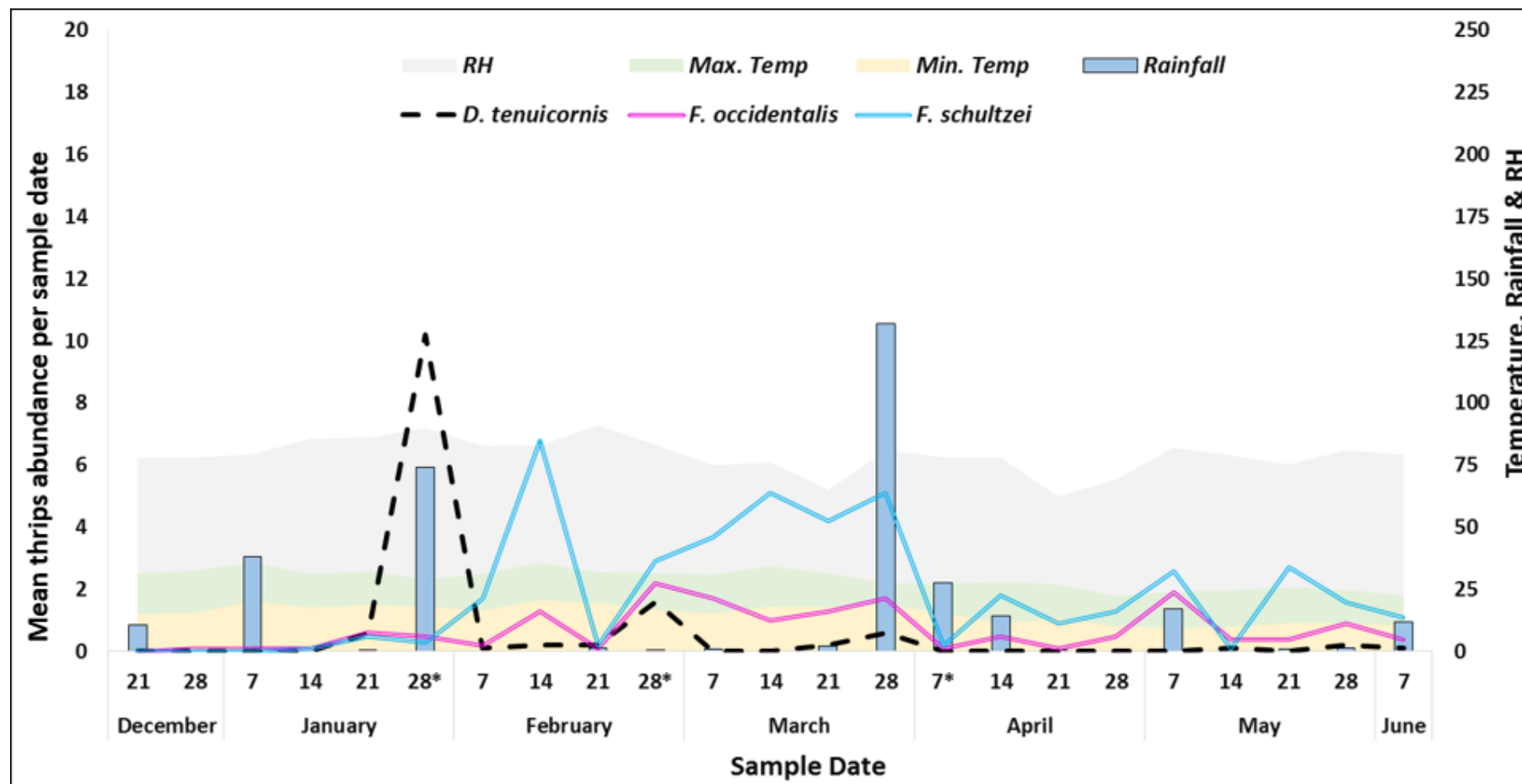


Figure 7.6 Weekly mean species abundance by sample date in year three (December 2013 to June 2014) in lettuce (* denotes a planting).

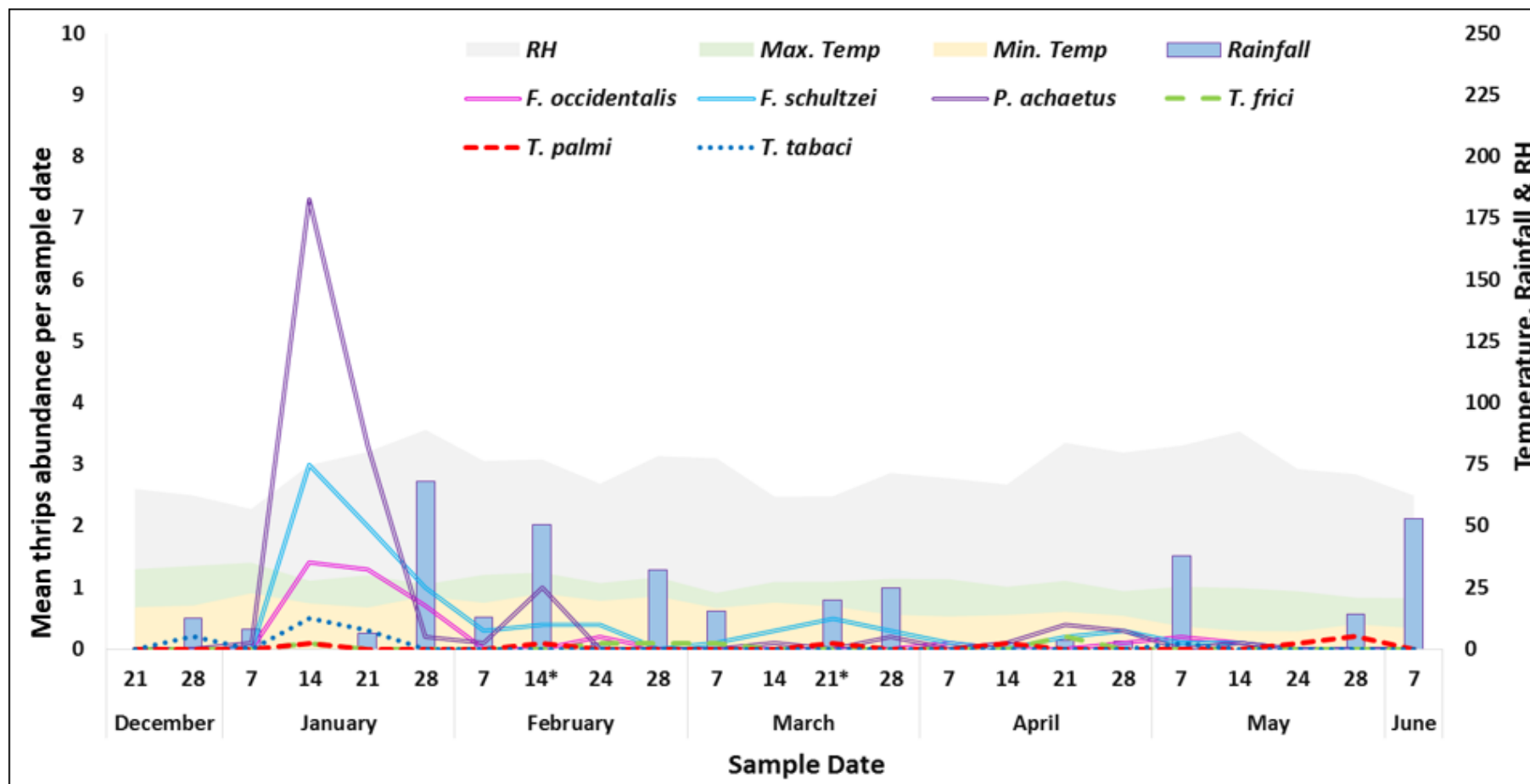


Figure 7.7 Weekly mean species abundance by sample date in year one (December 2011 to June 2012) in tomato (* denotes a planting).

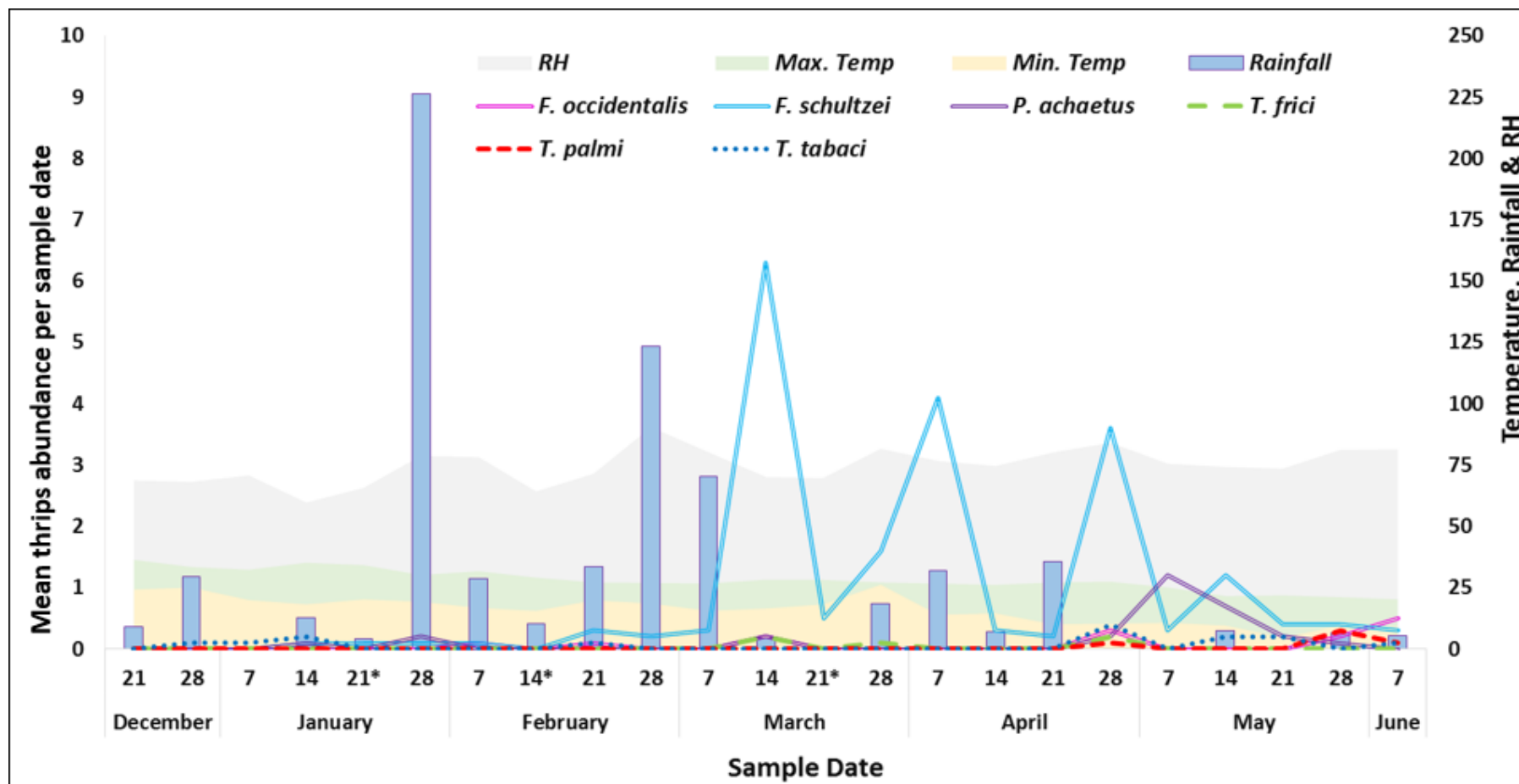


Figure 7.8 Weekly mean species abundance by sample date in year two (December 2012 to June 2013) in tomato (* denotes a planting).

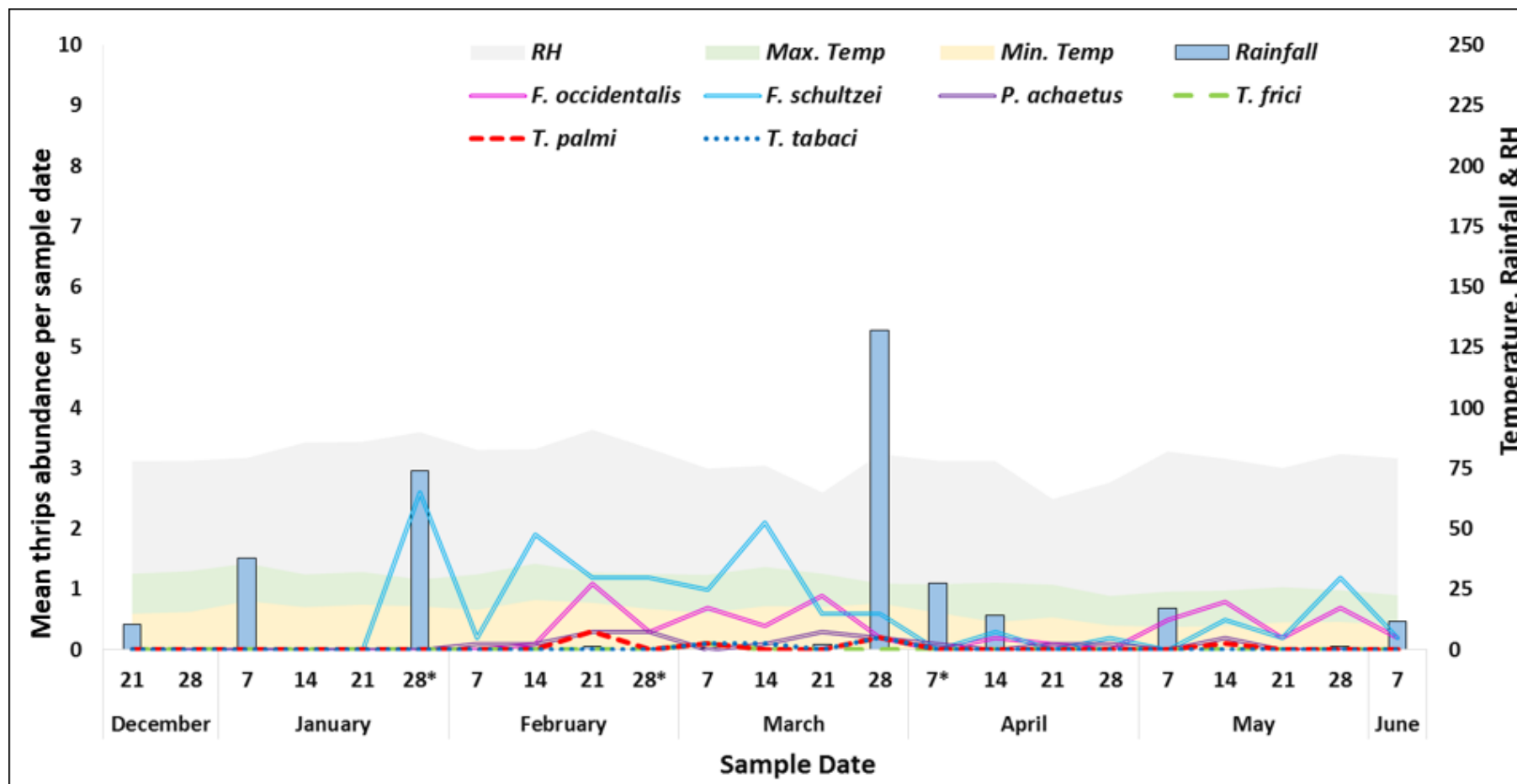


Figure 7.9 Weekly mean species abundance by sample date in year three (December 2013 to June 2014) in tomato (* denotes a planting.)

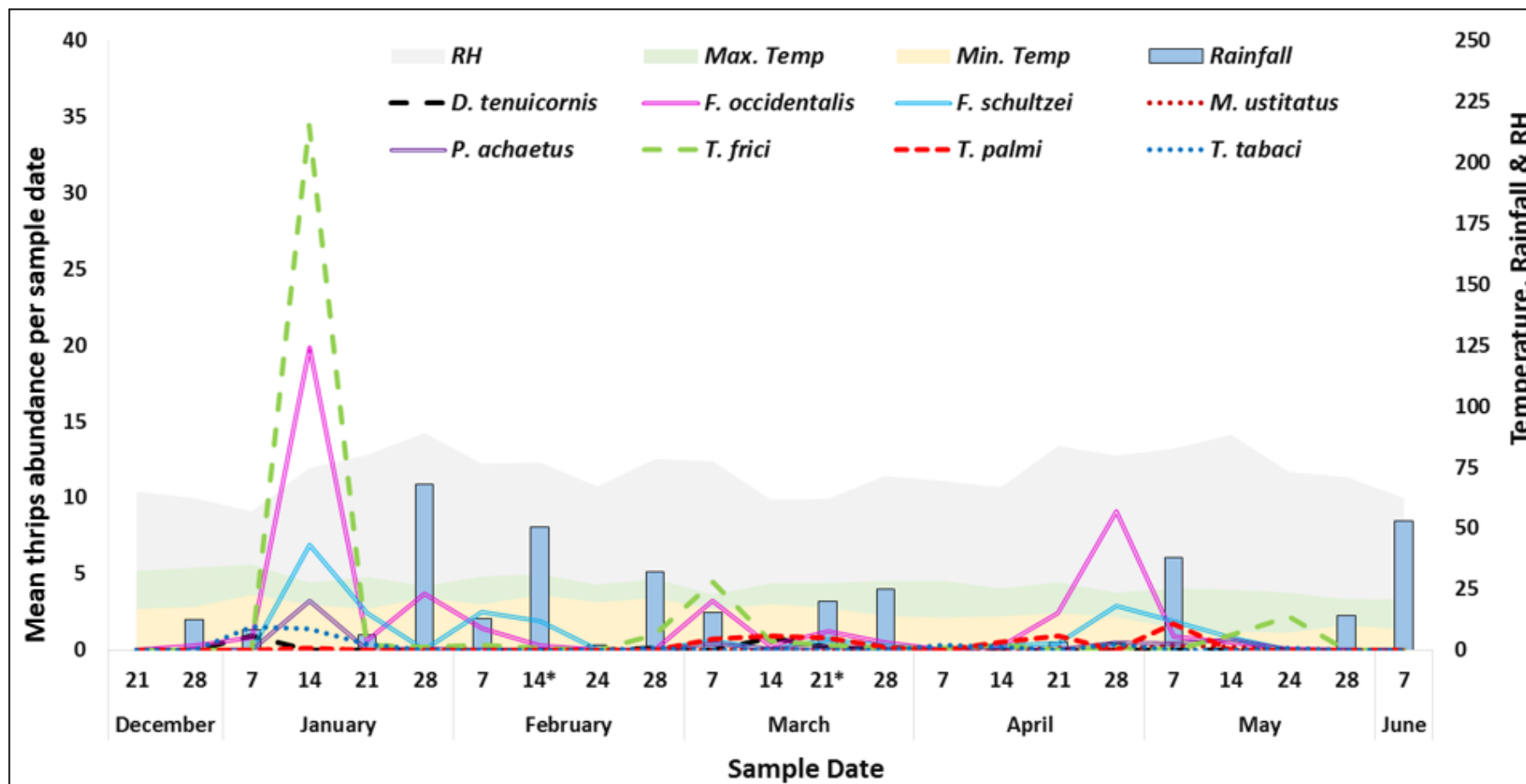


Figure 7.10 Weekly mean species abundance by sample date in year one (December 2011 to June 2012) in zucchini (* denotes a planting).

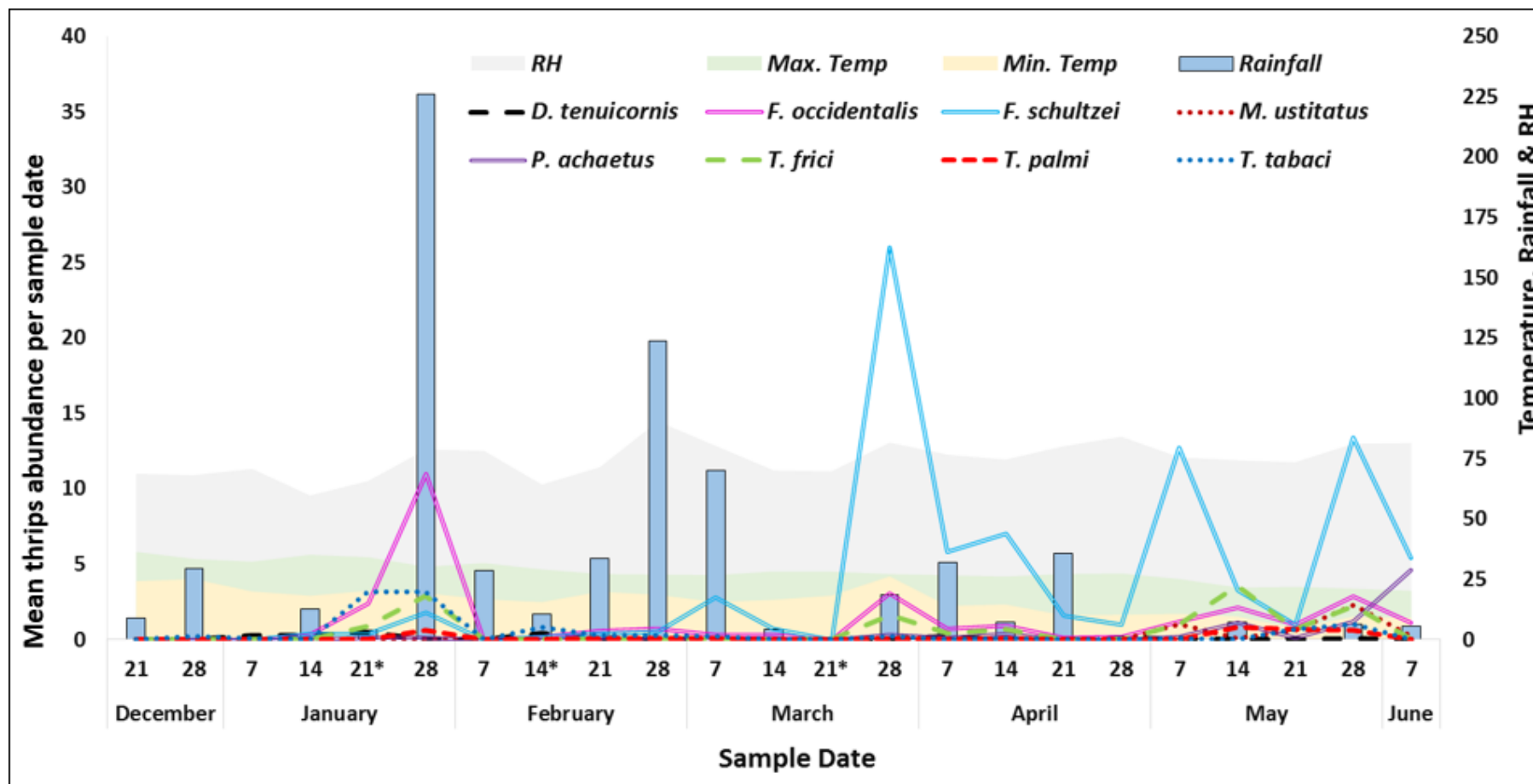


Figure 7.11 Weekly mean species abundance by sample date in year two (December 2012 to June 2013) in zucchini (* denotes a planting).

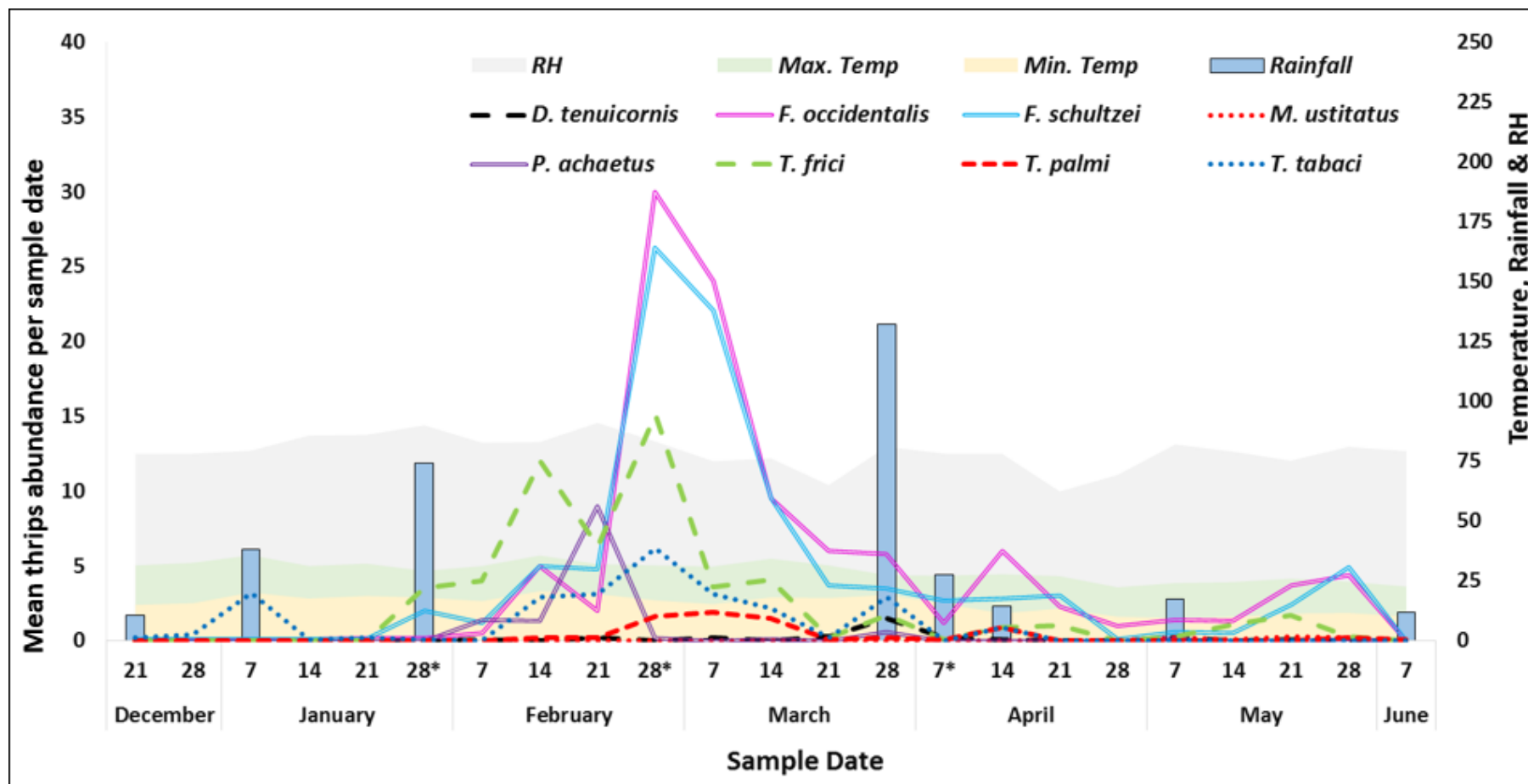


Figure 7.12 Weekly mean species abundance by sample date in year three (December 2013 to June 2014) in zucchini (* denotes a planting).

Binomial logistic regression

A binomial logistic regression was performed to ascertain the effect of crop age, rainfall, temperature, and relative humidity on thrips presence in each agro-ecosystem. In French bean, the logistic regression model was statistically significant $X^2(4) = 65.402, p < 0.005$. The model explained 63% (Nagelkerke R^2) of the variance in abundance, indicating that the reliability of the model to predict thrips presence in French bean, based on the predictive variables, was strong. Increasing crop age and temperature were associated with an increased likelihood of thrips being present in French bean (Table 7.1). Based on the Pearson correlation, there was a weak negative correlation between *D. tenuicornis* abundance and relative humidity, while *F. occidentalis* abundance was positively correlated with rainfall. *Megalurothrips usitatus* and *T. tabaci* presence were negatively correlated with increasing temperature, although the associations were weak. A weak positive association existed between *H. gowdeyi* and temperature. Pearson correlation coefficients for French bean are presented in Table 7.5.

The lettuce logistic regression model was statistically significant $X^2(4) = 69.030, p < 0.005$. The model explained 76% (Nagelkerke R^2) of the variance in abundance, indicating that the reliability of the model to predict thrips presence in lettuce, based on the predictive variables, was strong. Of the four predictive variables, only crop age was statistically significant (Table 7.2). *Desmothrips tenuicornis* abundance was positively correlated with increasing temperature and negatively correlated with relative humidity, both of which were weak. There was a weak negative correlation between *F. schultzei* abundance and rainfall, and a moderate negative correlation with temperature. Pearson correlation coefficients for lettuce are presented in Table 7.6.

The tomato logistic regression model was statistically significant $X^2(4) = 14.881, p = 0.001$. The model explained 20% (Nagelkerke R^2) of the variance in abundance, indicating that the model can only predict a

small proportion of thrips presence in tomato based on the predictive variables. None of the four variables had a significant effect on the presence of thrips in tomato (Table 7.3). There was a weak positive correlation between *F. occidentalis* abundance and rainfall and temperature, and a strong positive correlation with relative humidity. A positive weak correlation existed between *F. schultzei* abundance and rainfall, relative humidity and temperature. *Thrips palmi* abundance was negatively correlated with rainfall and temperature although the association was weak. Pearson correlation coefficients for tomato are presented in Table 7.7.

The zucchini logistic regression model was statistically significant $X^2(4) = 49.329, p < 0.005$. The model explained 44% (Nagelkerke R^2) of the variance in abundance, indicating that the reliability of the model to predict thrips presence in zucchini based on the predictive variables was good. Increasing rainfall and temperature were associated with a reduced likelihood of thrips being present in zucchini, while increased relative humidity was associated with an increased likelihood of thrips presence in the agro-ecosystem (Table 7.4). *Desmothrips tenuicornis* were negatively correlated with relative humidity and positively correlated with temperature, although the relationships were weak. There was a weak positive correlation between *F. occidentalis* abundance and rainfall, relative humidity and temperature. *Frankliniella schultzei* abundance was positively correlated with rainfall and relative humidity, although only weakly. The abundance of *M. usitatus* was negatively correlated with rainfall, which was at a moderate level of association. *Megalurothrips usitatus* abundance was also positively correlated with relative humidity and negatively correlated with temperature, although only weakly. There was a negative correlation between *P. achaetus* and *T. frici* abundance and rainfall, and a positive correlation with relative humidity, all of which were weak. *Thrips palmi* abundance was negatively correlated with temperature, while *T. tabaci* abundance was positively correlated with temperature; both were weak associations. Pearson correlation

coefficients for zucchini are presented in Table 7.8.

Table 7.1 Logistic regression predicting the likelihood of thrips presence in the French bean agro-ecosystem based on crop age, rainfall, temperature and relative humidity (RH%).

	<i>B</i>	SE	Wald	<i>df</i>	<i>p</i>	Odds Ratio	95 % CI for Odds Ratio	
							Lower	Upper
Crop age	0.214	0.015	210.773	1	0.000*	1.289	1.203	1.275
Rainfall	0.017	0.015	1.395	1	0.237	1.007	0.99	1.032
Temperature	0.011	0.011	0.926	1	0.003*	2.808	0.989	1.047
RH %	-0.005	0.006	0.727	1	0.011	0.929	0.88	1.220
Constant	-4.056	0.570	0.563	1	0.304	0.304		

(**p* < 0.005 based on Bonferroni correction)

Table 7.2 Logistic regression predicting the likelihood of thrips presence in the lettuce agro-ecosystem based on crop age, rainfall, temperature and relative humidity (RH%).

	<i>B</i>	SE	Wald	<i>df</i>	<i>p</i>	Odds Ratio	95 % CI for Odds Ratio	
							Lower	Upper
Crop age	-0.199	0.037	10.152	1	0.001*	0.888	0.826	0.955
Rainfall	-0.001	0.005	0.011	1	0.917	0.999	0.989	1.010
Temperature	0.070	0.029	5.673	1	0.017	1.073	1.103	1.137
RH %	-0.025	0.014	3.142	1	0.026	0.975	0.949	1.002
Constant	-0.217	1.684	0.017	1	0.805	0.805		

(**p* < 0.005 based on Bonferroni correction)

Table 7.3 Logistic regression predicting the likelihood of thrips presence in the tomato agro-ecosystem based on crop age, rainfall, temperature and relative humidity (RH%).

	<i>B</i>	SE	Wald	<i>df</i>	<i>p</i>	Odds Ratio	95 % CI for Odds Ratio	
							Lower	Upper
Crop age	-0.046	0.034	1.791	1	0.181	0.955	0.894	1.021
Rainfall	0.006	0.006	1.007	1	0.316	1.006	0.955	1.017
Temperature	0.039	0.031	1.624	1	0.202	1.040	0.979	1.105
RH %	0.022	0.013	2.973	1	0.085	1.022	0.997	1.048
Constant	-4.134	1.618	7.107	1	0.008	0.013		

(**p* < 0.005 based on Bonferroni correction)

Table 7.4 Logistic regression predicting the likelihood of thrips presence and relative humidity (RH%).

	<i>B</i>	SE	Wald	<i>df</i>	<i>p</i>	Odds Ratio	95 % CI for Odds Ratio	
							Lower	Upper
Crop age	-0.011	0.032	0.127	1	0.721	0.989	0.929	1.053
Rainfall	-0.014	0.004	11.543	1	0.001*	0.986	0.978	0.994
Temperature	-0.143	0.031	21.814	1	0.000*	0.867	0.817	0.921
RH %	0.030	0.009	11.954	1	0.001*	1.031	1.013	1.049
Constant	-1.514	1.140	1.764	1	0.184	0.220		

(**p* < 0.005 based on Bonferroni correction)**Table 7.5** Pearson correlation between species abundance and weather in French bean.

	Rainfall	Relative humidity	Temperature
<i>D. tenuicornis</i>	0.012	-0.053*	0.021
<i>F. occidentalis</i>	0.058*	0.044	-0.015
<i>F. schultzei</i>	-0.031	-0.017	0.001
<i>H. gowdeyi</i>	0.001	0.001	0.214*
<i>M. usitatus</i>	-0.055*	0.023	-0.200*
<i>P. achaetus</i>	-0.036	-0.040	0.036
<i>T. frici</i>	-0.024	-0.006	0.004
<i>T. tabaci</i>	0.001	0.045	-0.064*
N = 1210			

*Correlation is significant at the 0.05 level

Table 7.6 Pearson correlation between species abundance and weather in lettuce.

	Rainfall	Relative humidity	Temperature
<i>D. tenuicornis</i>	0.013	-0.085*	0.154*
<i>F. occidentalis</i>	-0.029	-0.015	0.011
<i>F. schultzei</i>	-0.096*	-0.012	-0.379*
<i>T. tabaci</i>	-0.038	0.009	0.003
N = 990			

*Correlation is significant at the 0.05 level

Table 7.7 Pearson correlation between species abundance and weather in tomato.

	Rainfall	Relative humidity	Temperature
<i>F. occidentalis</i>	0.098*	0.610*	0.055*
<i>F. schultzei</i>	0.086*	0.132*	0.057*
<i>P. achaetus</i>	0.003	-0.003	0.015
<i>T. palmi</i>	-0.057*	0.033	-0.068*
<i>T. tabaci</i>	-0.230*	0.015	-0.022
N = 1320			

*Correlation is significant at the 0.05 level

Table 7.8 Pearson correlation between species abundance and weather in zucchini.

	Rainfall	Relative humidity	Temperature
<i>D. tenuicornis</i>	-0.007	-0.168*	0.062*
<i>F. occidentalis</i>	0.060*	0.179*	0.057*
<i>F. schultzei</i>	0.053*	0.182*	0.032
<i>M. usitatus</i>	-0.441*	0.144*	-0.086*
<i>P. achaetus</i>	-0.084*	0.120*	-0.003
<i>T. frici</i>	-0.081*	0.089*	-0.006
<i>T. palmi</i>	0.006	0.037	-0.119*
<i>T. tabaci</i>	-0.041	0.026	0.156*
N = 880			

*Correlation is significant at the 0.05 level

Three-way ANOVA

There was no three-way interaction between year, planting and species for any of the four vegetable agro-ecosystems ($p > 0.05$) (Table 7.9). Year had no effect on thrips abundance in any of the four agro-ecosystems ($p > 0.05$) (Table 7.9).

Table 7.9 Main effect of planting and species for each vegetable agro-ecosystems in three-way ANOVA.

	French bean	Lettuce	Tomato	Zucchini
Year	$F(2, 660) = 81.48$, $p = 0.213$	$F(2, 330) = 34.61$, $p = 0.173$	$F(2, 330) = 52.00$, $p = 0.153$	$F(6, 770) = 65.07$, $p = 0.201$
Planting	$F(10, 660) = 3.23$, $p < 0.001$	$F(8, 330) = 18.39$, $p < 0.001$	$F(10, 330) = 17.51$, $p < 0.001$	$F(10, 770) = 68.53$, $p < 0.001$
Species*	$F(5, 660) = 69.56$, $p < 0.001$	$F(2, 330) = 101.87$, $p < 0.001$	$F(5, 330) = 49.26$, $p < 0.001$	$F(6, 770) = 54.50$, $p < 0.001$
Planting x Species	$F(50, 660) = 6.62$, $p < 0.001$	$F(16, 330) = 18.37$, $p < 0.001$	$F(20, 330) = 7.36$, $p < 0.001$	$F(60, 770) = 26.73$, $p < 0.001$
Year x Planting x Species	$F(17, 660) = 84.23$, $p = 0.14$	$F(14, 330) = 32.70$, $p = 0.116$	$F(17, 330) = 102.22$, $p = 0.093$	$F(18, 770) = 54.34$, $p = 0.120$

Planting and species had a significant effect on abundance in all four agro-ecosystems, including an interaction effect ($p < 0.05$) (Table 7.9). In French bean, based on pairwise comparison, planting one had the greatest total thrips abundance and planting four recorded the lowest abundance; however, there were few significant differences amongst the eleven plantings. Planting one had significantly more thrips compared to plantings four, eight, ten and eleven, and there was no difference in relative abundance between plantings three to eleven (Figure 7.13; means with a letter in common are not significantly different, $p > 0.05$. Planting number (1 to 11) followed by the month of planting (in brackets) are displayed in the figure).

In lettuce, results of the pairwise comparison of total thrips abundance between plantings are presented in Figure 7.14 (means with a letter in common are not significantly different, $p > 0.05$. Planting number (1 to 11) followed by the month of planting (in brackets) are displayed in the figure), with planting seven having significantly more thrips compared to all other plantings.

In tomato, pairwise comparison of total thrips abundance between plantings determined that there were significantly more thrips in planting one compared to all others (Figure 7.15; means with a letter in common are not significantly different, $p > 0.05$. Planting number (1 to 11) followed by the month of planting (in brackets) are displayed in the

figure).

In zucchini, there were significantly more thrips in planting nine compared to all other plantings (Figure 7.16; means with a letter in common are not significantly different, $p > 0.05$. Planting number (1 to 11) followed by the month of planting (in brackets) are displayed in the figure). The effect of species on thrips abundance is discussed in Chapter 4.

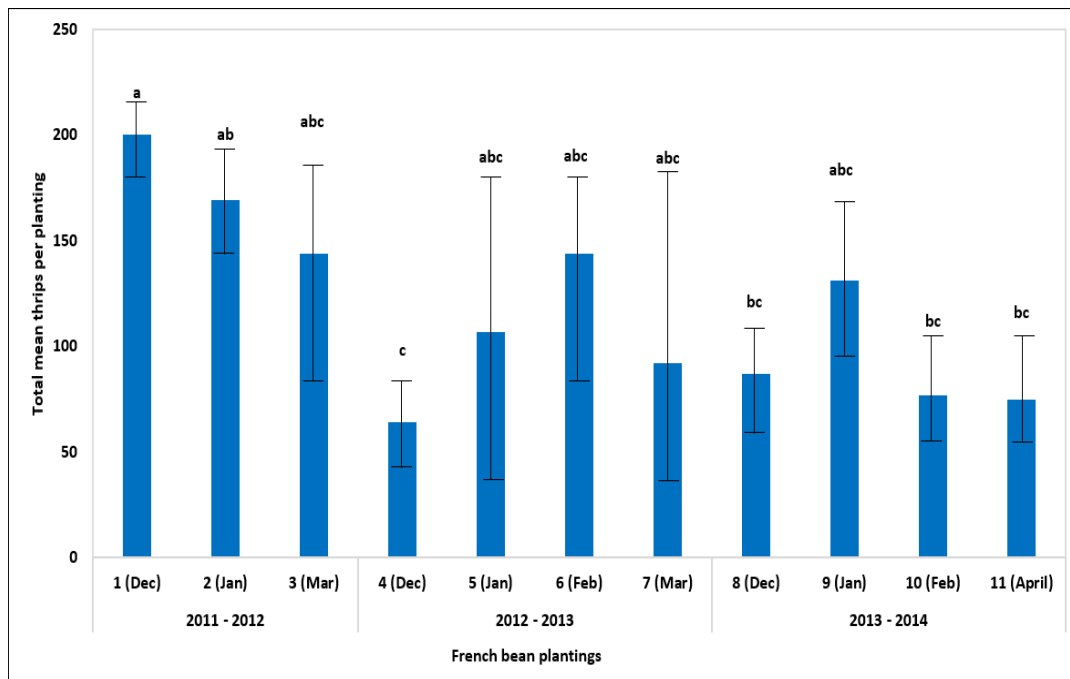


Figure 7.13 Pairwise comparison of total thrips abundance in each French bean planting.

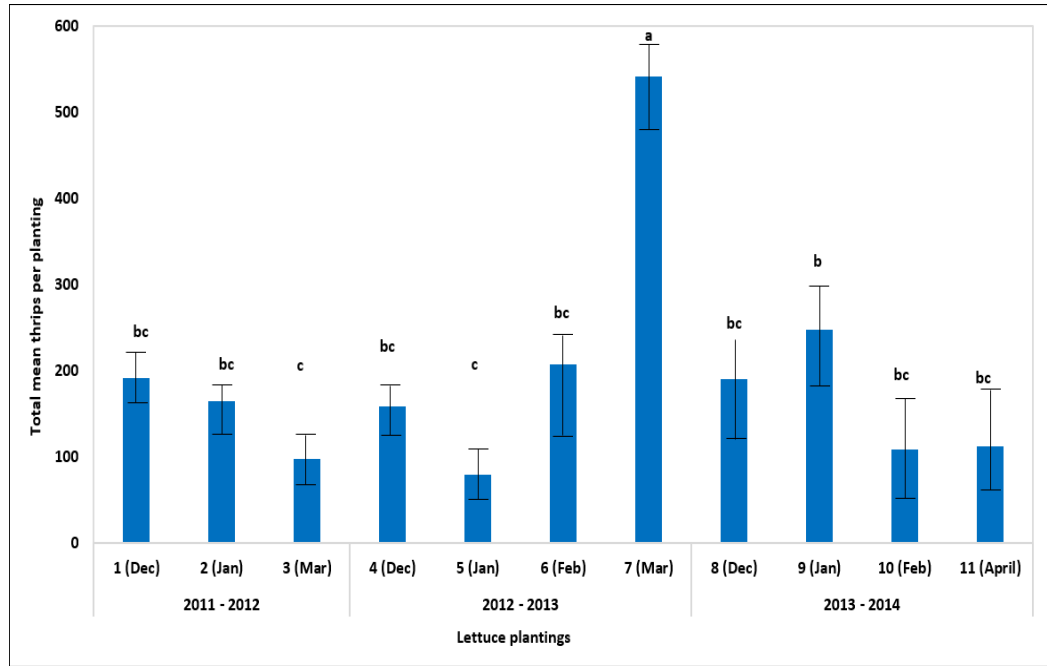


Figure 7.14 Pairwise comparison of total thrips abundance in each lettuce planting.

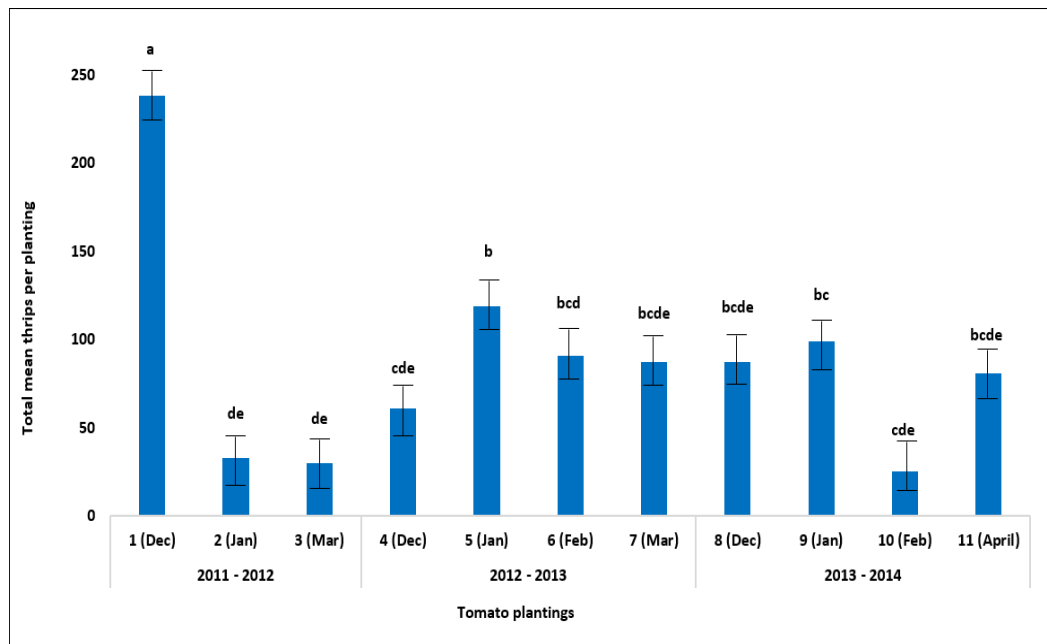


Figure 7.15 Pairwise comparison of total thrips abundance in each tomato planting.

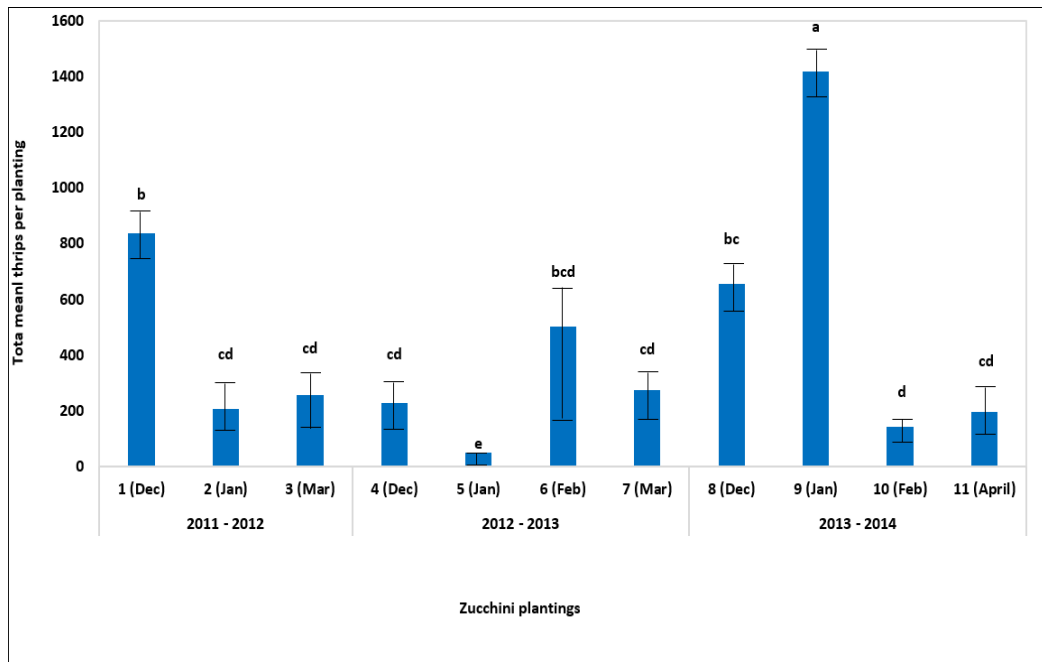


Figure 7.16 Pairwise comparison of total thrips abundance in each zucchini planting.

Discussion

A strong host association between a species and crop (feeding or breeding) will determine the presence of the species and its use of the plant for feeding or breeding. However, weather also has a direct effect on the abundance of an insect population, by increasing the rate of migration onto a plant or the reproductive rate of the insect dependant on the optimum conditions required. Based on the results of this study, rainfall, temperature and relative humidity had a direct effect on the presence of thrips within the four agro-ecosystems. The relative abundance of each of the species was highly variable, with some species displaying a more consistent relationship with weather regardless of the crop type, while others were much more variable in the abundance across the four crops.

Effect of weather on thrips presence

Temperature has long been viewed as an important factor in thrips population dynamics, largely by affecting the development time of many species and their ability to immigrate into a crop. For example, under high temperatures, many insect species, such as the nun moth, *Lymantria monacha* L., have a shortened egg, larval and pupal development time (Karolewski et al. 2007). Feeding, reproduction and the time spent invested in looking for suitable oviposition places is also associated with warm temperatures (Moore & Allard 2008). An increase in temperature and crop age was associated with a greater thrips abundance within the French bean crops. As temperature increases plant growth, the response of flowering in plants is also increased, often with longer flowering periods (Scaven & Rafferty 2013). This response would explain the increased thrips presence in French bean. Warmer temperatures would see increased movement of anthophilic thrips, into the crop in search of nectar and pollen to fuel their metabolic activity.

Weather had no effect on the presence of thrips within either lettuce or tomato. However, for the lettuce agro-ecosystem, increasing crop age had a direct effect on thrips in crop. The data is consistent with the physiological growth stage of the crop influencing a response in thrips moving into the crop. As lettuce has a reproductive association with both *F. occidentalis* and *F. schultzei* (see Chapter 6), this may be in response to the development of either species. Tomato supported the lowest thrips abundance in comparison to French bean, lettuce and zucchini (see Chapter 4), and is considered a poor reproductive host for all species (see Chapter 6). That there was no relationship with either weather or crop age and thrips presence in the crop, further suggests that tomato is a poor host for the thrips found in this study.

In zucchini, rainfall, temperature and relative humidity had an effect on the presence of thrips within the agro-ecosystem. An increase in rainfall and temperature, decreased the likelihood of total thrips

abundance in zucchini, while increased relative humidity increased the likelihood of abundance in the agro-ecosystem. Rainfall is considered to be an important suppressive weather factor on thrips populations (Palomo et al. 2015), and warm temperatures are generally favourable for thrips population growth (Cammell & Knight 1992; Deka et al. 2009; Harrington et al. 2001; Stacey & Fellowes 2002), while relative humidity can be highly variable in its relationship with insects (Jaworski & Hilszczański 2013). The negative association between rainfall and temperature in crop may be as a result of their effect on the physiology and growth of the zucchini plant, affecting thrips presence. Rainfall and temperature stress can cause zucchini flowers to drop (Napier 2009). As there were significantly more thrips collected from zucchini flowers compared to all other plant parts (growing tip and leaves) this would dramatically decrease the number of flowers available for thrips (see Chapter 5).

Effect of weather on thrips species abundance

High rainfall is generally considered to negatively impact thrips populations, with heavy precipitation causing mortality through drowning (Jones 1979). However, rainfall can promote plant growth and delay senescence of the crop and therefore prolong the period for reproduction or immigration to place (Morsello et al. 2008). This would explain the positive relationship between *F. occidentalis* and rainfall in French bean, tomato and zucchini. Morsello et al. (2008) found that dispersing *F. fusca* and *T. tabaci* were positively related to the number of days of precipitation, but negatively related to total rain volume. This is of relevance as often peak periods of *F. occidentalis* in French bean occurred after rain, with immediate declines in abundance coinciding with high rainfall events. *Frankliniella occidentalis* also displayed a positive relationship with relative humidity in tomato and zucchini, which is important for the development of this species. Greater than 80% relative humidity is necessary for pupation of late-stage second instar *F.*

occidentalis, with 90% the optimum level (Steiner et al. 2011). Similarly, increased relative humidity saw an increase in relative abundance of *T. frici* and *M. usitatus* in zucchini

Temperature had a direct effect on the abundance of *M. usitatus*, with population abundance greatest during the cooler autumn periods in French bean and zucchini. The findings here support those of Duff (2012) who found that *M. usitatus* numbers were higher in French bean between April and May compared to October to November in the Lockyer Valley in plantings in 2008 and 2012. The optimum temperature for *M. usitatus* development is 20°C, completing a lifecycle within 50 days (Chang 1987). Therefore, based on the outcome here and the lifecycle data generated by Chang (1987), this suggests that the thermal optimum for this species is low, and the survival and fitness of *M. usitatus* is suited to the autumn temperature range (mean temperature of 20 to 22°C) (BoM 2016). While extremely low temperatures can cause increased mortality, some insects are unable to complete their development cycle without a sufficient number of low temperature days (Jönsson et al. 2007; Netherer & Schopf 2010).

Temperature has been observed to have a strong effect on the development and reproduction of *T. tabaci*, by decreasing development time at warmer temperatures (Tsai et al. 1995). Kawai (1990) reported that mean generation time of *T. tabaci* at 15°C is 80.2 days, and only 20.5 days at 30°C. *Thrips tabaci* have been shown to tolerate low temperatures, with pupae surviving 8 days at 0°C (Tsai et al. 1995). In zucchini, there was a positive relationship between *T. tabaci* and temperature, supporting the findings of Tsai et al. (1995) and Kawai (1990), while in French bean the reverse was observed. This indicates that the responses of *T. tabaci* to temperature are altered dependant on the crop, and that understanding the effect of weather on the population dynamics of an insect cannot be generalised across a range of crops.

Desmothrips tenuicornis were directly affected by increased

relative humidity in French bean, lettuce and zucchini. Insects will often respond to slight differences in relative humidity outside the optimum range of 60 to 80%, by moving to an area of preferred humidity (Cammell & Knight 1992). French bean traps heat and moisture within the canopy of its foliage as a result of dense planting, and can sustain high relative humidity within the crop (Nyasani et al. 2013). Similarly, it is possible that lettuce and zucchini trap moisture and heat within the crop, creating a humid and unfavourable environment. Therefore, the decrease in *D. tenuicornis* abundance in association with increased relative humidity in these two systems may be as a result of it moving out of the crop or off the plant, to areas where the relative humidity is lower and more favourable. This inverse relationship between relative humidity and abundance has been recorded in many population dynamics studies (Waiganjo et al. 2008). For example, the development time of the spotted stalk borer, *Chilo partellus* (Swinhoe), took up to 70.2 days at 80% relative humidity and 22°C (Tamirum et al. 2012). However, the development period decreased to 26.5 days at 40% relative humidity and 30°C.

Frankliniella schultzei displayed a positive relationship with rainfall, temperature and relative humidity in tomato and zucchini; however, in lettuce the association with temperature and rainfall was negative. The relationship between *F. schultzei* and rainfall in lettuce may be a physiological effect of the crop. As interstitial dweller, thrips can move into flowers where they are protected from rainfall. In lettuce, a non-flowering crop, they may have been more vulnerable to drowning in high rainfall events. The negative association between *F. schultzei* and temperature in lettuce may be as a result of predation. *Desmothrips tenuicornis* are thought to be predatory on immature thrips, and the results of this study suggest that temperature may have increased the relative abundance of *D. tenuicornis* in lettuce, resulting in increased predation of immature *F. schultzei* (see Appendix C). As lettuce is a reproductive host of *F. schultzei* (see Chapter 6) this species would have

been particularly vulnerable to predation. However, laboratory assays assessing the predation potential of *D. tenuicornis* on immature *F. schultzei* failed to conclude if this was occurring (Appendix C).

Thrips palmi development is dependent on warm temperatures, with 25°C optimum (Capinera 2008; Yadav & Chang 2013), which is in direct contrast to the effect of temperature on this species in tomato and zucchini. This indicates that the relationships these species have with temperature are also dependant on their relationship with the plant and their behaviour on the plant (feeding or breeding).

Variation in abundance

For many of the species recorded in the four agro-ecosystem assemblages, there were large variations in abundance across the years and plantings, and in their relationship with the three weather variables measured in this study. The climatic conditions will mutually affect the growth of the plant and the thrips species, dependant on their climatic needs for optimal growth. The life history of many insects means that phenological synchrony exists between a plant and an insect, which will stimulate insect movement onto the plant based on the phenological life stage. Therefore, these variations are likely due to the suitability of the plants' nutritional characteristics, the climate within the canopy of the crop and the phenological stage of the crop, making it more or less suitable for thrips population growth (Brodbeck et al. 2002).

In this study, only the basic interactions between weather, crop and thrips abundance are reported. There are a multitude of specialised multi-trophic insect, plant and microbial complexes that are dependent on a range of abiotic factors, including climate, topography, land use history, soil quality and inter-specific competition for resources. Natural enemies, including predators, hymenopteran parasitoids, parasitic nematodes and fungal pathogens can play an important role in regulating thrips populations on plants in field grown agro-ecosystems (Loomans et

al. 1997). For example, Davidson and Andrewartha (1948) published data on the relationship between weather and *T. imaginis* reproducing on roses, without taking into account other factors such as seasonal inflorescence. The findings reflected only an increase in abundance during favourable periods that coincided with the rose flowering period. *Thrips imaginis* were also reproducing on surrounding host plants and moving into the rose flowers during this flowering period. This highlights the importance of assessing the relationship of weather and thrips populations in a holistic context, considering other possible variables within the agro-ecosystem, including crop phenology, and an understanding of the reproductive capability of a plant. Most importantly, variation in seasonal abundance of thrips will differ between years, therefore to better understand and determine the relationship between climatic variables and thrips, long-term studies need to occur.

Conclusion

Temperature, rainfall and relative humidity influenced the abundance of thrips populations both directly and indirectly, dependant on the species. Increasing temperature increased the likelihood of thrips presence in French bean, and increasing rainfall and temperature saw a decreased likelihood of thrips present in zucchini, whilst increased relative humidity saw the likelihood of thrips presence in zucchini increase. Increasing temperature had a negative relationship with *M. usitatus* abundance, and a positive relationship with *H. gowedyi* in French bean, whilst increasing temperature had a negative relationship with *F. schultzei* abundance in lettuce. Increasing relative humidity had a positive relationship with increasing *F. occidentalis* abundance in tomato and in zucchini, increasing rainfall had a negative relationship with *M. usitatus* abundance in crop. Based on the results observed in this study, temperature, rainfall and relative humidity play an important role in regulating thrips populations in each crop treatment; however, individual

species display variations in their association with these three variables in relation to individual crops.

Chapter Eight: The temporal and spatial evolution of thrips clusters within four vegetable agro-ecosystems

Introduction

Thysanoptera are opportunistic species capable of exploiting environments where the conditions for feeding, reproduction and shelter may occur only intermittently (Funderburk 2001). This characteristic, combined with the polyphagous nature of some species, means that thrips are extremely adaptable to a wide range of horticultural crops. The transient nature of thrips in optimum environments often results in quick colonisation and population establishment. The diversity of thrips species present in a vegetable crop can be very rich at any one time and the distribution of these populations may not be homogenous. Spatial heterogeneity of thrips is an important source of variability to be investigated as knowing the potential distribution, in space and time, is vital for understanding the growth of thrips populations in vegetable agro-ecosystems. This, in turn, will underpin the development of more effective thrips control strategies.

Spatial and temporal dynamics

Spatio-temporal studies of insect populations in vegetables aim to understand the heterogeneity of populations to determine the patterns of abundance within a crop along a temporal time scale, such as plant age (Vinatier et al. 2011). Population distribution patterns are almost never uniform and are influenced by the behavioural response of each individual species to the crop, the season and a multitude of other variables. In studies of population distribution patterns, spatial

distribution can be divided into three types: random, aggregated (clustered) and uniform (Begon et al. 1996). Thrips populations in field grown vegetable systems are almost always clustered. Changes in the spatial patterns of these clusters during crop development are likely to reflect species-specific associations with a crop (feeding or breeding), the subsequent redistribution throughout the crop occurring either as a result of the increase in population growth or dispersal ability. Environmental variables and weather conditions have a major effect on these processes. A pre-requisite for understanding these spatio-temporal patterns is accurate descriptions of the likelihood of thrips movement into a crop and the subsequent formation and growth of thrips clusters in a vegetable crop.

The temporal and spatial variation of the insect populations that exist within agro-ecosystems are affected by seasonal factors (van Helden 2010). Temporal distribution of important economic species such as *F. occidentalis* varies with season and crop phenology in French bean (Kasina 2009; Duff 2012; Nyasan 2013), tomato (Reitz 2002) and chilli (Walsh et al. 2012). However, information on the spatio-temporal distribution of thrips in vegetables on a macro-scale is limited, particularly in field grown systems. Spatial distribution is one of the most characteristic ecological properties of a species that can be used to define patterns of abundance in a crop, but is often not reported in vegetable crops as it is highly region specific (Taylor 1984). Population dynamics of a thrips species will differ between geographical locations and across host crops (Hill 1987), which may explain the limited information on the within-crop distribution of thrips in vegetables. However, distribution patterns of insects can stabilise over time, particularly in areas where perennial crops are planted or annual crops are planted in successive plantings, seasons or years, which is the case in many vegetable production systems (Moradi-Vajargah et al. 2011). Macro-scale spatio-temporal distribution studies of thrips may, therefore, be used in these situations to determine regional agro-ecosystem infestation patterns and

the subsequent growth of thrips populations.

There are many explanations for the cause of non-homogenous or aggregated insect population distributions, and distribution studies need to consider a multitude of abiotic and biotic factors. The distribution is affected by combined variations in crop phenology, local climate, season, site topography and the species itself (van Helden 2010; Sciaretta & Trematerra 2014). As many vegetable crops can support more than one thrips species, understanding the casual factors of spatio-temporal distribution of each species within a crop requires examination of multiple factors for each species. More importantly, the patterns of abundance of each species are likely not to be the same in all vegetable agro-ecosystems where the species is commonly found occurring.

Macro- and micro-scale distribution

Distribution studies on a micro-scale are concerned with the change in relative abundance of species within the plant. For example, Tamò et al. (1993) determined that *M. sjostedti* was spatially aggregated on cowpea plants, with a higher number of adults found on the inflorescence compared to leaf, stem and petioles. Abundance was distributed along a temporal crop phenological scale, with aggregation and abundance increasing as the crop began to flower. In a greenhouse study, Ugine et al (2006) determined that *F. occidentalis* were temporally and spatially distributed on garden impatiens, *Impatiens walleriana*. The adult and immature abundance significantly increased in flowers at each successive stage of bud development compared to the last, and in comparison, to the foliage of the plant (Ugine et al. 2006). Such studies are critical for developing an understanding of how thrips densities change in relation to the growth of the crop.

Macro-level studies focus on understanding the mechanisms of spatial distribution of insect populations throughout a landscape such as a vegetable agro-ecosystem (Dunning et al. 1992). Much of the spatio-

temporal research conducted on a macro-level has investigated distribution patterns to develop more accurate sampling protocols for pest populations. For example, Moradi-Vajargah et al. (2011) investigated the population density and spatial distribution of the alfalfa weevil, *Hypera postica* (Gyllenhal), on alfalfa in Iran. Based on collections in sample quadrant units of 0.25 m², Moradai-Vajargah determined that the weevil was spatially separated by its life stage. Larvae and adults were highly aggregated on the plant within these quadrants and throughout the experimental area, whilst the pupae had a more randomised distribution. Therefore, a higher sample number was required when sampling for adults. In pepper fields in Florida, Seal et al. (2006) found that chilli thrips, *S. dorsalis*, were highly aggregated on the top leaves of the plant in field plots of 24 m² and 48 m². The application of this information was sampling methods for interception of *S. dorsalis* in pepper fields, which involved examining the upper leaves of newly transplanted plants.

Studying the spatio-temporal patterns of thrips on a macro-level is an intensive practice, largely due to the necessity of conducting research over several plantings, seasons and years across a wide range of vegetable agro-ecosystems in relation to a specific thrips species. This explains the limited understanding of the spatio-temporal distribution of some of the key thrips found in French bean, lettuce, tomato and zucchini species assemblages. Many studies have investigated the influence of factors such as weather and host on the presence and abundance of thrips, such as the information presented in Chapter 7 in this study. However, the influence of crop and weather on the spatial distribution of thrips on a macro-scale is less understood. The spatial variation of insect populations in vegetable agro-ecosystems is becoming more important for the evolution of IPM programs. This is particularly pertinent for crops that can support one or more pest and non-pest species in large abundance at any one time.

One of the difficulties in ecological studies of insect populations is

that insect count data are discrete, and typically distributed in clusters throughout a crop, which means the data set consists of high zero counts (Ribiero Jr et al. 2009). Analysing such data can be difficult; therefore, it is appropriate to use models that incorporate a data generating mechanism such as Poisson distribution (Ribiero Jr et al. 2009). Alternatively, equations can be developed that characterise the data so that it is more uniform in its distribution and can be used in linear regression models to develop estimates and predictions of thrips movement into and throughout an agro-ecosystem.

As determined in Chapter four (Thrips species assemblage), the key species in each of the four vegetable agro-ecosystem species assemblages are *F. occidentalis* and *M. usitatus* in French bean, *F. occidentalis* and *F. schultzei* in lettuce and zucchini, and *F. schultzei* and *P. achaetus* in tomato. *Frankliniella occidentalis* and *F. schultzei* are commonly found in lettuce and zucchini (Kakkar et al. 2012b; Nyasani et al. 2012; Nyasani et al. 2013). Both are highly polyphagous and considered pests of a wide range of vegetable crops including lettuce and zucchini. In tomato, *F. occidentalis* and *P. achaetus* are often found in Australian crops; while the former is considered a pest, the hairless flower thrips (*P. achaetus*) has not been recorded causing injury to tomato crops. *Frankliniella occidentalis* commonly occurs in French bean crops (Duff 2012; Nyasani et al. 2013; Kasina et al. 2009) and is considered a pest, as is the bean blossom thrips *M. usitatus*, also found in French beans (Chang 1987; Duff 2012; Tang 2015). The spatial and temporal distribution of these species on a macro-level, within the respective agro ecosystems assemblages, is not well understood. Therefore, this may be one of the first attempts.

In this chapter, we investigate the spatial and temporal distribution of *F. occidentalis* and *F. schultzei* in lettuce and zucchini crops, *F. schultzei* and *P. achaetus* in tomato, and *F. occidentalis* and *M. usitatus* in French bean by determining the probability of each species to form a cluster, the number of thrips within a cluster, and the spatial size

of the cluster throughout the crop.

Materials and methods

Field design and sample protocol

As described in Chapter 3 (General research methodology), the field survey was conducted as eleven plantings over the course of a three-year period. Each planting consisted of four blocks and four crop treatments, with ten replicates per block. One plant sample (flower, growing tip, leaf and stem or whole plant) was collected from each replicate per crop, weekly, over the life of the crop. Flower and growing tip samples were collected into 95% ethanol. Stem and leaf and whole lettuce samples were removed in the field (destructive sampling) and collected into individual paper bags, deconstructed in the laboratory and beaten over a tray to dislodge thrips. Thrips were then collected into vials of 95 % ethanol. Tomato leaf and stem and growing tip samples were not destructively collected, but beaten over a tray in crop and thrips collected into 95% ethanol. All adult thrips were slide mounted and identified to genus and species, using the Oz Thrips interactive lucid key under a compound microscope. Immature thrips were assessed in Chapter 6 and not reported on here.

Average rainfall and temperature were recorded from the BoM weather station at the University of Gatton campus as described in Chapter 3.

Spatial distribution

To determine the spatial distribution of each species within the respective agro-ecosystem, each replicate was regarded as one spatial point, with the coordinates corresponding to the centre of the replicate within each crop. The data sample size was ten spatial points for each crop, which limited the spatial resolution of the observations to five points (replicates) along the length of the crop and two points across the width of the crop. The limited spatial data and resolution imposed challenges on statistical analysis.

Therefore, to account for the limited spatial data, two statistical equations were developed to characterise spatial distribution, which produced two new dependent variables, thrips cluster size and thrips count modulation

Thrips cluster size

Thrips cluster size is the physical size of the aggregation of thrips in space (spatial distribution) across the crop area. Thrips cluster size, L_{cl} , is defined as equation (1):

$$L_{cl} = K \frac{\sum_{i=1}^{10} \sum_{j=1}^{10} \frac{|c_i - c_j|}{(\Delta L_{ij})^n} \Delta L_{ij}}{\sum_{i=1}^{10} \sum_{j=1}^{10} \frac{|c_i - c_j|}{(\Delta L_{ij})^n}} = K \frac{\sum_{i=1}^{10} \sum_{j=1}^{10} \frac{|c_i - c_j|}{(\Delta L_{ij})^{n-1}}}{\sum_{i=1}^{10} \sum_{j=1}^{10} \frac{|c_i - c_j|}{(\Delta L_{ij})^n}}, \quad (1)$$

where ΔL_{ij} is the distance (m) between the i -th and j -th replicate, measured between the centre of the two replicates in a crop. c_i and c_j are the thrips counts in the i -th and j -th replicates respectively. i and j are the indices taking integer values between one and ten indicating different replicates in the crop. The cluster size is an average of the distances ΔL_{ij} between all possible pairs of replicates in a crop, weighted by the factors $|c_i - c_j|(\Delta L_{ij})^{-n}$. The parameter K is determined from the condition that the average cluster size L_{cl} must be equal to the size of one replicate, 4 x 3.75 m ($\sim 16 \text{ m}^2$) if only one replicate, in a crop, has non-zero counts. Therefore, the minimum cluster should be $\sim 16 \text{ m}^2$. The power n should be determined from the comparison of the calculated L_{cl} at different values of n with the actual distribution of the thrips counts. Therefore, cluster size is defined as a measurement of the diameter of the cluster in the block. This equation is useful for small sets of spatial data (as shown in this study), because permutation of the replicate data (Eq. (1)) results in effective smoothing of the cluster size variable (L_{cl}) compared to the

original highly scattered count variable. See appendix F for further methodology detail for these equations.

Thrips cluster modulation

Thrips cluster modulation is defined as the mean number of thrips within a cluster (aggregated thrips). Thrips cluster modulation M_{cl} is defined by equation (2), which was developed solely for use in this thesis:

$$M_{cl} = \frac{\sum_{i=1}^{10} |c_i - \min\{c\}|}{10}, \quad (2)$$

where $\min\{c\}$ is the minimum thrips count from each replicate, within a crop. M_{cl} is an average of the differences between thrips counts and the minimum thrips count in a crop. This equation provides the average magnitude of typical variation of thrips counts in a crop, thus quantifying the typical modulation of thrips counts across the crop. If the minimum thrips count is zero, the M_{cl} simply gives the average thrips count.

Statistical analysis

Only the two most abundant species in each crop (based on results in Chapter four) were included in the analyses. Species comparison of *F. occidentalis*, *F. schultzei*, *M. usitatus* and *P. achaetus* across all four crops was not possible due to the high zero recordings of some species, or their absence, in some crop treatments. For instance, *M. usitatus* does not occur in lettuce and was recorded in very low numbers in tomato. similarly, *P. achaetus* was only present in relative abundance in tomato, therefore could not be compared across crop treatments.

To characterise the spatio-temporal distribution of each species within the respective agro-ecosystem, the data was subjected to linear and logistic regression models. The model fit was estimated using the McFadden's R^2 , which is the most frequently reported coefficient of

determination in regression models (McFadden 1974; StataCorp 2015). This determines the percent of the variability of the dependant variable accounted for by the model. To demonstrate the likelihood of thrips clustering ($D > 1$ over-dispersion), the index of dispersion was calculated to determine if the count data was clustered (aggregated) ($D > 1$ over-dispersion), as $D = \sigma^2/\mu$, where σ^2 is the variance and μ is the mean count value (Upton & Cook 2014).

Data was further subjected to a logistic regression to determine the probability of thrips moving into a crop and forming a cluster in relation to crop age (weeks since planting), year (one – 2011/2012, year two – 2012/2013 and year three – 2013/2014), planting number (1 to 11) and weather (average rainfall and temperature). A linear regression model was used to investigate how cluster size (L_{cl}) and cluster modulation (M_{cl}) changed in relation to crop age, year, planting number and weather for each of the four agro-ecosystems. Linear regression models require the dependent variables (L_{cl} and M_{cl}) to be distributed normally. Therefore, the Tukey's ladder of transformations (Tukey 1977) was used to identify the required transformation of the dependent variables to ensure their normality in all models. All combinations of variables were investigated and the best predictive models were selected accordingly. Interactions between all pairs of predictor variables in all models were checked and demonstrated to be statistically insignificant ($p > 0.2$) and therefore interactions were not considered. Crop age was categorised when statistical significance was not achieved using the numerical time variable (comparison of values progressing from one week after planting onward) and the corresponding R^2 coefficient could be improved. Variables that exceeded the adopted level of statistical significance, at the $p < 0.15$ level, were not included in the final models and are therefore not reported.

Year was included in both regression analyses to determine if there was consistency in presence and clustering across the years. Whilst

we cannot discuss the behaviour of species dependency across the years, nor the implication for management of these pest populations in each crop. Inclusion of year, along with crop age and weather, will indicate if there is consistency of presence of thrips species and clustering amongst the years. Or indicate the possibility of other variables outside of these equations that might be a causal factor in the likelihood of thrips presence and clustering that could be included in future model based on difference between years.

The figures presented show the 95% prediction intervals rather than confidence intervals to illustrate the typical spread of the experimental measurements around the predicted points and curves (Figures 8.1 to 8.5). The 95% prediction intervals are not an indication of significant differences between the corresponding dependencies. All weather variables were calculated as mean values between samples dates.

Results

Frankliniella occidentalis and *F. schultzei* were much more aggregated in zucchini compared to all other crops, based on the indices of dispersion (Table 8.1).

French bean

The probability of *F. occidentalis* moving into French bean and forming a cluster increased from three weeks after seeding (Table 8.2; Figure 8.1c). The size of *F. occidentalis* clusters in French bean increased exponentially with increasing temperature (Figure 8.1a) and, inversely, the size decreased with increasing rainfall greater than 25 mm (Table 8.1; Figure 8.1b). For *M. usitatus* the probability of cluster formation was very low in the first three weeks after seeding, followed by a significant increase between week four and five, and again from week six onward, with an almost probable chance (0.9) of *M. usitatus* clusters forming over

the last five weeks (Table 8.2; Figure 8.1d). Unlike *F. occidentalis*, the size of *M. usitatus* clusters were not dependent on weather, except for plantings two and three (Table 8.1). There was no statistically significant dependence of cluster modulation on crop age, planting, year or weather for either species ($p > 0.15$)(variables that exceeded the adopted level of statistical significance, at the $p < 0.15$ level, were not included in the final models and are not reported). Therefore, modulation was calculated using the intercept only (Table 8.3). *Frankliniella occidentalis* had a higher mean cluster modulation than *M. usitatus* (Table 8.3).

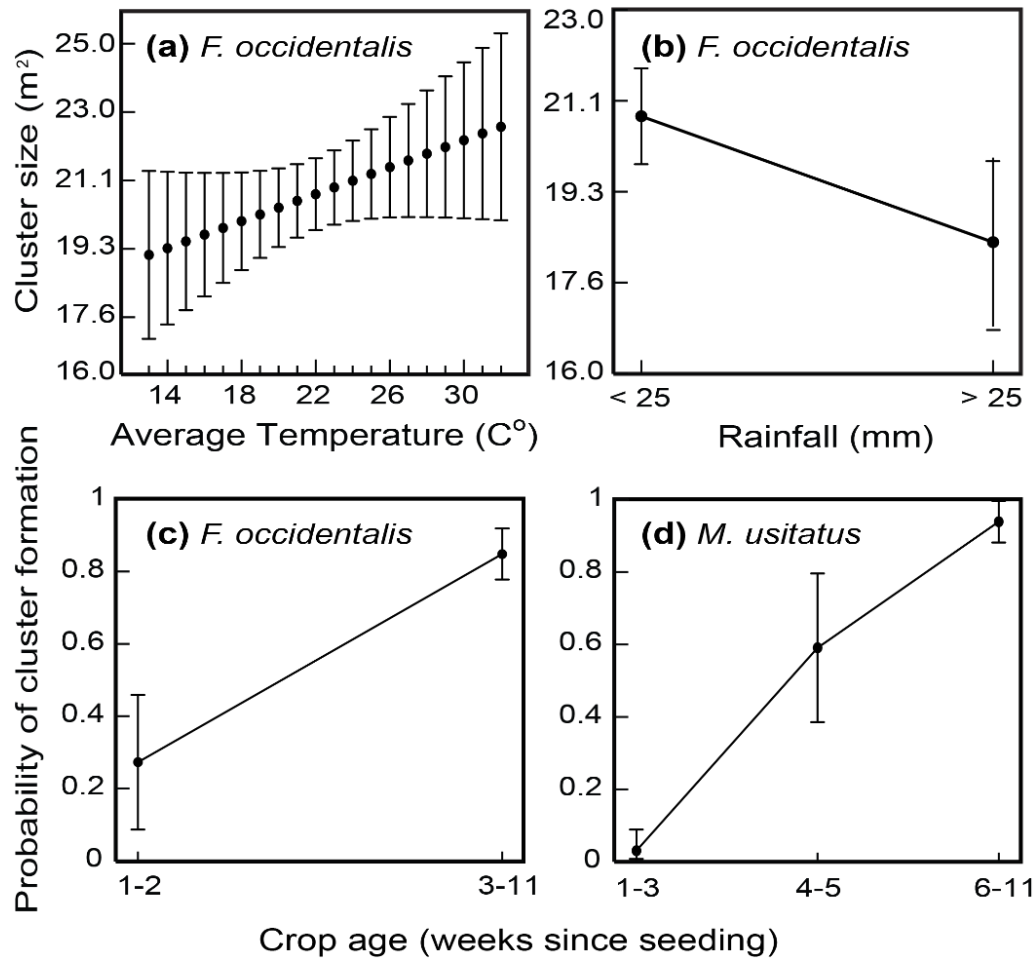


Figure 8.1 The dependency of *F. occidentalis* cluster size on (a) temperature and (b) rainfall. The probability of cluster formation for (c) *F. occidentalis* and (d) *M. usitatus* in French bean dependent on crop age.

Lettuce

Unlike French bean, the probability of *F. occidentalis* clustering in lettuce was not dependent on the age of the crop; however, rainfall reduced the probability of *F. occidentalis* cluster formation, particularly in week one (Table 8.2; Figure 8.2c). The size of *F. occidentalis* clusters were dependant on rainfall, with larger cluster size corresponding with > 25 mm rainfall, and inversely a smaller cluster size at < 25 mm rainfall (Table 8.1; Figure 8.2a). Cluster size under different rainfall was significantly different between years being the highest at > 25 mm in year three (2013 to 2014) (Figure 8.2a). There was no statistically significant dependence of cluster modulation on crop age, planting, year or weather for *F. occidentalis* in lettuce ($p > 0.15$), and therefore was calculated using the intercept only (Table 8.3). Mean cluster modulation of *F. occidentalis* was lower in lettuce than French bean (Table 8.3).

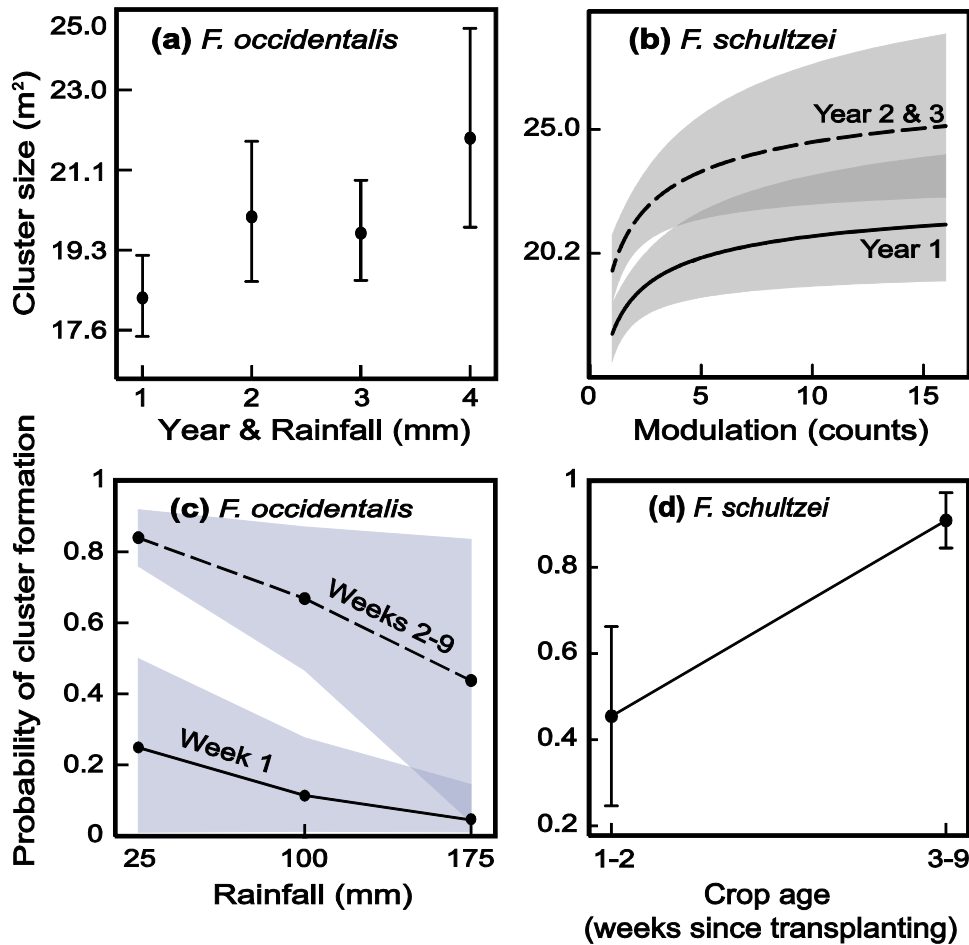


Figure 8.2 a) The dependency of *F. occidentalis* cluster size on rainfall (b) The dependency of *F. schultzei* cluster size on thrips cluster modulation. (c) The probability of *F. occidentalis* cluster formation in lettuce dependent on rainfall, and (d) *F. schultzei* dependant on crop age.

The probability of *F. schultzei* cluster formation in lettuce was dependent on crop age (Table 8.2), with a low probability between weeks one and three, increasing after this period (Figure 8.2d). The size of *F. schultzei* clusters were dependant on cluster modulation, which were the only species to display this dependency (Table 8.2; Figure 8.2b). This dependency between modulation and size is to be expected as increasing modulation (thrips counts) could be expected to cause spatial spreading (growth in the physical size of the cluster). The dependence of year three (2013 to 2014) was statistically indistinguishable from year two (2012 to 2013) (Table 8.2; Figure 8.2b). Mean cluster modulation of *F. schultzei* in lettuce was 1.70 (Table 8.3).

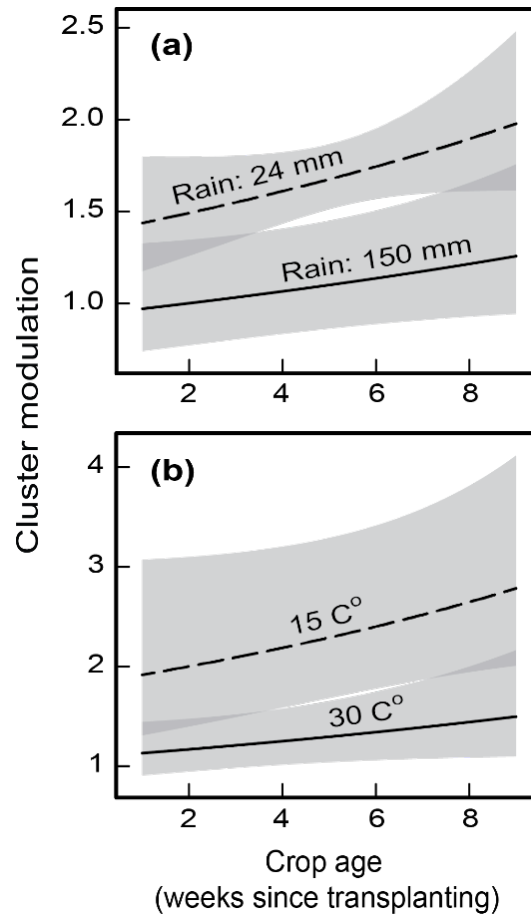


Figure 8.3 The dependency of *F. schultzei* cluster modulation in lettuce on crop age and (a) rainfall and (b) temperature.

Frankliniella schultzei cluster modulation, on lettuce resulted in a significant dependence ($R^2 \% = 24.7$) on crop age (reg. coeff. -0.015 , $p = 0.09$), rainfall (reg. coeff. 0.0015 , $p = 0.003$) and temperature (reg. coeff. 0.015 , $p = 0.028$), with the transformation $(M_{cl})^{-1/2}$. *Frankliniella schultzei* cluster modulation increased from one week after transplant (Figure 8.3). When plotted at average rainfall of 24 mm, modulation increased from below 1.5 mean thrips to around 2 at week eight (Figure 8.3a), and decreased with increased rainfall. At a mean temperature of 22.7°C , the model indicates a reduction in average temperature to 15°C increased modulation with crop age (Figure 8.3b). However, at $\geq 30^{\circ}\text{C}$, cluster modulation decreased (Figure 8.3b).

Tomato

For *F. schultzei* in tomato, the probability of cluster formation was not dependent on crop age, but was dependent on temperature (Table 8.2; Figure 8.4a), while the size of *F. schultzei* clusters was significantly dependant on the year (Table 8.1). Mean cluster modulation was calculated as 1.29 (Table 8.3). The probability of *P. achaetus* cluster formation in tomato was dependent on crop age and was significantly different between years (Table 8.2; Figure 8.4b). The probability of *P. achaetus* cluster formation was higher in year one compared to year two and three, which were statistically indistinguishable (Table 8.2). The probability of *P. achaetus* cluster formation occurring decreased at week eight in year two and three, and at week ten in year one (Figure 8.4b). There was no statistically significant dependence of cluster modulation on crop age, planting, year or weather for either *F. schultzei* or *P. achaetus* ($p > 0.15$). Cluster modulation for both species was calculated using the intercept only (Table 8.3). For *P. achaetus*, modulation was non-linear after transformation (Table 8.3).

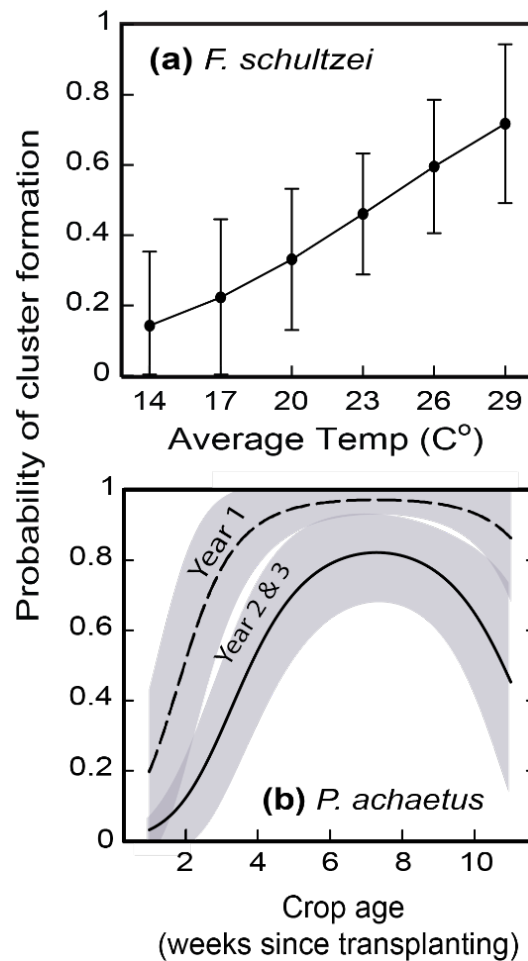


Figure 8.4 The probability of *F. schultzei* cluster formation in tomato dependent on (a) temperature and (b) *P. achaetus* cluster formation dependant on crop age.

Zucchini

In zucchini, the probability of *F. occidentalis* and *F. schultzei* cluster formation was dependent on crop age (Table 8.2; Figure 8.5c and d respectively). The result showed that there was a higher probability of *F. occidentalis* cluster formation in year one compared to year two and three, with probability declining after week six in year two and three (Figure 8.5c). Similarly, *F. schultzei* cluster formation declined after week six (Figure 8.5d). The size of *F. occidentalis* and *F. schultzei* clusters in zucchini were significantly dependant on crop age, increasing from one week after seeding until week eight (Table 8.1; Figure 8.5a and 8.5b

respectively). There was no statistical significant dependence of cluster modulation on crop age, planting, year or weather for *F. occidentalis* or *F. schultzei* ($p > 0.15$), therefore cluster modulation was calculated using the intercept (Table 8.3). *Frankliniella schultzei* had the greatest mean modulation overall in zucchini, indicating there was a higher mean abundance of *F. schultzei* within each cluster.

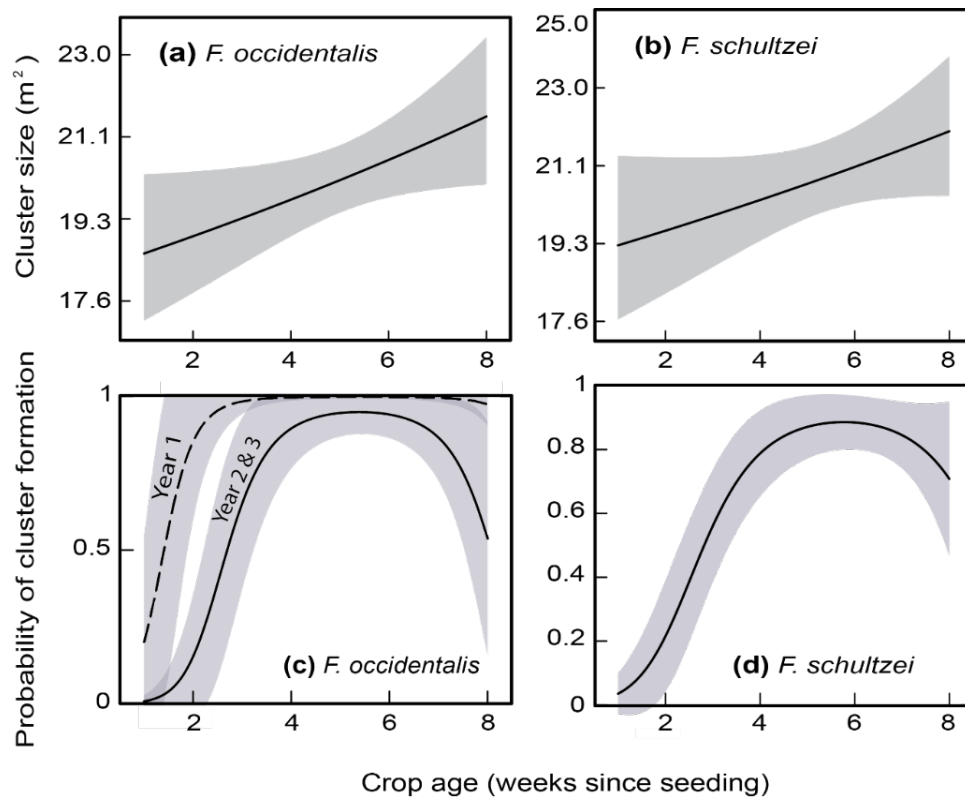


Figure 8.5 The dependency of (a) *F. occidentalis* and (b) *F. schultzei* cluster size on crop age. The probability of (c) *F. occidentalis* and (d) *F. schultzei* cluster formation in zucchini dependent on crop age

The mean average temperature was lower in year one compared to year two and three (Figure 8.6).

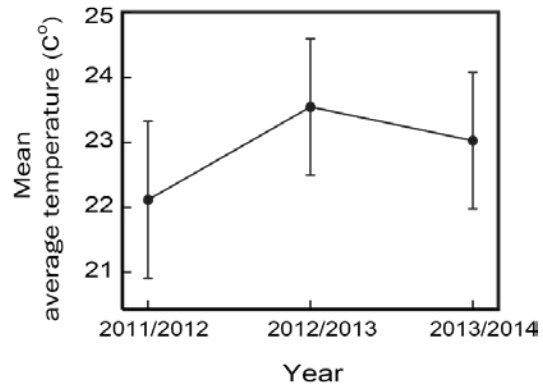


Figure 8.6 Mean average temperature between year one, two and three

Table 8.1 Linear regression models for the dependency of cluster size for each species, within each crop, based on crop age (weeks), rainfall, temperature, year of planting, planting number and cluster modulation (eq. (2) $(M_{cl})^{-1/2}$).

Crop	Species	Predictor Variable	Base Category	Transformation	Reg. Coeff.	p-value	R ² (%)	Index of Dispersion
French bean	<i>F. occidentalis</i>	Av. Temp. °C	< 25° C	Identity	0.02	0.120	8.4	1.26
		Rainfall (mm)	< 25 mm	Identity	-0.28	0.012		
	<i>M. usitatus</i>	Planting 2 & 3	Planting 1 & 4	Identity	-0.23	0.020	7.1	1.30
Lettuce	<i>F. occidentalis</i>	Rainfall	< 25 mm	$(L_{cl})^{-3}$	-0.0016	0.026	10.0	1.69
		Year 2014	Year one & two	$(L_{cl})^{-3}$	-0.0013	0.035		
	<i>F. schultzei</i>	Week 2 – 9	Week 1	$(L_{cl})^{-3}$	-0.0002	0.120	26.8	1.70
		Cluster modulation		$(L_{cl})^{-3}$	0.0048	< 0.001		
		Year two	Year one	$(L_{cl})^{-3}$	-0.0022	0.001		
Tomato		Year three	Year one	$(L_{cl})^{-3}$	-0.0016	0.016		
	<i>F. schultzei</i>	Year two & three	Year one	$(L_{cl})^{-3}$	-0.0019	0.005	9.6	1.22
	<i>P. achaetus</i>							1.10
Zucchini	<i>F. occidentalis</i>	Week 2 - 8	Week 1	$(L_{cl})^{-3}$	-0.00036	0.040	7.7	2.08
		Av. Temp. °C	< 25° C	$(L_{cl})^{-3}$	-0.00014	0.150		
	<i>F. schultzei</i>	Week 2-8	Week 1	$(L_{cl})^{-3}$	-0.0003	0.100	5.2	2.26

Table 8.2 Logistic regression models for the probability of cluster formation of each species, within each crop, based on the predictive variables crop age (weeks since planting or seeding), rainfall, temperature and year of planting.

Crop	Species	Predictor variable	Base category	Reg. Coeff.	p-value	R ² %
French bean	<i>F. occidentalis</i>	Week 3–11	Week 1-2	2.70	< 0.001	20.1
	<i>M. usitatus</i>	Week 4-5	Week 1-3	3.83	0.001	56.9
		Week 6-11	Week 1-3	6.21	< 0.001	
Lettuce	<i>F. occidentalis</i>	Rainfall (mm)	< 25mm	- 0.01	0.020	18.3
		Week 2-9	Week 1	2.76	< 0.001	
	<i>F. schultzei</i>	Week 3-9	Week 1-2	2.48	< 0.001	20.2
Tomato	<i>F. schultzei</i>	Week 2-11	Week 1	2.17	< 0.001	35.0
		Av. Temp. °C	< 25 °C	0.18	0.030	
	<i>P. achaetus</i>	Week 2-11	Week 1	1.83	< 0.001	30.8
		Year two	Year one	- 1.17	0.010	
Zucchini	<i>F. occidentalis</i>	Year three	Year one	- 2.03	0.005	51.5
		Week 2–8	Week 1	4.35	< 0.001	
		Year two	Year one	- 3.47	0.011	
	<i>F. schultzei</i>	Year three	Year one	- 2.55	0.053	31.5
		Week 2–8	Week 1	2.71	< 0.001	

Table 8.3 Mean values of cluster modulation for each species in the corresponding crop, including required transformations.

Crop	Species	Mean Cluster Modulation	95 % CI		Transformation
			Lower	Upper	
French bean	<i>F. occidentalis</i>	1.40	1.21	1.68	$(M_{cl})^{-1/2}$
	<i>M. usitatus</i>	1.43	1.23	1.48	$(M_{cl})^{-1}$
Lettuce	<i>F. occidentalis</i>	1.25	1.17	1.34	$(M_{cl})^{-1}$
	<i>F. schultzei</i>	1.70	1.52	1.92	$(M_{cl})^{-1/2}$
Tomato	<i>F. schultzei</i>	1.29	1.20	1.40	$(M_{cl})^{-1/2}$
	<i>P. achaetus</i>	1.09	1.04	1.14	$(M_{cl})^{-1}$
Zucchini	<i>F. occidentalis</i>	2.00	1.66	2.40	$\ln(M_{cl})$
	<i>F. schultzei</i>	2.04	1.73	2.46	$(M_{cl})^{-1/2}$

Discussion

The movement of a thrips species throughout a vegetable agro-ecosystem is dependent on a range of factors, including the crop type. Consequently, temporal and spatial distribution and density patterns will differ between thrips species (Kennedy & Margolies 1985). In this study, the four thrips species displayed different responses moving into a crop and forming a cluster, and subsequent growth in physical size and density in each of the vegetable agro-ecosystems. The calculated indices of dispersion (Table 8.1) for each species in the respective vegetable agro-ecosystem were greater than 1, indicating that data for each species counts were clustered (Upton & Cook 2014). The variation in species response to a crop was particularly evident in *F. occidentalis* and *F. schultzei*, which were found across more than one vegetable crop in this study. This indicates that the way a species responds to a particular crop is not equal in terms of their spatial and temporal distribution throughout the agro-ecosystem on a macro-level.

In French bean, clusters of *F. occidentalis* were likely to be found at the 2- to 3- leaf stage, at one to two weeks after seeding, with the likelihood of presence increasing by a magnitude of four after this time.

Unlike *F. occidentalis*, the probability of finding clusters of *M. usitatus* in French bean was very unlikely from one week after seeding to week three. However, at week four, when the French bean plant begins to form inflorescence (pre-budding), the probability of finding *M. usitatus* clusters increased substantially. By week six the chances of finding *M. usitatus* in French bean was almost twice as likely as the previous weeks (four and five). Week six coincides with the onset of flowering, which suggests that *M. usitatus* may prefer the later stages of the crop. However, the presence of *F. occidentalis* clusters does not appear to be as strongly dictated by flowering as does for *M. usitatus*, which suggests the onset of flowering increases the response of *M. usitatus* to move into the crop. Aggregation of insects is presumed to be associated with finding resources such as floral parts of the plant for feeding and breeding (Kao 1984). As the phenological changes of the crop occur, insects move into and out of an area based on the nutritional quality of the crop and its physiological stage in relation to the reproductive needs of the thrips (oviposition sites).

While the probability of *F. occidentalis* and *M. usitatus* cluster formation in French bean was driven by crop age, growth in the size of *F. occidentalis* clusters was a response to change in weather. The spatial spreading of the physical size of the clusters across the French bean crop increased with increasing mean temperature and declined with increased rainfall. Periods of warm and favourable weather can stimulate feeding and breeding and cause a rapid increase in population abundance (Cammell & Knight 1992), which in turn can lead to a crowding effect and induce dispersion (Mackay & Lamb 1996). For moderately mobile insects, such as thrips, population build up is considered to increase gradual spatial spreading, to accommodate the larger abundance in crop (van Helden 2010). However, in this study, cluster size was found to be dependent on abundance (defined in this study as modulation) for *F. schultzei* in lettuce only.

The decrease in *F. occidentalis* cluster size in relation to rainfall

was likely due to increased mortality. Nyasani et al. (2013) also found that *F. occidentalis* populations in French bean were negatively correlated with rainfall. Thrips survivorship is significantly affected by rainfall intensity (moderate, heavy and violent rainfall) and abundant precipitation can affect the mortality of insects (Norris et al. 2002; Patterson et al. 1999). An increase in rainfall can cause an immediate decline in adult thrips numbers remaining on the plant, through run-off and drowning, which would reduce the physical size of thrips clusters occupying a crop.

Unlike in French bean, the probability of clusters of *F. occidentalis* present in lettuce was not dependant on the age of the crop. However, the probability of cluster formation was dependant on rainfall events, which was categorised into two crop age groups - week one, and weeks two to eleven. At the time of transplanting, the lettuce plants were five weeks old, with approximately nine unfolded true leaves present, increasing in leaf number and size until full head formation at week seven. When rainfall was less than 25 mm, the chances of finding *F. occidentalis* in the crop was very low, but increased to near absolute probability after week two. However, with rainfall greater than 25 mm in the first week after transplanting in the field, the probability of *F. occidentalis* cluster formation in lettuce was very low, decreasing with increased rainfall. Similarly, from week two as rainfall increased the probability of *F. occidentalis* cluster formation also decreased. However, there was still a much larger probability of the species being present in comparison to week one. The unfolded leaves and small size of the lettuce in the initial week after transplanting would have provided little protection during high rainfall events, compared to the physiological growth stage of the plant after week two. This would have provided a greater area for the thrips to survive, on the crop, and therefore allow for a high chance of their presence in the crop.

The size of the *F. occidentalis* clusters in lettuce were also inversely dependant on rainfall. Increased rainfall was associated with an

increase in the size of the clusters of *F. occidentalis* in the crop. While cluster size was categorised by year and rainfall, the results indicate that under a higher rainfall (> 25 mm) there was greater spatial spreading across the crop, with the size of the cluster increasing. Inversely, rainfall events below < 25 mm saw less spatial spreading, with smaller cluster size. The response of this species to rainfall in lettuce was very different to French bean, which suggests that it is related to the different structures of the crop. It is possible that the thrips were moving around seeking shelter more readily under the large canopy of the lettuce plant. However, how thrips respond to rainfall events to protect themselves is poorly understood (McFarlane et al. 2015; Pellegrino et al. 2013), and therefore further research is needed before any conclusions can be drawn.

The response to crop age and weather was very pronounced for the temporal and spatial distribution of *F. schultzei* in lettuce. Two weeks after transplanting, *F. schultzei* cluster formation was likely, with the probability of formation in crop high from three weeks after transplanting. The cluster modulation, or average number of thrips counts, of *F. schultzei* in lettuce was dependant on crop age, temperature and rainfall. Modulation increased exponentially as the crop matured, with the highest counts in the last weeks of the crop life. High rainfall decreased the modulation of *F. schultzei* clusters, likely because of increased mortality through drowning, while lower rainfall saw an increase in modulation (Norris et al. 2002; Patterson et al. 1999). Cluster modulation increased at lower temperatures, and decreased with high temperatures. Submok and Uraichuen (2015) found that increased temperature decreased the mean number of thrips on lettuce in a glasshouse trial. They also concluded that a temperature range from 24 to 32°C was optimal for *F. schultzei* growth, which contrasts with the results here. Therefore, the dependency of *F. schultzei* cluster modulation at lower temperatures may be geographically specific, differing between the two locations. The differences may also be directly affected by the

environmental conditions of the protected glasshouse operation in comparison to an open field agro-ecosystems. Lettuce is a primary reproductive host for *F. schultzei* (see Chapter 6), and increased *F. schultzei* cluster modulation in relation to temperature and rainfall may have been due to reproduction taking place as a result of the adequate conditions of the agro-ecosystems, leading to increased cluster modulation of *F. schultzei* in crop. That there was no effect of cluster modulation on cluster size for any other species in each of the four agro-ecosystems suggests that there were other variables not included in the model that may have affected the outcome.

The size of *F. schultzei* clusters in lettuce were dependant on cluster modulation, with the spatial distribution of *F. schultzei* increasing with increased modulation. Increase in *F. schultzei* cluster size is a direct response to the increase in numbers within these clusters. Availability of space on a plant can influence the distribution of thrips, moving to other plants in search of available protection, food and shelter. For example, Salifu and Hodgson (1987) found a higher degree of aggregated distribution at higher densities of *M. sjostedti* (Trybom) on cow pea, *Vigna unguiculata* L.. Therefore, the increase in spatial distribution of *F. schultzei* in lettuce is likely a growth function of the species in the crop, occupying a greater aggregated distribution over an area as the number of thrips increases and a resulting need for food and resources. Fluctuations of insect populations are affected by density dependant factors (biotic) and density independent (abiotic) factors such as rainfall and temperature (Pongpraset 2005). The differences in the characterisation of the distribution of the two species suggest that they have different responses to rainfall in lettuce agro-ecosystems.

In tomato, the probability of *F. schultzei* cluster formation was only dependant on temperature. As mean average temperature increased, the probability of finding *F. schultzei* in tomato increased, with this species most likely to be found in crop at 29°C. The probability of cluster formation by *P. achaetus* in tomato along the crop age temporal

scale was different between year one and the two following years; however, the results indicated that as the crop matured, the probability of finding clusters in crop decreased. For the first year, this period of decrease occurred later in the crop around week ten, while it was very pronounced for the following two years, declining at week eight. Tomato was transplanted at five weeks old, and was flowering not long after transplanting, which would explain the increase in probability from two weeks after planting. As the plant grows, it provides abundant niches for various thrips to move into and occupy (Irwin 1991). As the leaves senesce and flowers drop, these niches decline rapidly and so too does the attractiveness of the plant to the insect, and therefore the temporal distribution of many thrips species is dictated by the phenology of the plant (Irwin 1991). This was displayed in the present study, when cluster formation of *P. achaetus* probability decreased at weeks eight and ten, which coincided with a cease in flowering and fruit set. Therefore, the plant may no longer have been suitable for *P. achaetus* explaining the decline in the probability of cluster formation at the end of the crop life.

In zucchini, the probability of cluster formation of both *Frankliniella* species and the spatial distribution of these clusters increased in size with the progression of the crop's growth, displaying a natural pattern of a population growth (Rathcke & Lacey 1985). *Frankliniella occidentalis* and *F. schultzei* displayed similar cluster probability responses to crop age, with probability increasing exponentially at week two, and decline at a certain age point in the crop. As both species are known to be associated with flowers, the life-history strategy would suggest that a fluctuation in the likelihood that either species would be present in zucchini and form a cluster may be dependent on flower production. Therefore, movement into the crop to use pollen for feeding and breeding would explain the higher probability of occurrence during flowering, followed by a subsequent decrease as flower production declines and flower drop occurs. Rhainds and Shipp (2003) found that *F. occidentalis* were more likely to disperse from

senescent chrysanthemum inflorescences than healthy inflorescences, and were more likely to move onto healthy inflorescence compared to those that were senescing. Therefore, the probability of formation of clusters displays a cyclic relationship in zucchini in response to the flowering cycle of repeated flushes of the zucchini crop (Mound & Teulon 1995).

The size of the clusters in zucchini were also dependant on crop age for both *F. occidentalis* and *F. schultzei*. The dependant relationship of spatial distribution with flowering explains the increase in the size of the cluster, increasing as more resources become available. The size of the cluster subsequently increases along a spatial scale as increased flowering occurs and the population sources more food and shelter (Kao 1984). This is particularly relevant for *F. occidentalis*, for which pollen is important for fecundity and egg production (Kirk 1997).

There were observed difference in *F. occidentalis* and *F. schultzei* cluster size in lettuce and zucchini, and *P. achaetus* cluster probability in tomato between the three observed years. The first year was significantly cooler in comparison to the following two years across the study period, and it is likely that this influenced the responses of cluster formation and size. For *P. achaetus* cluster formation, the decline in probability was less prominent in year one compared to year two and three, indicating that the cooler temperatures may have had a direct effect on the species in tomato.

Conclusions

The combined effects of variation in crop phenological stage and weather resulted in an aggregated spatial distribution of all species within each of the four vegetable agro-ecosystems. These clusters evolved over time due to specific species-plant interactions. The presence of thrips and the ensuing decline in their cluster formation were largely

dependent on age or phenological growth stage of the crop, particularly in the flowering crops. Size and subsequent spatial growth of populations were largely dependent on temperature and rainfall. The variation in the spatial and temporal distribution of each species is an indication of the different mechanisms driving their cluster formation and growth in the four vegetable agro-ecosystems. This demonstrates the need for further research across a wide range of vegetable agro-ecosystems to occur, under different climatic and weather conditions to better understand these spatio and temporal distributions. This is particularly important for species associated with a wide range of crops, such as *F. occidentalis* and *F. schultzei*. As demonstrated in this study, their spatial and temporal distribution and the subsequent evolution of each species clusters will differ between crops under the same environmental conditions at the same point of time.

Chapter Nine: General discussions and future research

Overview

The speed at which thrips can establish themselves in a crop and the propensity of key pest species to cause vast damage to vegetable production agro-ecosystems has seen Thysanoptera categorised as a pest order (Ainsworth 1991; Ananthakrishnan 1993). This is, however, a misrepresentation, as less than 1% of the circa 5500 described species in the order Thysanoptera are considered economic pests (Morse & Hoddle 2006). Due to the serious nature of the very few pest species, primarily *F. occidentalis*, *S. dorsalis* and *T. tabaci*, much of the research conducted on thrips population dynamics is focused on understanding the relationship between each of these species and the vegetable agro-ecosystem in which they occur. The research predominantly aims to achieve better control by targeting and minimising the damage caused in vegetable production systems by pest thrips species. Chemicals are the dominant control strategies used in the vegetable industry for thrips management, and their use is based on this research (Byrne et al. 2013; Gillett-Kaufman et al. 2009).

More recently, studies on the ecology of the key pest species have explored alternative thrips management strategies. The outcomes of this type of work have seen the introduction of Integrated Pest Management (IPM) programs developed around the populations of specific pests. Importantly, this has produced an in-depth understanding of the ecology and biology of key pest thrips in specific vegetable agro-ecosystems where these species cause considerable economic injury through feeding, oviposition or tospovirus transmission. However, while the research has focused on understanding these key pests in specific vegetable crops, a large knowledge gap exists in our understanding surrounding the population dynamics of the key pests in many other vegetable agro-ecosystems, as well as all other thrips species within these

agro-ecosystems. This gap must be filled if effective IPM programs for pest thrips management are to be widely adopted by the vegetable industry.

The study of population dynamics encompasses a wide range of factors, inclusive of the interactions between an insect and the environment, the crop and the weather. The main aim of such research is to better understand the mechanisms that drive change in a particular species population, from: establishment in the crop, subsequent growth in abundance, and movement throughout the physical agro-ecosystem area. The difficulty in population dynamics studies is the breadth of intertwined relationships that cause an insect population to fluctuate in density, particularly as the change in population dynamics of a particular species is dependent on its relationship with a specific crop. It is widely accepted that different thrips species are associated with different vegetable agro-ecosystems. However, as determined throughout this study, not all species interact with crops in the same manner; and their presence, abundance and interaction (feeding or breeding) change with the crop type. Ecological surveys to better understand the dynamics of a specific insect population are limited not only by the multitude of biotic and abiotic factors and the complex interactions between them, but also by limitations in time, funding and experimental space, particularly for agricultural based ecological research.

The aim of this study was to develop a comprehensive understanding of the dynamics of thrips populations in French bean, lettuce, tomato and zucchini agro-ecosystems. Five key research areas were examined: the thrips species assemblage, the temporal and spatial distribution of thrips populations, the relationship between weather and thrips abundance, and the reproductive host association of key species in each of the four agro-ecosystems. The research findings from each of these areas were presented in previous chapters. This chapter discusses the combined effects of variations in thrips population abundance in relation to each of the key research areas. The findings are discussed within a context of field grown vegetable agro-ecosystems consisting of a complex of multi-trophic interactions between plants and environmental elements each between thrips species.

An improved understanding of thrips species assemblage

Thrips species are rarely restricted to only one type of habitat (Redhead et al. 2016). The 17 species recorded in this study are diverse in their abundance within each of the four vegetable agro-ecosystem species assemblages studied. For at least the lettuce, tomato and zucchini agro-ecosystems, the literature suggests this is the first documented account of the assemblages that exist in these crops.

Although there was some overlap, the four assemblages differed in the high abundance of one or two key species. Both French bean and zucchini agro-ecosystems were found to support high species diversity and thrips abundance, indicating that they are both suitable hosts to a broad range of species that use the crops for feeding or breeding. In comparison, lettuce and tomato supported a less diverse species assemblage, and in tomato much lower thrips abundance. The species composition of each assemblage varied between the agro-ecosystems by the diversity of thrips supported, and the abundance and absence of some key species. However, the presence of a species within an assemblage does not permit conclusions to be drawn regarding the nature of the association between the species and the vegetable crop.

Regular occurrence and high abundance alone does not define the type of host association that exists between thrips and the plant, or even the strength of this association. Nor does it indicate how these species populations will change in relation to the weather or the phenology of the crop. As highlighted by Milne et al. (1996a), too often the collection of a species from a plant is used as evidence to demonstrate a host association. This too can be the case when determining the type of association between thrips and crop, based merely on their abundance. The determination of the species assemblage does however provide the baseline data for further investigation of the fluctuation in numbers of these various species in relation to the crop type, the weather and crop phenology.

A detailed literature search failed to find any record of thrips species

assemblages for lettuce, tomato or zucchini. This lack of literature lends support to the notion of a poor understanding of thrips species diversity and thus the dynamics of thrips populations in a range of vegetable agro-ecosystems. From an ecological perspective, poor documentation of species diversity and the assemblages that exist in vegetable crops means that any attempt to better understand the dynamics of these populations is limited. There is a lack of knowledge of pest and non-pest species present in a crop and an understanding of which species are causing damage. This leads to the unnecessary application of chemical, or selection of ineffective insecticides, which, in turn, affects production efficiency (Gillet-Kaufman et al. 2009). The decision for a grower to employ a control strategy, such as insecticides, affects their crop management regime and subsequently their productivity (Demirozer et al. 2012). Incorrect insecticide use or unnecessary application on a non-pest species can result in the elimination of natural predators, outbreaks of target and non-target pests and the subsequent development of insecticide resistance in thrips (Demirozer et al. 2012). Therefore, in order to develop effective IPM programs and better chemical usage, the first step is to identify the thrips species assemblage in a vegetable agro-ecosystem in order to target key pests at critical stages in their development (Funderburk 2002).

An improved understanding of the temporal distribution of key thrips in the species assemblage

Frankliniella occidentalis and *F. schultzei* often co-occur within the same vegetable agro-ecosystems, including Fabaceae, Solanaceae and Cucurbitaceae (Kakkar et al. 2012b; Nyasani et al. 2012; Nyasani et al. 2013; Walsh et al. 2012). Therefore, it was not surprising, that these two species were found in relative abundance in each of the four agro-ecosystems was not surprising, and adds further support to the conclusion that they have an association with a wide range of horticultural crops. However, *F. occidentalis* and *F. schultzei* displayed different temporal distributions between French bean, lettuce, tomato

and zucchini, indicating that despite the ability of these two species to use the four crops, their interaction with the crops varied with crop growth stage. Changes in herbivorous insect abundance in vegetables are known to coincide with phenological changes in their host plants (Scaven & Rafferty 2013). Therefore, the establishment and abundance of these two species are affected by the crop age. Vegetable production is generally a mono-culture planting system, with large areas planted to two or three crop types. Therefore, the temporal distribution of thrips populations along a crop age scale, from planting/seeding to harvest, and distribution amongst these crops, will be dependent on the suitability of one or more crops as a host at any point in time.

Frankliniella occidentalis and *F. schultzei* moved into all crops in very small numbers from one week after transplanting or seedling emergence, with numbers building and peaking just prior to flowering in French bean, tomato and zucchini and around the pre-heading stage in lettuce when the leaves were loosely arranged. *Frankliniella occidentalis* displayed more of an affinity for the flowering crops, with French bean, tomato and zucchini supporting high abundance. In comparison, there were significantly more *F. schultzei* in lettuce. *Frankliniella occidentalis* had higher fecundity and larval development when fed on a diet inclusive of pollen (Trichilo & Leigh 1986), while *F. schultzei* has been reported to perform equally as well with or without pollen (Milne et al. 1996b). Based on these findings, the results of this study support the conclusion that the presence of flowers may be less important for the success of *F. schultzei* compared to *F. occidentalis*. This conclusion is further supported by the temporal distribution between zucchini and French bean crops for *F. occidentalis*, and between zucchini and lettuce for *F. schultzei*.

As the zucchini crop began to flower, *F. occidentalis* and *F. schultzei* abundance increased in the flowers, with high abundance found between weeks three and six, which coincides with the peak flowering period. At six weeks after seeding, flower production in the zucchini started to decline, which suggests that both thrips species could detect a

change in the nutritional quality of the plant and moved onto a more suitable host. The ephemeral nature of flowers appears to lead to a host switch in *F. occidentalis* and *F. schultzei* from zucchini to lettuce or French bean, to maintain population growth as zucchini begins to reduce flowering and nears senescence. While these two species are the most commonly occurring thrips species found in the four vegetable agro-ecosystem species assemblages, their temporal distribution between the crops indicates that their use of different vegetable crops is dissimilar.

Chemical control is the most used management tool for thrips (Cañas 2015). The decision on when to apply insecticides is critical. Ineffective thrips control can be exacerbated by the poor knowledge of when to apply insecticides in relation to critical periods of immigration and colonisation in the crop. If dispersal is linked to changes in food quality, which the results of this study suggest, then French bean and lettuce that are about to enter their most susceptible phenological stage, planted near a zucchini crop, are at risk of probable damaging infestations by the two pest species. For French bean, the period of greatest risk is at flowering, when thrips feed on the developing pods, causing scarring, stunting and distortion (Duff 2012). Historically, French bean growers routinely apply insecticides to control thrips infestations as the flower opens rather than when increased thrips densities are found in crop (Harper & Horne 2012). Therefore, if French bean and zucchini are planted within the same area, as is often the case in mixed cropping enterprises, results of this study indicate that targeted sprays at week four to five, when the flower is opening, will be ineffective at controlling *F. occidentalis* populations dispersing into the crop around week six. Therefore, control should instead take place as populations increase in zucchini flowers from week two. Similarly, for lettuce planted in the vicinity of zucchini crops, *F. schultzei* should be controlled in zucchini prior to the period of dispersal into lettuce. Alternatively, at risk crops should be planted at periods that do not coincide with dispersal.

varies with the composition of the nectar (Wäckers & van Rijn 2012), and the colour, shape, smell and spatial distribution of the flowers (Begum et al. 2004; Vollhardt et al. 2010). The movement of *F. occidentalis* and *F. schultzei* from zucchini into French bean and lettuce is an important topic for future research. The management of mobile insect pests in mixed cropping enterprises is a major challenge both in theory and practice of IPM (Shelton 1995). The mechanisms for thrips dispersal in relation to the nutritional quality of French bean, lettuce and zucchini need to be assessed to better understand the mutual relationship between *F. occidentalis* and *F. schultzei* and these crops.

Improved understanding of the reproductive host association between thrips and French bean, lettuce, tomato and zucchini

Reproductive hosts largely influence the population dynamics of insects, as it is this plant-insect association that allows for increased abundance by providing a suitable environment for life-cycle completion. Differences in the level of host association will further influence the intrinsic rate of population increase. Secondary hosts are suitable for reproduction, but usually only in very small numbers, and a species will use these plants until a more suitable primary host becomes available. A primary host provides optimum conditions for large, and generally fast, breeding and lifecycle development to occur (Reitz et al. 2002).

All four vegetable crops in this study supported immature thrips, displaying some level of reproductive association with at least two thrips species. The results indicated that French bean was a primary reproductive host for *M. usitatus* and *T. tabaci*, and a secondary reproductive host for *F. schultzei*. Further research is needed to determine whether French bean is a primary reproductive host for *F. occidentalis*. Lettuce was found to be a primary host for *F. occidentalis*.

and *F. schultzei*, but while *T. tabaci* can reproduce on this plant, it was only a secondary host. All other reproductive associations were secondary.

It was clear that for some of the key thrips in each agro-ecosystem species assemblage, that the relatively high abundance found in each crop was a result of a species moving in to the crop and feeding, or due to breeding in the crop. Based on the host association results, it can be determined that the high abundance of *M. usitatus* in French bean was as a direct result of their primary reproductive association, and that French bean was suitable for breeding, survival and development of immature thrips. Likewise, for lettuce, it was concluded that the high abundance of *F. occidentalis* and *F. schultzei* in the crop was due to a primary reproductive association. For tomato, the low species diversity and abundance in the species assemblage reflected their poor reproductive association with the thrips found on the crop in this survey.

When the reproductive association findings are analysed in relation to the temporal segregation of *F. occidentalis* between zucchini and French bean, and *F. schultzei* between zucchini and lettuce, further conclusions can be drawn regarding their association with these three vegetable crops. *Frankliniella occidentalis*, *F. schultzei* and *T. tabaci* are capable of reproducing on zucchini; however, the very low number of immatures collected and reared indicates that as in tomato, the crop is only a secondary reproductive host. In regards to the temporal distribution of the two *Frankliniella* species, the results indicate that *F. occidentalis* and *F. schultzei* were feeding on the pollen and nectar of the zucchini flowers in the earlier weeks of the crop life, after which time *F. occidentalis* dispersed into French bean, and *F. schultzei* into lettuce, where each species was using the respective crop to reproduce. Increased abundance was, therefore, observed in the lettuce and French bean crops at later phenological stages.

The practical implication of understanding these primary

breeding associations is targeted control at periods prior to oviposition of key thrips species. Secondly, this information is critical in relation to the ability of *F. occidentalis*, *F. schultzei* and *T. tabaci* to vector the three tospoviruses present in Australia – tomato spotted wilt virus (TSWV), capsicum chlorosis virus (CaCV) and iris yellow spot virus (IYSV) (CRCTPP 2007). Only early instar larvae feeding on an infected plant can acquire the virus, in a period less than 30 minutes of feeding. Once the larvae acquire the virus, it circulates and multiplies with the insect and is then transmitted to other plants once the thrips reaches maturity (CRCTPP 2007; Funderburk et al. 2011). Lettuce, tomato and zucchini are all known hosts of tospovirus, and are, therefore, at risk of infection. While zucchini and tomato are not considered primary reproductive hosts, their secondary host association has implications for the spread of tospovirus to other crops as only a small number of infected thrips are needed to spread the disease. The virus-vector relationship is a particular challenge in efforts to manage tospoviruses (Funderburk 2009), and the lack of knowledge regarding reproductive hosts serving as virus sources only increases the risk of infection through inadequate control. Therefore, in mixed cropping enterprises growers need to be alert for increases in *F. occidentalis*, *F. schultzei* and *T. tabaci*, particularly in zucchini crops, as subsequent dispersal may result in a spread in tospovirus amongst neighbouring crops.

The status of zucchini as a feeding host also requires further research. For example, the finding that one of the key species in zucchini, *T. frici*, was not reared from field collected sub-samples provides further evidence that the thrips supported within the zucchini species assemblage have a stronger feeding association than a reproductive association. Paini et al. (2007) stated that a clear distinction needs to be made between plants on which only adults are found, and plants supporting both adults and larvae, to conclusively determine that a reproductive association exists. Based on this, Paini et al. (2007) classified feeding hosts as those with only adults present. A feeding

association would explain the high diversity and thrips abundance supported within the zucchini agro-ecosystem. It is likely that many of the other species within this assemblage were moving into the crop and feeding before moving to a more suitable reproductive host.

Further research needs to be undertaken to provide further insight into the nutritional qualities of the plant, and the effect on reproduction, lifecycle development and fecundity. This would provide a broader understanding of the association between zucchini and thrips and the effect this relationship has on the dynamics of these populations, in terms of increasing or decreasing the fitness of the population. Future research is also needed to explain the higher abundance of thrips in female zucchini flowers compared to male as determined in this study, particularly as female flowers do not contain pollen which is considered important for the development of various thrips species, including *F. occidentalis*.

Improved understanding of the relationship between rainfall, temperature and relative humidity and thrips relative abundance

Climate has a significant impact on the population dynamics of insects, and changes in rainfall, temperature and relative humidity will have a different effect on individual species with different development requirements. As ectothermic animals, insects are highly dependent on the thermal conditions of the environment; their rate of development and dispersal increasing or decreasing with changes in temperature. For small insects, such as the Thysanoptera, heavy rainfall can have a large impact on populations, reducing abundance through drowning or dislodgment from the plant. While the relationship between insects and humidity is not as characteristically distinct as it is for temperature (Jaworski & Hilszczański 2013), large variations in relative humidity can

directly impact the development of thrips, with many species reported to prefer a level between 70 to 90% (Kirk 1997).

Collectively, the effect of rainfall, temperature and relative humidity affected the species assemblage in each vegetable agro-ecosystem differently. In French bean, increasing temperatures resulted in a greater likelihood of the presence of thrips. In zucchini, increased rainfall and temperature were associated with a lower likelihood of thrips presence in the crop, while an increase in relative humidity was associated with a higher likelihood of thrips presence. For lettuce and tomato, rainfall, temperature and relative humidity had no effect on the likelihood of thrips presence in the vegetable agro-ecosystems. Individual species within these assemblages also displayed specific associations with the three weather variables measured in this study. Only *M. usitatus*, *F. occidentalis* and *D. tenuicornis* were consistent in their relationship with weather across two or more crop types. *Desmothrips tenuicornis* displayed a negative association with relative humidity and a positive association with temperature in French bean, lettuce and zucchini. *Frankliniella occidentalis* was positively correlated with rainfall, relative humidity and temperature across French bean, tomato and zucchini. *Megalurothrips usitatus* was negatively correlated with temperature in French bean and zucchini. In this study, this consistent association across the different crops indicates that these species are more constant in their relationship with the weather variables, regardless of the host crop they were found.

French bean was a reproductive host for *M. usitatus* and *F. occidentalis*. Based on their observed relationship with weather variables, the higher periods of abundance of these species in the respective crops was concluded to be as a result of a combination of optimum weather conditions for reproduction and the preferred phenological period of the crop. For *M. usitatus* this period was during the cooler autumn season of the survey, and for *F. occidentalis* during the spring and summer periods. With thrips pest management largely dependent on chemical control,

understanding the response of thrips population growth to weather is critical for optimising insecticide application. Based on the information in this study, the two dominant pest species within the French bean species assemblage occupy separate climate periods: *F. occidentalis* the warm conditions and *M. usitatus* the cooler periods. Often, by the time thrips populations are detected by the grower, control is futile, as feeding and breeding has already taken place. Therefore, this seasonal information is critical for optimising planting regimes and planning IPM programs.

Frankliniella schultzei had a negative relationship with rainfall and temperature in lettuce, indicating that peak abundance occurred during periods of mild temperature and low rainfall, likely providing optimum conditions for reproduction in the crop. In zucchini, both *F. occidentalis* and *F. schultzei* abundance was positively correlated with rainfall and relative humidity, which for the latter was in direct contrast to its relationship with these variables in lettuce. It is likely that the positive correlation between rainfall and relative humidity in zucchini was due to the climatic conditions being poor for thrips dispersal into French bean or lettuce, resulting in more thrips present in zucchini. Rainfall suppresses thrips dispersal (Lewis 1997), and high humidity reduces thrips movement (Derksen 2009). This would also explain the different association between rainfall and *F. schultzei* in lettuce, where higher rainfall was associated with fewer thrips in the crop.

There are around 300 species (~ 6%) of thrips that prey on other arthropods (zur Strassen 1995). *Desmothrips tenuicornis* are thought to prey on immature thrips and other small arthropods (Pereyra & Mound 2010). The results indicate that higher temperatures increased the relative abundance of *D. tenuicornis* in lettuce, while resulting in decreased *F. schultzei* in this crop, which may have been as a result of a combination of weather and through predation by the potentially predatory *D. tenuicornis*. Weather affects the establishment of insect biological control agents in the field. For example, Funderburk et al. (2000) found that the pirate bug, *Orius insidiosus* (Say), was an effective

predator of thrips in capsicum during the spring period when temperatures were warm. However, compared to protected cropping systems, the examples of biological control options are very few in field grown agro-ecosystems. A series of controlled choice and no choice tests evaluating the predation potential of female *D. tenuicornis* on immature *F. occidentalis* and *F. schultzei* failed to find any signs of predation occurring (Appendix C). There is much that is not known about the diets of many thrips species (Kirk 1995). Therefore, the results indicate that *D. tenuicornis* did not predate on these two species in this study, which suggests they may not be effective predators of *F. schultzei* and *F. occidentalis*, and the reason for their high abundance in lettuce has not yet been established.

The combined effects of variations in the plant phenological stage, the microclimate within the canopy of the crop or plant, insect behaviour on the plant (feeding or breeding) and weather directly affect the presence and abundance of species. To model the effect of weather on thrips abundance related to this complex set of interacting factors, repeated, long-term ecological surveys need to be conducted. Future research needs to incorporate other variables, such as wind speed and direction, soil temperature, and air pressure and density; to develop a greater understanding of how changes in weather influence the presence of a species in a crop, and the subsequent growth of the thrips population. Further research is also needed to study the response of *D. tenuicornis* populations to warm weather and their potential as a naturally occurring biological control agent in thrips IPM programs.

An improved understanding of the spatial distribution of key thrips within the vegetable agro-ecosystems

The combined effects of the plant physiological stage and weather resulted in clustered spatial distribution of *F. occidentalis* and *M. usitatus*

in French bean, *F. occidentalis* and *F. schultzei* in lettuce, *F. schultzei* and *P. achaetus* in tomato and *F. occidentalis* and *F. schultzei* in zucchini.

Differences in the spatial patterns of these species reflect a species-specific association with each of the crop types. The variation in the distribution of each species is an indication of the different mechanisms influencing the presence of the species and the subsequent growth in the size of the clustered distribution throughout the respective agro-ecosystems.

In French bean, *F. occidentalis* were more likely to form a cluster in the crop from two weeks after seeding, while *M. usitatus* were more likely to cluster in the later stages of the crop's life, coinciding with flowering. *Megalurothrips usitatus* prefer to live and feed on flowers, and will feed on young leaves and pods when inflorescences are scarce. These results support the conclusion of Tang et al. (2015), that the temporal distribution of *M. usitatus* clusters is dependent on the flowering period of the plant. *Frankliniella occidentalis* were less restricted in their use of the French bean crop in relation to the phenology of the crop. The relative abundance of *M. usitatus* was associated with cooler temperatures. However, the clustering of *M. usitatus* in French bean was not dependant on temperature or rainfall as it was for *F. occidentalis*. This indicates that the growth of *M. usitatus* populations is more dependent on the age of the crop, particularly the flowering stage, than on weather. Warm temperatures and low rainfall induced an increase in the physical size of *F. occidentalis* clusters in French bean, increasing spatial spreading throughout the agro-ecosystems.

For both of the *Frankliniella* species in zucchini, and *P. achaetus* in tomato, the probability of clusters of each species forming in the crop coincided with the formation of inflorescence, followed by a decline with the onset of senescence and flower set decrease. For both the *Frankliniella* species in zucchini, the size of these clusters increased exponentially with the progression of the crop life. The decline in the probability of cluster formation in zucchini coincided with the period

where both species were thought to be moving out of the crop and into either French bean or lettuce. From week three to nine in lettuce, the probability of cluster formation was high. This corresponded to the period of dispersal of *F. schultzei* from zucchini at week six, and their declined probability in the zucchini crop.

Unlike French bean and zucchini, *F. occidentalis* cluster formation in lettuce was not dependent on the age of the plant, but was affected by rainfall, as was the spatial distribution and growth in cluster size. This indicates that for *F. occidentalis* in lettuce, crop phenology was not a factor for cluster formation. Conversely, *F. schultzei* cluster formation was highly dependent on the age of the crop; and the growth of these clusters, in relation to physical size and relative abundance was likely due to reproduction. Increased abundance through reproduction would increase spatial spreading throughout the crop to accommodate the higher abundance in the crop.

One of the difficulties in ecological research on insect populations is the highly aggregated data, which often has large zero or absence counts, therefore, the data is not of a normal distribution and analysis and interpretation is difficult. To overcome this problem in this study, two equations were developed. These equations are directly applicable to the general case of spatially distributed data as insect populations are almost never homogenous and always highly aggregated regardless of the survey size (van Helden 2010). Therefore, these equations could be used on large survey areas that contain a large number of replicates or for small sets of spatial data as shown in this study, because the permutation of the replicates allows for effective smoothing of the data. The development of these two new approaches to analyse highly scattered count variables is critical for studies of thrips management, but also other pest populations in vegetable agro-ecosystems. The development of these two equations would not have been possible without running successive field trials over a three-year period. Further trials are needed to refine the modelling outputs even further.

The value in such research is in refining the biological data to produce more precise predictive outcomes that can be used to develop accurate and targeted IPM programs. For example, Yudin and Tabashnik (1990) developed empirical models based on weekly field-collected data to predict tomato spotted wilt virus incidence at harvest in lettuce crops. This allows lettuce growers to predict disease incidence and implement management decisions early in the planting cycle to reduce damage and, therefore, economic loss. With the development of the two new equations in this study, models can potentially predict the presence and subsequent growth of thrips pest populations in vegetable agro-ecosystems with the same management impact demonstrated by Yudin and Tabashnik (1990).

Conclusion

To develop a comprehensive understanding of the population dynamics of thrips in vegetable agro-ecosystems, a holistic approach is required to investigate the mechanisms that affect the presence of a species, and the subsequent increase and growth of the population. In this study, some thrips species demonstrated an ability to use a wide range of crops, with their presence and abundance varying between crops with changes in weather conditions and the phenological stage of the crop. This is best demonstrated by *F. occidentalis* and *F. schultzei*. Other thrips species, such as *M. usitatus*, have shown very clear species-specific interaction with only one crop. Crop type has a large influence on determining the species that are present within the agro-ecosystem, as demonstrated by the four species assemblages that exist in French bean, lettuce, tomato and zucchini.

One of the most important factors influencing the population dynamics of thrips in this study was the phenological growth stage of the crop. The temporal and spatial distribution of thrips in this study were dependant on the age of the plant in all four agro-ecosystems, which influenced when a species was likely to be present in the crop, the

relative abundance of the crop and the subsequent population decline. The temperature was also associated with increased or decreased relative abundance, according to the thrips species' optimum conditions for reproduction, development and population increase. The relative abundance was extremely dependant on the reproductive association with the crop, particularly French bean and lettuce. It is also likely that the existence of a thrips feeding association with zucchini had an effect on the high diversity and abundance found in this agro-ecosystem.

Studies need to integrate the relationship between the behavioural responses of thrips and the physiological and phenological stages of the crop, in terms of feeding or breeding interactions. This should be considered together with the effect of the weather on the plant and the insect, to advance our understanding of thrips populations in vegetable agro-ecosystems. By better understanding these interactions, it will be possible to better predict thrips population outbreaks, and develop targeted and more effective integrated pest management programs accordingly.

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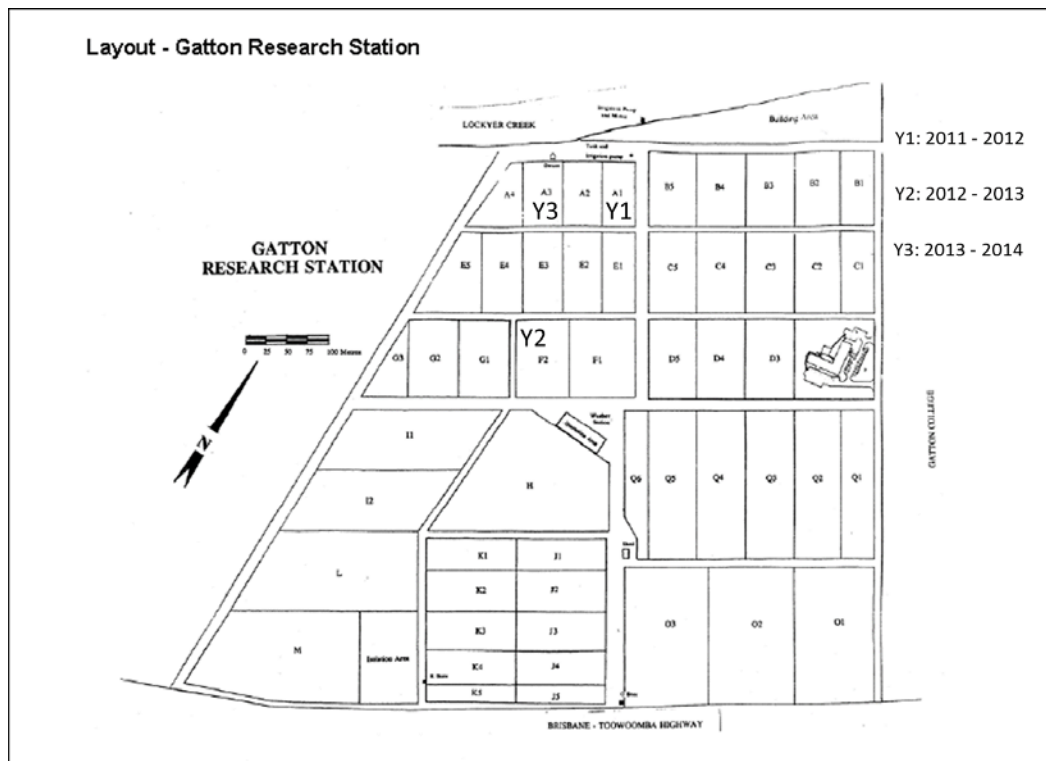
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Appendix A: Experimental design – trial layout

Field Trial Location

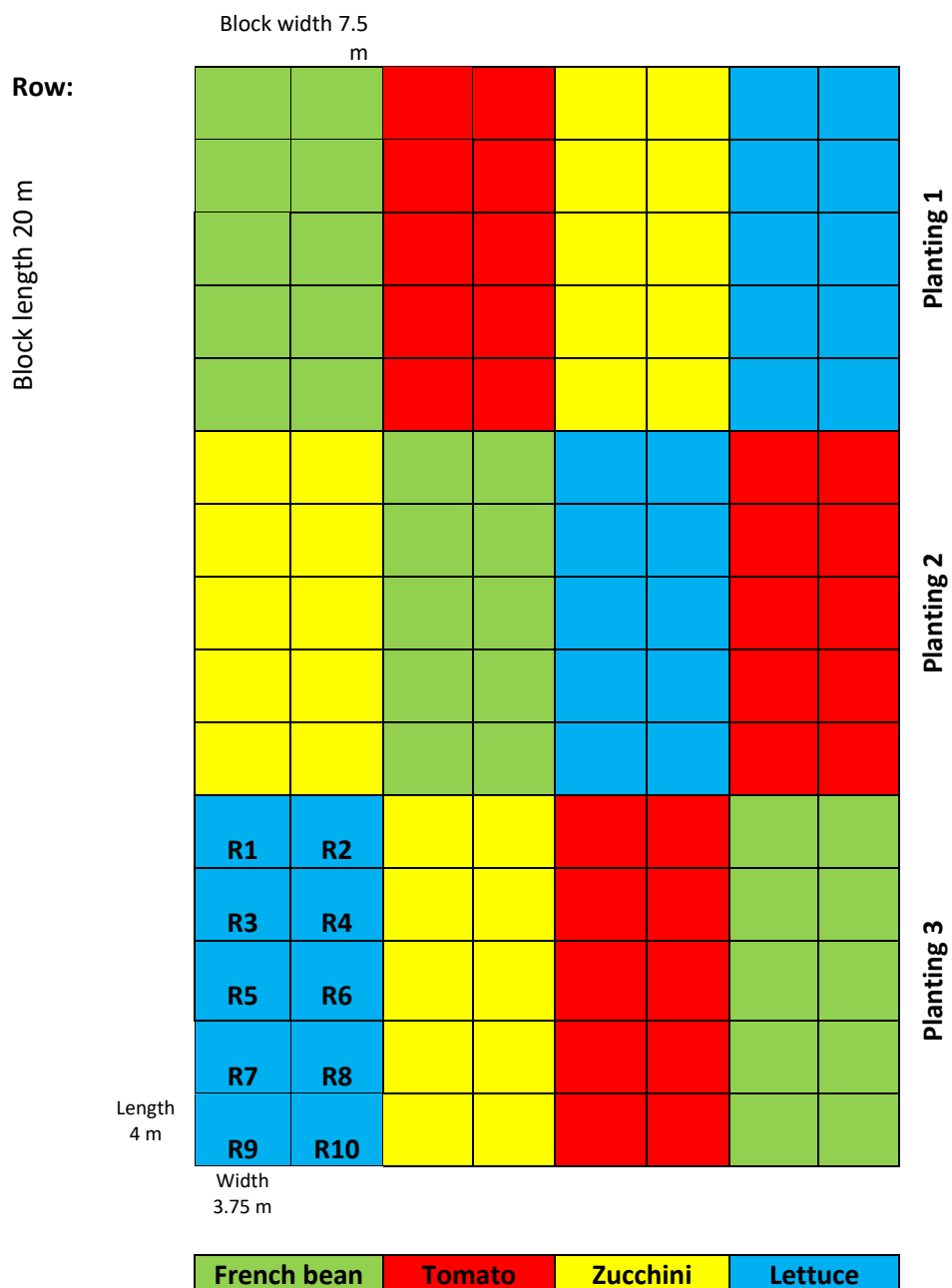


Trial Layout



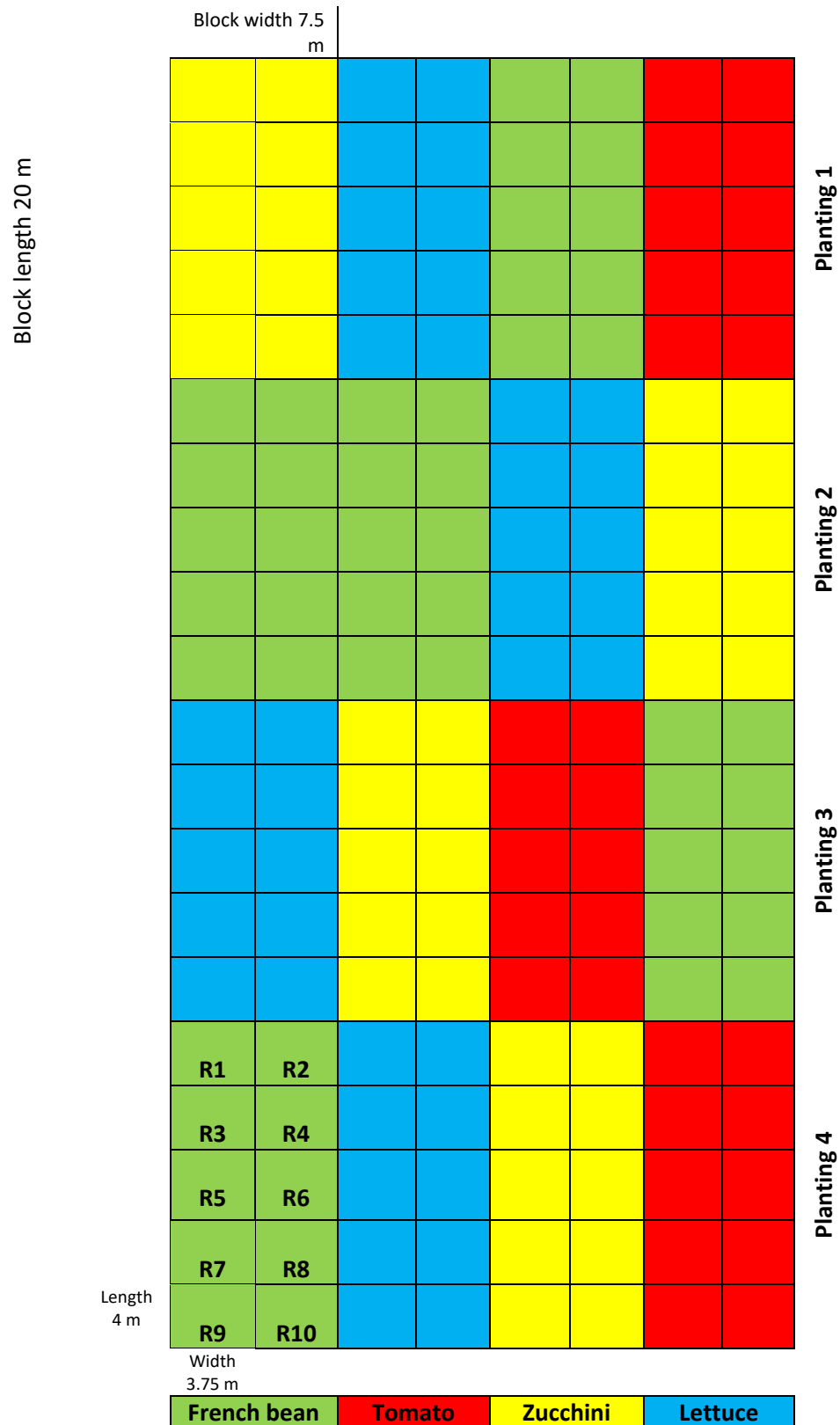
Season 1: December 2011 to June 2012

Column: 1 2 3 4



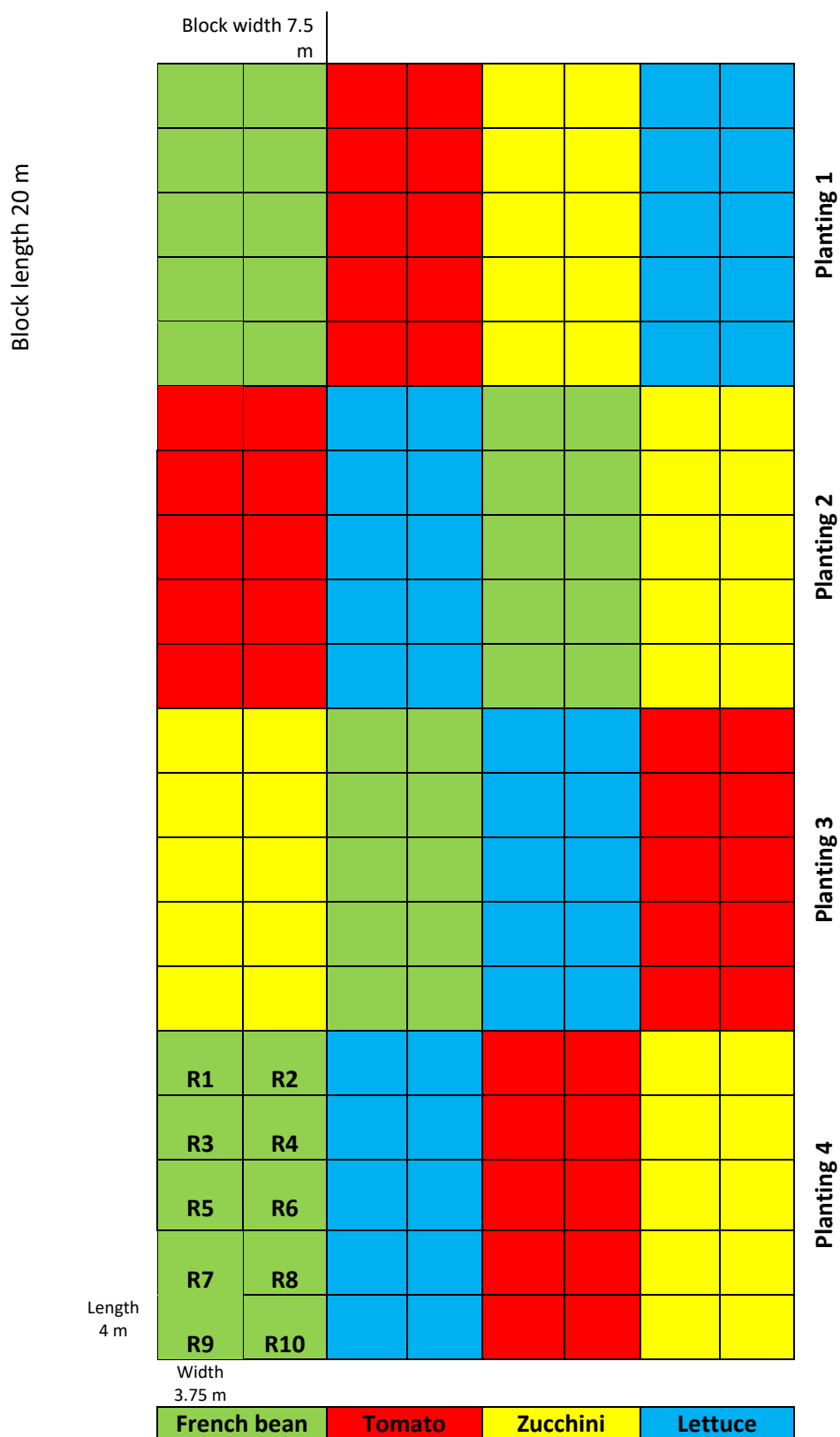


Season two: December 2012 to June 2013





Season three: December 2013 to June 2014



Appendix B: Identification sheets

Sample Sequence No :							
Date:	Rep:	Crop:	Type:				
Thrips spp.							
			Male	Female	Totals	ID & Mounted Totals	
<i>F. occidentalis</i>							
<i>F. schultzei</i>							
<i>T. tabaci</i>							
<i>T. palmi</i>							
<i>T. imaginis</i>							
<i>Tenothrips frici</i>							
<i>M. usitatus</i>							
<i>P. achaetus</i>							
<i>Aeolothripidae</i>							
Other sp.							
Vial nymphs:							
Petri Nymphs:							
Mounted Samples							
	Male	Female	Specimen		Mounted#	Unmounted#	Identification
a)							
b)							
c)							
d)							
e)							
f)							
g)							
Notes:							
Vials Processed			Slides ID				
Slides Mounted			Entered				

Appendix C: Predation potential of *Desmothrips tenuicornis*

General Overview

The use of naturally occurring biological control agents for thrips control in vegetable agro-ecosystems is very rare, and in comparison to protected cropping systems, control strategies based solely on biological control agents in field grown vegetable agro-ecosystems are uncommon (Morse & Hoddle 2006). Therefore, with the high abundance of the potentially predatory *D. tenuicornis* recovered from lettuce in this study, attempts were made to investigate the predation capacity of this species on key pests *F. occidentalis* and *F. schultzei*. With the limited use and availability of biological control agents in field grown vegetable systems, identifying a naturally occurring predator would be a valuable addition to IPM programs. With limited information on the biology, ecology and predation ability of this species, the findings from the predation experiments from this study are included in this thesis as it may be used in the planning of future *D. tenuicornis* predation trials.

Introduction

Biological control strategies rely on beneficial organisms such as parasites, predators and pathogens to control insect pests. A number of thrips specific hymenopteran parasitoids attack thrips eggs (Mymaridae: *Megaphragma* sp.) and larvae (Eulophidae: *Ceranisus* sp.) (Loomans 2006). Most natural enemies that attack thrips are generalist predators that occur naturally within the agro-ecosystem (Ananthakrishnan 1993). Predatory bugs in the genus *Orius* have successfully reduced thrips in field settings. In Japan and Florida, natural populations of *Orius* spp. have been documented colonising capsicum and eggplant fields, suppressing thrips and halting the spread of Tospoviruses (Ramachandran et al. 2001; Reitz et al. 2002; Reitz et al. 2011). While these examples highlight the suppressive capacity of thrips predators,

control strategies based solely on biological control agents in field grown vegetable agro-ecosystems are uncommon (Morse & Hoddle 2006). Therefore, chemical control is still the predominant tool used in field grown vegetable production to control pest thrips in crop (Cañas 2015).

Some thrips are facultative predators of small insects such as mites and other thrips, their eggs, larvae and pupae and insect secretions (Kirk 1995; Mound & Teulon 1995). There are approximately 300 species (~ 6%) that are considered predators, however there is still very little known about their nutritional requirements or predation ability (zur Strassen 1995). Predatory species have been observed to reduce pest thrips numbers, for example high densities of the predatory species *H. victoriensis* were recorded in strawberry crops, along with low *F. occidentalis* numbers and low crop damage. Follow up laboratory trials confirmed that *H. victoriensis* was predating *F. occidentalis*. Some polyphagous pest species will predate small arthropods, for example *F. occidentalis* has been observed predating spider mite eggs in cotton crops (Trichilo & Leigh 1986). Some thrips, such as *Scolothrips* spp. and *A. fascipennies* are obligate predators of mites and scale insects.

Desmothrips tenuicornis are thought to be facultative predators of thrips nymphs (Minaei & Mound 2008; Pereyra & Mound 2010). However, there is very little information on the biology and ecology of *D. tenuicornis*, including the predation capacity of this species. With much of the emphasis on thrips management in field grown agro-ecosystems reliant on chemical control, identification of a naturally occurring biological control agent could benefit the horticulture industry. If *D. tenuicornis* is shown to feed on pest thrips species, then it is also important that they are not mistakenly targeted with insecticide sprays. Literature suggests that predators will generally predate on passive and active choice prey (Peckarsky & Penton 1989): passive choice being no option but to consume a given prey, whether from lack of choice or inability to predate; active choice being the ability of the predator to successfully seek out and consume a prey type.

Peckarsky & Penton (1989) stipulate that in predator-prey experiments run under controlled conditions, nil results can be as a consequence of dissimilar natural environments. Therefore, this experiment was run as controlled laboratory assays (Petri dishes) and as a potted plant experiment using lettuce and French bean to attempt to re-create field based conditions in the laboratory. The predation potential of female adult *D. tenuicornis* was evaluated in a series of choice (active) and no choice (passive) predation tests to identify their predation potential on immature *F. occidentalis* and *F. schultzei*. These two *Frankliniella* species were the most commonly occurring adult and immature pest species throughout the field surveys, particularly in lettuce where *D. tenuicornis* was most abundant.

Materials & Methods

A series of choice and no choice predation tests was run in Petri-dish assays, and in potted lettuce and French bean plant experiments. Female *D. tenuicornis* were collected from lettuce plants in the field survey and starved prior to use in the experiments. Immature *F. occidentalis* and *F. schultzei* were sourced from cultured colonies. The experiments aimed to determine if predation had occurred based on absent immature prey specimens, *D. tenuicornis* actively feeding on immatures or presence of injured immature thrips.

Desmothrips tenuicornis collection

Attempts were made to culture *D. tenuicornis* for use in these experiments. A range of alternate vegetables were used as an oviposition medium, including eggplant, French bean pods, cucumber and lettuce, with the addition of French bean flowers to provide a source of pollen and nectar. However, a culture could not be started therefore *D. tenuicornis* used in the experiments were collected as adults from the field.

Fifteen lettuce plants were collected from the field into paper bags and taken back to the laboratory. Plants were deconstructed and adult *D. tenuicornis* were removed and kept in individual clear 90 mm plastic vials, with holes in the lids to allow airflow. In total, 45 female adult *D. tenuicornis* were collected from the lettuce plants. Vials were placed in the refrigerator for approximately five minutes to slow the specimens down to allow for identification and sexing under the stereo microscope. Identification was performed using the Oz Thrips lucid key (2016). Distinguishing features were: yellow third antennal segment, with the extreme apex being dark; the forewing brown at the extreme base, but clavus with apex pale and the median brown area long; the distant transverse area almost parallel-sided with the pale coastal vein. This means the forewings are heavily banded, which distinguishes them from *F. occidentalis* and *F. schultzei*, the other dominant thrips found in lettuce (Chapter 4). Adults were starved for 48 hours before the predation experiments to standardise feeding across the specimens.

Desmothrips tenuicornis were collected from lettuce plants on three occasions, from planting one on February 22nd and planting two on 16th March 2013, and from planting one on 7th February 2014. All specimens were used only once.

Attempts were made to determine if *D. tenuicornis* were pupating in the soil, and hence better understand the biology of this species in order to be able to start a laboratory colony. Clear plastic containers were placed in the field, each with a yellow sticky trap placed on the upper, inner surface of the container with the glue side facing down. Traps were intended to capture emerging adults that may have been pupating in the soil. Traps were placed in lettuce, French bean, tomato and zucchini plots, as well as in nearby Eucalyptus sp. surrounding the trial area.

Prey species collection and culturing

Immature *F. occidentalis* and *F. schultzei* used in the experiments were sourced from laboratory colonies cultured at GRF. Adult *F. occidentalis* and *F. schultzei* were removed from plants collected from lettuce plots in the field survey. Adults were then cultured on Lebanese cucumber as per the adapted method of De Graff & Wood (2009) in Manners et al. (2013) described in Chapter 6. *Frankliniella occidentalis* and *F. schultzei* colonies were cultured on two occasions, sourced from lettuce plants collected from the field on the 3rd January 2013 (planting one) and 8th January (planting one) 2014.

Twenty lettuce plants were collected on each date from the outside rows of the lettuce planting, so as not to affect the weekly survey samples. Lettuce were collected into individual brown paper bags, taken to laboratory and deconstructed as per the method for *D. tenuicornis*. Vials were placed into the refrigerator to slow the specimens' movement, and then identified under a stereo microscope according to the Oz Thrips lucid key (2016). Thirty adult *F. occidentalis* and thirty *F. schultzei* were used to start a culture of each species. Cultures was reared through to the second generation (the field collected adults being the first generation), before being used in the first Petri dish predation assay, which took place on 25th February 2013. The third generation was used on the 19th March in the second Petri dish experiment. Second generation immatures were used in the potted experiments which took place on 10th February 2014. All *F. schultzei* and *F. occidentalis* specimens used in the experiments were 2nd instar immatures.

The cultures were kept in an insect rearing room, at a temperature of $24^{\circ}\text{C} \pm 3^{\circ}\text{C}$. The room was naturally lit by large windows, with light and dark hours approximately 11:13 (light: dark) in March. The predation experiments were conducted in a laboratory attached to the insect rearing room, with the same temperature and light: dark periods.

Petri dish predation experiments

The petri dish predation experiments consisted of three prey

treatments: two no choice tests, with *D. tenuicornis* provided with *F. occidentalis* or *F. schultzei*, and one choice test, with *D. tenuicornis* provided with both *F. occidentalis* and *F. schultzei*. There were also three controls containing prey thrips as described for the prey treatments, but with no *D. tenuicornis*, giving a total of six treatments. Controls allowed for observation of natural mortality of each species. There were ten replicates of each treatment, a total 60 Petri dishes. Each treatment consisted of four prey specimens, with the choice treatment consisting of two prey specimens of each species and one *D. tenuicornis*, and the no choice consisting of four prey specimens of one species and one *D. tenuicornis*. Only one *D. tenuicornis* was used in each treatment as initial observations documented that if more than one adult were in the same arena, the thrips displayed aggressive behaviour, flicking their abdomens up at each other (Terry 1995). Past predation experiments with two or more predators have resulted in one predator consuming another or expending energy on fighting (Peckarsky 2006). Prey specimens were added to the Petri dishes from the colony using a fine brush. *Desmothrips tenuicornis* adults were added after the prey specimens were in place due to their ability to move quickly and escape the Petri dish. The lids of the Petri dishes were secured using microfilm tape. Each petri dish was labelled with the treatment and replicate (1 to 10).

Short term disappearance rates were planned to be measured through hourly observations and compared between the treatments to determine if *D. tenuicornis* would eat more of one prey species (consumption rates), and if the rate of consumption was faster, including determining if *D. tenuicornis* would actively choose between the two prey species in the choice treatment. The absence of an immature specimen in a Petri dish was used as an indication that predation had taken place. Experimental set up at began at 7 am, taking approximately one hour. The first observation took place at 9 am, and Petri dishes were then checked every hour until 6 pm. The experiment ran for three days; on the second and third day observations were made from 7 am until 6 pm. To

determine which prey species had been eaten in the choice treatment, *D. tenuicornis* gut content was planned to be analysed. This experiment was run on two occasions to determine the repeatability of the experiment.

Potted French bean and lettuce predation experiments

The lettuce and French bean potted predation experiments consisted of the same choice, no choice and control treatments as the Petri dish experiments. There were three replicates of each treatment on French bean and lettuce, giving eighteen French bean and eighteen lettuce plants in total. The potted plants used in these experiments were excess sentinel French bean and lettuce plants used in Chapter 6 (March 2014). Each potted plant was caged, using the plastic cylinders as described in Chapter 6.

Experimental setup and observational methodology followed that of the Petri dish experiments. Immature prey thrips were placed onto the leaves of the plant from the *F. occidentalis* and *F. schultzei* colonies using a fine paint brush. Once the prey specimens were in place, a paint brush was used to transfer the adult *D. tenuicornis* onto the leaf of the plant, and the plastic cylinder was put in place over the top of the plant. Prey thrips were placed randomly on leaves of the plants, each on a separate leaf. *Desmothrips tenuicornis* were placed on a leaf with no prey specimens present. White sand was placed around the stem of the plant to aid in observing any thrips that may have fallen from the foliage. Plants were observed every hour from 8 am (immediately after setup, which began at 6.30 am) on day one, until 6 pm, and then from 7 am to 6 pm on the second and third day.

Results, discussion and future research

No immature thrips were recorded as absent in any of the treatments, including the controls, in the Petri dish experiments or the potted plant experiments.

The results in this study indicate that under controlled conditions *D. tenuicornis* do not predate immature *F. occidentalis* or *F. schultzei*. However, there are many factors that may have led to this outcome, including the dissimilarity to the natural environment, incorrect instar preferable for predating or lack of alternate food sources including pollen and nectar of specific plants. In each experiment, *D. tenuicornis* were starved before use in the predation experiments. However, it is possible that the specimens were already satiated, and even after starving for 48 hours had no interest in feeding. *Desmothrips tenuicornis* may in fact not predate on these particular species, and may feed on other thrips species or arthropods. Therefore, before it can be determined conclusively that *D. tenuicornis* do not feed on immature *F. occidentalis* or *F. schultzei* and further experiments need to take place.

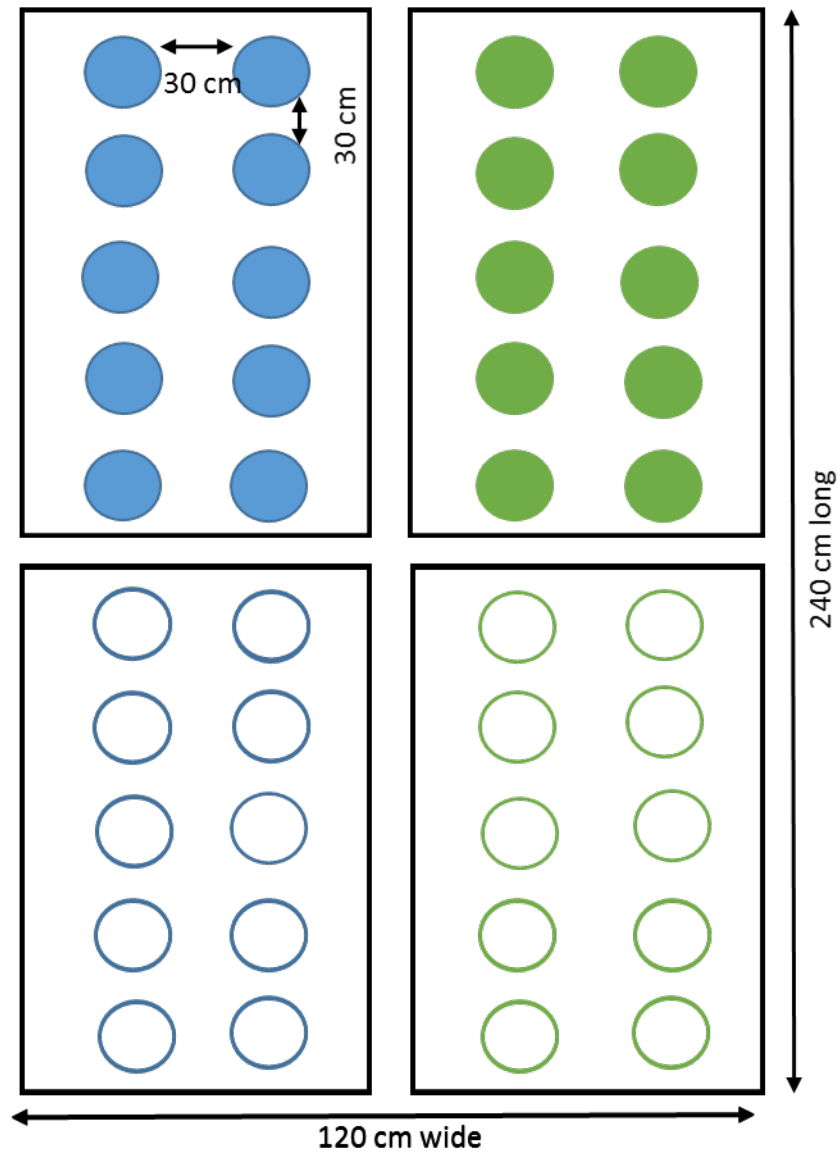
No *D. tenuicornis* were recovered on any traps placed in the vegetable plots or in the Eucalyptus surrounding the trial area. This suggests that this species does not pupate in the soil, or were not present in sufficient numbers to be trapped. The life cycle of this species has not been documented and there is very little known about its biology.

As a member of the Aeolothripidae family of which many are known facultative predators, it is thought that *D. tenuicornis* are also predators of other small arthropods and their eggs. However, with no published literature this is just speculation, and without field and laboratory evidence it cannot be concluded that *D. tenuicornis* are a predatory species. However, the results here do not provide enough evidence to conclude that they are not a predatory species. Further research needs to occur using alternate prey, different life stages and under different conditions (temperature, light, relative humidity etc.). In horticulture, the reliance on chemical insecticides to control pest thrips indicates the need for alternate methods of control. Therefore, further investigation on the biology and ecology of *D. tenuicornis* is required to increase our knowledge of this species, and identify if it could in fact be a naturally occurring biological control agent of pest thrips in vegetables.

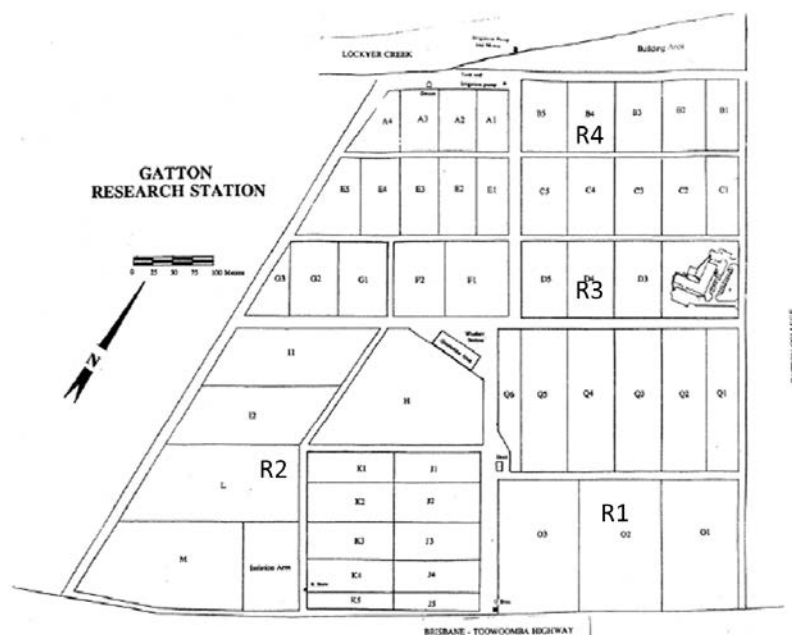
Appendix D: Immature sub-sample collection dates

		Sub-sample collection		
	Planting	1	2	3
Year one 2011 - 2012	1	18/01/2012	7/02/2012	29/02/2012
	2	29/02/2012	28/03/2012	17/04/2012
	3	12/04/2012	24/04/2012	27/05/2012
Year two 2012 - 2013	4	15/01/2013	4/02/2013	
	5	4/02/2013	8/03/2013	26/03/2013
	6	14/03/2013	4/04/2013	23/04/2013
	7	19/04/2013	13/05/2013	29/05/2013
Year three 2013 - 2014	8	9/01/2014	4/02/2014	26/02/2014
	9	26/02/2014	19/03/2014	
	10	19/03/2014	17/04/2014	8/05/2014
	11	1/05/2014	21/05/2014	

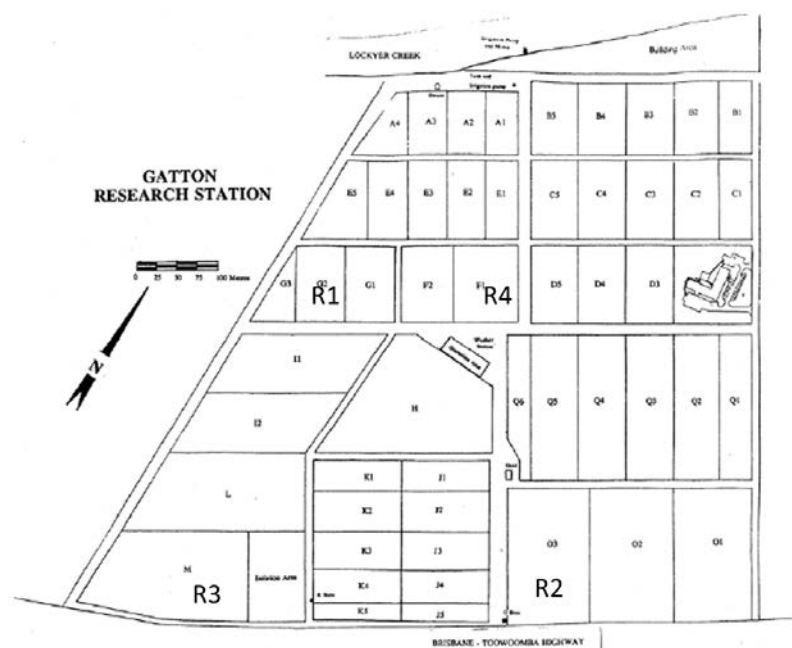
Appendix E: Sentinel trial layout



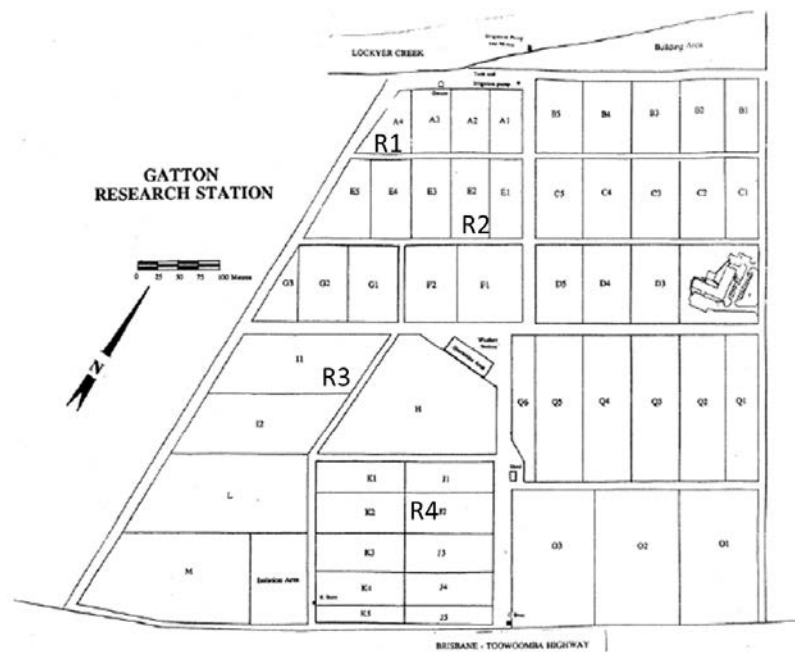
Experiment one: 2nd October 2012 - replicate location



Experiment two: 5th March 2013 – replicate location



Experiment three: 4th October 2013 – replicate location



Experiment four: 1st March 2014 – replicate location

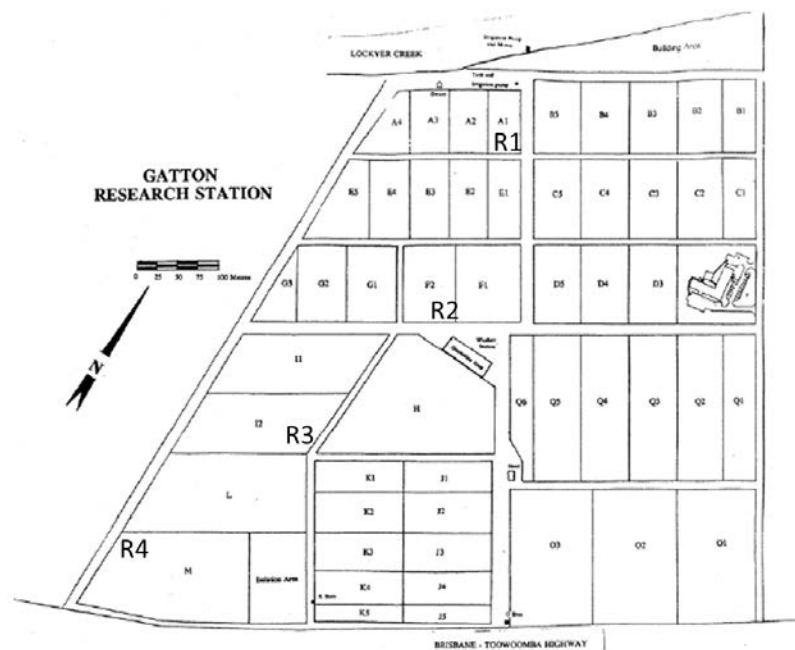




Figure 2. Sentinel plants removed from the field after exposure, re-caged.

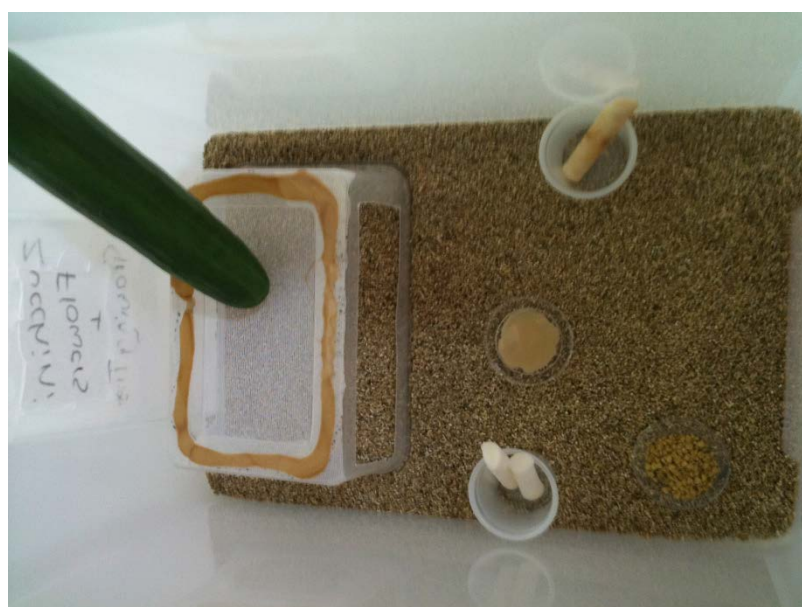


Figure 3. Sub-sampled immature thrips culture

Appendix F: Statistical Methodology – Thrips cluster size and Thrips cluster modulation

To determine the spatial distribution of each species within the respective agro-ecosystem, each replicate was regarded as one spatial point, with the coordinates corresponding to the centre of the replicate within each crop. The data sample size was ten spatial points for each crop, which limited the spatial resolution of the observations to five points (replicates) along the length of the crop and two points across the width of the crop. The limited spatial data and resolution imposed challenges on statistical analysis. For instance, the calculated index of dispersion $D = \sigma^2/\mu$, where σ^2 is the variance and μ is the mean count value (Upton and Cook, 2014), demonstrated the likelihood of data clustering (overdispersion) in the data sets. However, it would be difficult to determine possible clustering, followed by analyses using Ripley's K and L functions (Ripley, 1976; Dixon, 2002), based on the available spatial data within the considered planting blocks as a result of the 2×5 m mesh of spatial points. Therefore, to account for the limited spatial data, two statistical equations were developed to characterise spatial distribution, which produced two new dependent variables, thrips cluster size (equation 1) and thrips count modulation (equation 2).

Thrips cluster size – equation 1

In this thesis, thrips cluster size L_{cl} in a planting block was defined as:

$$L_{cl} = K \frac{\sum_{i=1}^{10} \sum_{j=1}^{10} \frac{|c_i - c_j|}{(\Delta l_{ij})^n} \Delta l_{ij}}{\sum_{i=1}^{10} \sum_{j=1}^{10} \frac{|c_i - c_j|}{(\Delta l_{ij})^n}} = K \frac{\sum_{i=1}^{10} \sum_{j=1}^{10} \frac{|c_i - c_j|}{(\Delta l_{ij})^{n-1}}}{\sum_{i=1}^{10} \sum_{j=1}^{10} \frac{|c_i - c_j|}{(\Delta l_{ij})^n}}, \quad (1)$$

where Δl_{ij} is the distance (m) between the i -th and j -th rectangular replicates measured between the centres of these two replicates within the selected block, c_i and c_j are the thrips counts in the i -th and j -th replicates, respectively, i and j are the indices taking integer values between one and ten indicating different replicates in the selected planting block, and K and n are the two parameters still to be determined.

Mathematically, cluster size definition is an averaging of the distances Δl_{ij} (m) between all possible pairs of replicates within one planting block, weighed by the factors $|c_i - c_j|(\Delta l_{ij})^{-n}$ (see the left side of Eq. (1)). The use of these weight was based the assumption that within a thrips cluster (defined as an area with significantly higher thrips abundance), thrips counts should be relatively constant and large. Therefore, the size of the cluster should be determined by the distance within which the thrips counts change significantly. As a result, the distances within which the thrips counts change significantly will have a significant contribution to the determined average cluster size L_{cl} , and that this notion is consistent with the increased weights $|c_i - c_j|(\Delta l_{ij})^{-n}$ where c_i becomes significantly different from c_j . Distances within which the thrips counts remain relatively the same (i.e., where $c_i \approx c_j$) should not have a significant contribution to the average cluster size L_{cl} ,

which is consistent with the small weights $|c_i - c_j|(\Delta L_{ij})^{-n}$ where $c_i \approx c_j$. Large distances ΔL_{ij} corresponding to replicates that are significantly spaced away from the cluster should not have significant contribution to the average cluster size, which is consistent with the reduction of the weights $|c_i - c_j|(\Delta L_{ij})^{-n}$ with increasing ΔL_{ij} . Therefore, the average cluster size L_{cl} has will have the units of distance presented in equation one above.

The parameter K is determined from the condition that the average cluster size L_{cl} must be equal to the size of one replicate, 4×3.75 m (~ 16 m²) if only one replicate, in a crop, has non-zero counts. Therefore, the minimum cluster size should be ~ 16 m². The power n should be determined from the comparison of the calculated L_{cl} at different values of n with the actual distribution of the thrips counts. The power n should be determined from the comparison of the calculated L_{cl} at different values of n with the actual distribution of the thrips counts in several typical examples of the planting blocks.

Using this as a calibration procedure, three possible values of $n = 1, 2$ and 3 were considered. The corresponding values for the scaling coefficient K were then found to be 2.80 (for $n = 1$), 3.27 (for $n = 2$), and 3.64 (for $n = 3$). To choose an appropriate value of n , three characteristic planting blocks with significantly different thrips distributions (figure 1) were considered. The cluster sizes calculated from Eq. (1) for these three blocks were: L_{cl} (Block 1) = 5.93 m, 5.56 m, and 5.10 m (for $n = 1, 2$, and 3); L_{cl} (Block 2) = 4.15 m, 4.17 m, and 4.23 m (for $n = 1, 2$, and 3); and L_{cl} (Block 3) = 4.33 m, 4.35 m, and 4.37 m (for $n = 1, 2$, and 3). As shown in these calculations, the differences between the calculated average cluster sizes for the three different powers n in Eq. (1) were very small, particularly as so zero thrips were recorded in some replicates. This demonstrates the validity of the adopted cluster evaluation approach that

is rather insensitive to the the n parameter in Eq. (1). Therefore, as a result of the comparison between the calculated values of L_{cl} with the actual count distributions within the example blocks (figure 1; the dashed curves indicate the approximate clusters determined by Eq. (1) with $K = 2.80$ and $n = 1$; $L_{cl} \approx 5.93$ m (Block 1), 4.15 m (Block 2), and 4.33 m (Block 3). , the value of $n = 1$ and the corresponding $K = 2.80$ were adopted for further analysis.

Planting Block 1			Planting Block 2			Planting Block 3	
0	0		1	0		4	3
0	0		4	0		9	2
0	0		0	0		5	1
1	1		2	5		4	3
2	1		0	0		3	2

Figure 1. Illustration for the definition of thrips clusters on the example of three planting blocks with characteristically different spatial distribution of thrips counts, displayed as numbers within the replicates.

The thrips clusters corresponding to the adopted values of K and n are demonstrated by dashed curves. The use of $n = 1$ ensured the selection of the largest size of the cluster for Block 1. This vale was chosen as the thrips were distributed approximately evenly throughout the four neighbouring replicates (with a small count maximum of two). In block two and three (figure 1) the count maximums are more pronounced, indicating significantly tighter thrips clustering around the replicates with these maximums. This was reflected in smaller sizes of the corresponding clusters.

It is important to note that the adopted definition of thrips clusters (Eq. (1)) defines the clusters as areas with significantly increased thrips counts, whether on the background of otherwise zero counts, as shown in blocks one and two in figure 1, or on the background of significantly lower but non-zero counts as shown in block three in figure

1. This definition is practically useful as it allows identification and characterisation of the areas with significantly increased thrips counts.

The developed equation is critical for use in small sets of spatial data due to the permutation of the replicates, which results in effective smoothing of the cluster size variable (L_{cl}) compared to the original highly scattered count variable (high zero's). The developed equation for cluster size is also directly applicable in the general case of any spatially distributed data that might contain a large number of replicates or other measurement points.

Thrips cluster modulation – equation 2

The second dependent variable developed for the characterisation of thrips counts was the cluster modulation M_{cl} defined for a selected planting block as:

$$M_{cl} = \frac{\sum_{i=1}^{10} |c_i - \min\{c\}|}{10}, \quad (2)$$

where $\min\{c\}$ is the minimum thrips count out of all 10 replicates in the considered block. Mathematically, M_{cl} is an average of the differences between the thrips counts within the selected block and the minimum thrips count in the same block. It gives the average magnitude of typical variation of thrips counts within the selected planting block, thus quantifying the typical modulation of the thrips counts over the block. If the minimum thrips count in the block is zero (Blocks 1 and 2 in Fig. 1), the M_{cl} simply gives the average thrips count on the block. M_{cl} is another important characteristic of the thrips clusters, quantifying the degree of variation of thrips counts.