Thrips vectors and resistance to *Tomato spotted wilt virus* (TSWV) in potato

by

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Preface

This study was formulated to examine the attributes of onion thrips (*Thrips tabaci* Lindeman) in relation to its vectoring role of *Tomato spotted wilt virus* (TSWV) in commercial and seed potato crops in Australia. Outbreaks of TSWV in potato have been sporadic, often not occurring for several years, but on occasion devastating, affecting up to one-third of some crops, and causing millions of dollars in industry losses. The accumulation of knowledge of TSWV disease epidemiology in potato has been limited due to its sporadic nature and low incidence outside Australia. Work conducted by Charles Jericho (2005) greatly increased this knowledge, but left many questions unanswered, not least of which is the ongoing confusion over the role of *T. tabaci* as a vector of TSWV in Australia.

This thesis consists of a general introduction followed by four research chapters and concludes with a thesis summary and general discussion. **Each of the research chapters has been prepared as an independent, publishable manuscript, except that here, figures and tables have been numbered to fit with the thesis format. For this reason, on occasion, there is some repetition between chapters.** The chapters are as follows:

Chapter 1 provides a general introduction and literature review
Chapter 2 examines three field trials undertaken in Tasmania and South Australia looking at differences in TSWV foliar and tuber infection levels, and *T. tabaci* numbers across a number of potato cultivars.
Chapter 3 examines the colour preferences of *T. tabaci*, *F. schultzei* and *F. occidentalis* for green, yellow, blue, red and white, as well as the preference of *T. tabaci* for different intensities of green. This chapter also contains a spectral analysis of potato cultivars.
Chapter 4 examines the host preferences of *T. tabaci*, *F. schultzei* and *F. occidentalis* for potato compared to a number of other plant hosts, and also the preferences of *T. tabaci* for potato at the cultivar level. This chapter also examines the oviposition preferences of *T. tabaci* for potato cultivars in choice and no-choice tests.
Chapter 5 examines the vector competence and transmission efficiency of several populations of *T. tabaci* in a number of acquisition-transmission host combinations, and relates this to the source hosts from which these populations were collected, and the relationship of these populations in a phylogenetic analysis.
Chapter 6 consists of a thesis summary and concluding remarks, with recommendations for further research and for industry.

Abstract

This study was formulated to examine the efficiency of *Tomato spotted wilt virus* (TSWV) transmission by onion thrips (*Thrips tabaci* Lindeman) and factors associated with host resistance in potato; in particular to investigate the suggestion that potato cv. Bismark has a high level of resistance to thrips, and to examine why onion thrips have failed to transmit TSWV in laboratory experiments in previous studies. Three field trials were conducted in Tasmania and South Australia to evaluate differences in potato cultivar resistance to thrips and TSWV (Chapter 2). TSWV-infection levels were moderate in two trials, with TSWV-incidence varying from 9-26 percent in Tasmania and 3-22 percent in South Australia, but only 0-6 percent in the second Tasmanian trial. Thrips counts showed the highest numbers of *T. tabaci* on Bismark and lowest thrips numbers were found on Shepody. There were no significant differences in TSWV foliar or tuber infections between cultivars, and no correlation between thrips numbers and TSWV incidence.

A population of *T. tabaci* was subjected to choice experiments to test for colour preference (Chapter 3), and host preference and oviposition choice (Chapter 4), using a number of commercial potato cultivars and coloured cards. Populations of western flower thrips (*Frankliniella occidentalis* Pergande) and tomato thrips (*Frankliniella schultzei* Trybom) were also tested for colour and host preference alongside onion thrips in separate experiments. Colour preference tests showed strong colour preferences amongst all three thrips species tested. Western flower thrips and tomato thrips strongly preferred green to red, blue and white; but preferred yellow to green. Onion thrips preferred green and yellow equally and over the other three colours. Onion thrips showed a strong preference for light-green over darker shades of green. Host preference tests showed differences in potato cultivar preference by onion thrips, with higher attraction to cultivars with lighter green foliage: Shepody and Russet Burbank. Oviposition choice tests showed almost the opposite, with higher numbers of hatched juvenile thrips on darker green potato cultivars: Atlantic, Bismark, Royal Blue and Tasman.

Several female-only, parthenogenetic populations of *T. tabaci* were collected from Tasmania, New South Wales and South Australia from potato, onion and *Chrysanthemum*. These populations were tested for their ability to transmit TSWV to potato and other hosts, and subjected to a phylogenetic analysis following DNA extraction and PCR amplification of mitochondrial gene cytochrome c oxidase subunit 1 (COI) (Chapter 5). Vector competence was associated with the host from which the populations were collected, with three populations collected from potato transmitting TSWV, but three populations collected from onion failing to transmit the virus. This ability to transmit TSWV was also associated with differentiation in COI, with vector competent and non-competent populations separating into subgroups within the 'L2' European clade of Brunner *et al*. (2004).

This is the first study to link genetic differentiation of *T. tabaci* to both source host and vector competence, and provides a credible explanation for why many studies have failed to achieve any transmission of TSWV by this species. Strong colour preferences and some host preferences were also demonstrated, however field experiments suggest that potato cultivar resistance to thrips is unlikely to provide a reliable method for reducing TSWV infection levels in commercial potato crops.

Chapter 1 - General Introduction

Potato production in Australia

History and economic importance

The first potatoes grown commercially in Australia were at the settlements of Sydney, New South Wales and Risdon Cove, Tasmania, around 1803, but were also planted in Tasmania in the 1790s by French explorers at Recherche Bay, and by Captain Bligh on Bruny Island in 1792 (Taylor, 2003). While the area of land planted to potato has not increased greatly in the last 150 years, yields have increased markedly (Taylor, 2003). Potato production in Australia in the 2009/2010 growing season consisted of 1,176 growers producing 1,278,118 tonnes from 36,379 hectares (35 t/ha), amounting to $614m in gross value, representing approximately 20 percent of vegetable production in Australia (ABS, 2011). Three quarters of Australia's potato production occurs in the southern States of Victoria, Tasmania and the southern parts of South Australia, with the remainder of the crop grown in NSW, Queensland and Western Australia (ABS, 2011).

Despite having neither the greatest area planted to potatoes, nor the highest production of the States, Tasmania has the highest number of individual growers (391), and the highest yields (50 t/ha) in the country (ABS, 2011). The potato industry in Tasmania has a farm gate value of $114 million (Griffiths, 2011), making up approximately 50 percent of the total value of vegetable production, and over 10 percent of all agricultural production in the State (Griffiths, 2011). Within Tasmania, processing potatoes make up 80 percent, fresh sales 10 percent, and the seed potato market 10 percent of production (Griffiths, 2010). Of the 1.3 million tonnes of total potato production in Australia in 2010, Tasmania produced 330,000 tonnes (ABS, 2011). The industry is segmented into seed production, fresh-market production and processing. The processing sector includes chips (french fries), wedges and other crisping products, but also includes some semi-processed products such as pre-peeled potatoes for the catering trade. This accounts for about 55 percent of total production. The fresh market, consisting of washed and brushed potatoes, accounts for about 35 percent and seed production is a little under 10 percent (Cummings, 2006). An enormous variety of potato cultivars are grown in Australia.

The adoption of newer machinery, such as more efficient harvesters, better cultivation practices, such as raised bed soil cultivation, and improved management of weeds and disease has led to substantial productivity gains (Taylor, 2003). Tasmania's abundant water resources, which provide for cheaper water and less variability in water licence allocations, have also contributed. Yield reductions due to widespread viral infection led

to the introduction of a certified seed scheme in the 1930s, which to this day remains central to the industry's disease management program. In more recent years however, noticeably from the mid-1990s, the frequency of *Tomato spotted wilt virus* (TSWV) epidemics Australia-wide has increased (Jericho, 2005; Jericho & Wilson, 2003).

Potato cultivars

Eight commercially available potato cultivars were selected for this study - Atlantic, Bismark, Royal Blue, Russet Burbank, Shepody, Coliban, Spunta and Tasman. Atlantic, Russet Burbank and Shepody were chosen because they constitute the main processing varieties in southern Australia, while the other cultivars were chosen because of their varying characteristics, with some indications that Bismark and Royal Blue may possess some resistance to thrips and TSWV (Jericho, 2005).

Cv. Atlantic is widely grown throughout Australia. It has become the main variety used for direct processing into crisps in Victoria and dominates the production of certified seed potatoes. The plants are medium to large, and upright; with thick stems that are purple at the base with an irregular pigmentation pattern upward. The leaves are smooth, bright green, and moderately pubescent. Tubers are oval to round, smooth, with lightly netted to heavily scaled white skin, with shallow white eyes and white flesh (Wilson, 1999).

Cv. Bismark is an early maturing cultivar with long, oval creamy white tubers and flesh with purple eyes. It is excellent for boiling as an immature potato, and is suitable for chipping when mature, but it is not a good baking type. Plants are of medium height, open and erect. The leaves are a medium-green colour, of medium size, and its flowers are light purple. Misshapen tubers are common, particularly when soil moisture fluctuates widely (DPIPWE, 2003).

Cv. Russet Burbank is a multi-purpose potato suitable for both the fresh market and processing, being excellent for baking and French fry production, but not ideally suited to boiling. It is a late-maturing type with highly russetted long cylindrical tubers, and white flesh, making it excellent for french fries. The eyes are shallow and numerous but not well distributed at the stolen end. It is subject to tuber malformation, particularly if planted at low density and given water erratically, and to hollow heart when grown in cold, wet seasons. It is susceptible to common scab and eelworm. The plants are tall, semi-upright, with large, light to medium green leaves, and white flowers (Peeten *et al*., 2011; Wilson, 1999).

Cv. Royal Blue has very dark green leaves, with almost a bluish tinge. The tubers have purple skin and yellow flesh. Typically smaller than the processing varieties, the tubers are a long, oval shape. They are good for mashing, roasting, frying or microwaving (PMCWA, 2011).

Cv. Shepody potatoes are an early maturing variety with long, large oval tubers. These qualities and their high yield are the reason they have become a major processing variety. The tuber skin and flesh is cream-coloured with shallow eyes. The plants are tall with red-violet flowers (ECPD, 2005).

Cv. Tasman is a useful all-purpose mid season type with bright pink tubers, fairly shallow red eyes and white flesh. It can be used for boiling, chipping and baking. Uniform tuber size and general attractiveness of the tubers, especially when washed, makes this potato visually attractive, however it has a tendency to break up during boiling and it can produce dark coloured chips and baked potatoes. It is highly susceptible to powdery scab. Plants are large, erect and vigorous with fairly dense, medium green, medium sized leaves. Flowers are pale purple with paler tips (DPIPWE, 2003).

Cv. Coliban is a white fleshed potato, somewhat floury, that is good for mashing, baking and roasting, but poor for boiling, with some tendency to disintegrate. It is a major fresh market variety, and one of the most commonly sold as a washed potato in the major supermarkets. The plants are tall and erect, with wiry, pigmented stems and small, open dark-green leaves. The flowers are white and purple. The tubers are round, with bright, white waxy skin (Wilson, 1999).

Cv. Spunta has tubers that are typically long, with shallow eyes, white skin and pale yellow flesh, which are good, boiled or steamed. Plants are tall, upright to semi-upright, with white flowers, and medium to large, dark green leaves (Peeten *et al*., 2011).

Tomato spotted wilt virus

History and economic importance

Tomato spotted wilt virus (TSWV) was first reported in 1915 in Victoria, in south-eastern Australia, by Brittlebank (1919), who named the disease caused by this pathogen "Spotted Wilt". However several earlier reports of unknown diseases with similar symptoms in tomato in Ohio, USA, 1895, and tobacco in Eastern Cape, South Africa, 1905, combined with a very wide host range, suggest that TSWV has been around for much longer, and makes its origin unclear (Peters, 1998). Within a short space of time following the first official reports, disease symptoms were found across mainland Australia and overseas (Best, 1968). That the disease arose from a thrips-vectored virus was confirmed in the 1920s, and named *Tomato spotted wilt virus* by Samuel (Samuel *et al*., 1930). TSWV has since been reported in more than 1100 plant species (Parella *et al*., 2003; Peters, 2004), across horticultural crops, ornamentals and weeds in Europe, North and South America, Asia, Russia, Africa, Australia, and New Zealand (Abad *et al*., 2003; Al-Shahwan *et al*., 1997; Anfoka *et al*., 2006; Broughton & Herron, 2007; Carrieri & Sorrentino, 2011; Cho *et al*., 1986; Clift *et al*., 1999; Conroy *et al*., 1949; Crosslin *et al*., 2009; Daughtrey *et al*., 1997; Dewey *et al*.,1996; German *et al*., 1992; Gitaitis *et al*., 1998; Golnaraghi *et al*., 2001; Gracia *et al*., 1999; Hill & Moran, 1996; Hristova *et al*., 2001; Jenser *et al*., 2009; Jericho & Wilson, 2002, 2003; Johnson *et al*., 1995; Latham & Jones, 1996, 1997; Mertelík *et al*., 1996; Mumford *et al*., 1996; Nischwitz *et al*., 2006a, 2006b; Ochoa *et al*.,1999; Peters, 1998; Sakimura, 1962; Wangai *et al*., 2001; Williams *et al*., 2001; Wilson, 1998a, 1998b, 2001; Yardimci & Kiliç, 2009; Zheng & Huang, 2010).

Outbreaks of TSWV on mainland Australia have been associated with *T. tabaci* and *F. schultzei* (Conroy *et al.*, 1949; Jericho & Wilson, 2003; Magee, 1936; Norris & Bald 1943; Norris 1951a & 1951b; Pittman 1927; Samuel *et al.*, 1930; Thomas & Jones, 2000), and more recently with *F. occidentalis* (Baily & Caon, 2000; Broughton & Herron, 2007; Herron *et al*., 1996; Latham & Jones, 1997; Malipatil *et al.*, 1993; Persley *et al*., 2006). Epidemics have been devastating to crop yields and economic returns in South Australia (Baily & Caon, 2000) and Western Australia (Broughton & Herron, 2007). All instances of TSWV in Tasmania have been attributed to *T. tabaci* because it is the the only known vector trapped in open cultivation (Jericho & Wilson, 2002; Wilson, 1998a).

The widespread and devastating nature of TSWV, and its expansion in the last twenty years, has prompted extensive study of the virus (German *et al*., 1992; Mumford *et al*., 1996; Ullman *et al*., 1997; Ullman *et al*., 2005). Despite this considerable research, and indeed a not inconsiderable body of researchers dedicated to understanding the relationship between thrips and tospoviruses, TSWV continues to cause widespread and

severe crop loss in tropical, subtropical, arid and Mediterranean climates. This is partly due to the difficulties in managing the disease, but also because *F. occidentalis,* which vectors TSWV more efficiently than *T. tabaci*, has rapidly expanded its geographic distribution and host range in the last twenty to thirty years (Ullman *et al*., 1997; Wijkamp *et al*., 1995). This has been especially important in growing regions where *T. tabaci* was previously the main vector of TSWV.

Major crop losses due to TSWV have occurred in Mexico, with 90 percent losses recorded in *Chrysanthemum* (Ochoa *et al*., 1999), and in Georgia, USA, with 100 percent losses recorded in capsicum and tomato (Gitaitis *et al*., 1998). Smaller, but still devastating losses of 30-60 percent in tobacco, peanut, tomato and capsicum have occurred in Georgia and Florida, USA (Bertrand, 2000, 2001; McPherson *et al*., 2003). Protected and field crops of tomatoes and capsicum have been devastated in France and Spain (EPPO/CABI, 1997), with up to 100 percent crop loss (Berling *et al*., 1990; Rodriguez, 1990). Production of tomato, melon, tomato and capsicum have been dramatically curtailed in parts of north-east Spain since the first introduction of TSWV in 1987, as growers were no longer prepared to shoulder the high risk of total crop loss (Cebolla-Cornejo *et al*., 2007; Jorda & Osca, 1991; Moriones *et al*., 1998). Argentina experienced several devastating outbreaks of TSWV in the 1990s, in tomato, lettuce, and capsicum (Gracia *et al*., 1999).

TSWV has caused significant damage to lettuce crops in Tasmania on a number of occasions over the last fifteen years (Wilson, 1998a; C. Wilson, personal communication, 2005), with losses in epidemic years ranging from five to sixty percent. Field tomato production in the Derwent Valley of Tasmania was brought to an end due to unacceptably high losses from TSWV infection (C. Wilson, personal communication, 2005). Potato crops have been badly affected in the south-east States of the United States (Abad *et al*., 2003) and across the southern States of Australia (Broughton & Herron, 2007; Clift & Tesoriero, 2002; Medhurst *et al*., 2003; Wilson, 2001). Capsicum, tomato, stonefruit, tobacco, peanuts, lettuce, chickpea, eggplant, celery, rhubarb and ornamental crops have suffered large losses from TSWV in Australia, New Zealand, the United States, Eastern, Western and Southern Europe, and in Eastern and Southern Africa (Chatzivassiliou *et al*., 1996; Cooke *et al*., 2009; EPPO/CABI, 1997; Jenser *et al*., 2003; Klesser 1966; Louro 1996; Persley *et al*., 2006; Roselló *et al*., 1996; Sharman & Persley, 2006; Thompson & van Zijl, 1996; Teulon & Penman, 1996; Wangai *et al*., 2001). Several entire ornamental flower crops have been destroyed by *T. tabaci*-vectored TSWV in nurseries in Hobart, Tasmania (P. Cross, DPIPWE, personal communication, 2008).

Glasshouse crops frequently suffer severe losses from thrips-vectored TSWV. Although pest control is sometimes easier in protected environments, due to the more efficient deployment of biological control agents, and easier application of pesticides, the warmer temperatures increase over-winter survival of thrips and accelerate thrips development (Chatzivassiliou *et al*., 2001; Daughtrey *et al*., 1997). TSWV is an increasing problem, due to recent extensive spread by natural and human means, expansion in geographic distribution and host range of *F. occidentalis* (Kirk & Terry, 2003; Morse & Hoddle, 2006), and increasing insecticide resistance, predominantly in *F. occidentalis* (Bielza *et al*., 2007, 2008; Broadbent & Pree, 1997; Brødsgaard, 1994; Espinosa *et al*., 2002; Herron & James, 2005, 2007; Immaraju *et al*., 1992; Jensen, 2000; Kontsedalov *et al*., 1998; Martin & Workman, 1994; Robb *et al*., 1995; Zhao *et al*., 1995), but also more recently in *T. tabaci* (Herron *et al*., 2008; MacIntyre *et al*., 2005; Shelton *et al*., 2006). Losses caused by TSWV are not limited to reductions in yield and quality. Economic costs also include the expense of additional management measures, such as insecticides and roguing of infected plants.

TSWV in potato crops in Australia

Tomato spotted wilt virus causes disease in Australian potato crops that, while sporadic in incidence, is highly damaging and difficult to control (Persley *et al*., 2006). Despite extensive work by Jericho (2005), much is still unknown about the epidemiology of the virus in potato, mainly because of the low number of TSWV epidemics in potato outside of Australia, limiting the incentive to research and the scope for doing so. Recurring, unpredictable and debilitating outbreaks of TSWV in the potato industry result in lost production and income, hinder industry expansion, and may lead to detrimental changes in crop rotation sequences and regional cropping opportunities. TSWV epidemics are particularly damaging to crops of processing potatoes. Virus infections cause internal necrosis or orange-brown discolouration making them unmarketable and unsuitable for processing, but often this does not become apparent until after the potatoes have arrived at the processing facility, after growing, harvesting and transport costs have already been incurred (Jericho, 2005; C. Wilson, personal communication, 2005). TSWV in southern Australia, while intermittent and highly variable in its effects, remains a serious threat to the economic viability of the Australian potato industry and related activities.

Because the ecological and epidemiological factors underpinning TSWV outbreaks in Australia are not well understood, managing TSWV and vector thrips is an enormous challenge for growers, processors and scientists (Herron & Cook, 2002; Jericho, 2005; Jericho & Wilson, 2003; Norris, 1951a, 1951b; Wilson, 1998b). Following early Australian

work by Pittman (1927), Samuel *et al*. (1930), Samuel & Bald (1931) and Bald (1937); research was conducted on TSWV in potato crops by Magee (1936), Norris & Bald (1943), Conroy *et al*. (1949), and Norris (1951a, 1951b), and more recently by Wilson (1996, 1998a, 1998b, 2001), Jericho *et al*. (2002), Jericho & Wilson (2003), Jericho (2005) and Wilson *et al*. (2006, 2009). Extensive outbreaks of TSWV occurred in potato in Victoria and New South Wales between 1945 and 1948. Losses were significant, and in some cases crops were abandoned (Conroy *et al*., 1949; Norris, 1951a, 1951b). As they are today, these outbreaks were sporadic and unpredicted; however Conroy *et al*. (1949) did observe a correlation between the outbreaks and dry summers. Over the following forty years few accounts of TSWV in Australia were produced, until the early 1990s, when reports and interest in TSWV and vector thrips began to increase, following an increase in the frequency and severity of TSWV epidemics in many crops (Clift *et al*., 1999; Hill & Moran, 1996; Jericho, 2005; Jericho & Wilson, 2003; Latham & Jones, 1996, 1997; Moran *et al*., 1994; Wilson, 1998a; Wilson, 2001).

A similar pattern of decline and resurgence of TSWV occurred in much of Western Europe and the United States, however this did not occur to the same extent in some other areas, such as Eastern Europe, South America and South Africa, where TSWV was an ongoing problem (Goldbach & Peters, 1996; Sakimura, 1963a). Kirk and Terry (2003) have discussed the spread from the late 1970s of *F. occidentalis*, which is a more efficient TSWV-vector than *T. tabaci* (Ullman *et al*., 1997), from the United States and Canada to Europe, northern Africa and Australia. This is one reason for the increase in the number and extent of TSWV epidemics in Australia in a range of crops (Malipatil *et al*., 1993; Persley *et al*., 2006). The rise in TSWV across the world in the 1980s and 1990s has also been attributed to increased pesticide use to control thrips and other insects in greenhouses in western countries (Peters *et al*., 1996). In fact these two contributing factors can be linked, in so much as the intensive insecticide use in the United States during the 1970s and 1980s selected for insecticide resistant populations of *F. occidentalis*. These populations then established in glasshouses across North America, and from there spread around the world with an increasing horticultural trade, particularly in cut flowers (Kirk & Terry, 2003). *F. occidentalis* was first recorded in Australia in 1993 (Malipatil *et al*., 1993), yet reports of TSWV outbreaks in Australia preceded this.

TSWV was first recorded in potato in Tasmania in 1982 (Sampson & Walker, 1982). Over the following decade infections were reported in potato in NSW (Clift *et al*., 1999), in Western Australia (Latham & Jones, 1997), and in South Australia and Tasmania (Wilson, 2001). Broughton and Herron (2007) reported devastating outbreaks in potato

in South Australia around 2000/2001. Surveys by Jericho and Wilson (2003), during the seasons of 2001/2002 and 2002/2003, recorded outbreaks of TSWV in a number of potato crops in South Australia, Victoria and New South Wales. These outbreaks resulted in 30 percent of seed potatoes failing certification in Ballarat, Berrigan, Portland, Colac and Gippsland (Jericho, 2005). Disease incidence in Tasmania at this time varied from trace to 28 percent, resulting in up to 1000 tonnes of seed failing certification (Jericho, 2005).

Tomato spotted wilt virus now appears in potato crops in Australia every year, although the level of incidence and severity varies significantly from year to year. The disease has been recorded in potato in all Australian States, except for the Northern Territory (Table 1.1, updated from Jericho, 2005).

Table 1.1 Reports of TSWV in Australia

Location	**Year**	**Crop/weeds**	**Reference**
Victoria	1917-1919	Tomato	Brittlebank, 1919
New South Wales	1927	Tomato	Pittman, 1927
South Australia	1930	Tomato	Samuel *et al.*, 1930
South Australia	1931	Tomato	Bald & Samuel, 1931
New South Wales	1935	Lettuce and potato	Magee, 1936
New South Wales	1937	Tomato	Bald 1937
New South Wales	1941	Potato	Norris & Bald 1943
New South Wales	1946-1947	Potato	Conroy *et al.*, 1949
New South Wales (including ACT) & Victoria	1945-1947	Potato	Norris 1951a &1951b
Queensland	1961	Peanut	Helms *et al.*, 1961
Location	**Year**	**Crop/weeds**	**Reference**
Australia wide	1994	Potato	Moran *et al.*, 1994
Western Australia	1996	*Capsicum*, tomato & *Dahlia*	Latham & Jones 1996

Western Australia	1993-1996	Broad bean, *Capsicum*, celery, chilli, eggplant, globe artichoke, lettuce, paprika, potato, tomato, native flora & weeds.	Latham & Jones, 1997
Tasmania	1994-1995	Lettuce & weeds	Wilson, 1998
New South Wales, Victoria, Tasmania, Queensland	1992-1999	Potato, tomato, lettuce, & *Capsicum*	Clift *et al.*, 1999
Australia wide	1998-2000	Potato	Horne & Wilson, 2000
Tasmania, Victoria, South New South Wales	2001	Potato	Wilson, 2001
South Australia	1999-2000	Potato	Baily & Caon, 2000
Australia wide	1994-2001	Various crops	Clift & Tesoriero, 2002
Tasmania, Victoria, South Australia & New South Wales	2001-2002	Potato	Jericho & Wilson, 2002
Tasmania, Victoria, South Australia & New South Wales	2001-2003	Potato	Jericho & Wilson, 2003
Tasmania, Victoria, South Australia & New South Wales	2003	Potato	Jericho & Wilson, 2003
Western Australia	2003	*Capsicum*	Thomas-Carroll & Jones, 2003
Western Australia	2003	Lettuce	Broughton & Herron, 2007
Australia-wide	1993-2003	Various crops	WFT Newsletters (No. 1-30) Medhurst *et al*., 1993-2003

Taxonomy of TSWV

TSWV is a *Tospovirus*, which is a genus of thrips-transmitted, tripartite, ambisense, single-stranded (ss) genome RNA viruses within the family Bunyaviridae. *Tospovirus* is the only plant-infecting genus within the family; the other four genera (*Bunyavirus*, *Phlebovirus*, *Nairovirus*, *Hantavirus)* being animal-infecting viruses (Elliot 1990; Francki *et al*., 1991). The structure of TSWV has been studied widely (de Ávila *et al*., 1993; de Haan *et al*., 1989, 1990, 1991; German *et al*., 1992; Goldbach & Peters, 1994, 1996;

Kormelink *et al*., 1992, 1994; Mohamed *et al*., 1973; Mumford *et al*., 1996; Qiu *et al*., 1998; Sin *et al*., 2005; Soellick *et al*., 2000; Tas *et al*., 1977; Tsompana *et al*., 2005).

Tospoviruses consist of three single-strand RNA molecules, known simply as S (Small), M (Medium), and L (Large), being c. 2.9 kb, 4.8 kb and 8.9kb, respectively (Cortez *et al*., 2001). The S-RNA and M-RNA are both ambisense, while the L-RNA is of negative polarity (Cortez *et al*., 2001). The genome codes for six proteins via five different open reading frames (ORFs). The S-RNA produces the nucleocapsid (N) proteins that are used to construct the virion capsid and a non-structural protein (NSs) of unknown function (Cortez *et al*., 2001). The M-RNA produces two envelope precursor glycoproteins (G1 and G2) and a viral movement protein (NSm) for cell-to-cell transfer (Cortez *et al*., 2001). The L-RNA produces a RNA-dependent polymerase (RdRp) for viral replication and genome transcription (Whitfield *et al*., 2005). Each RNA segment is packaged by nucleocapsid proteins and small amounts of RNA polymerase, creating a quasi-spherical particle, 80-120 nm in diameter. The mature particle is usually enclosed in a lipid membrane, which is formed by budding from the Golgi of the host and incorporating the viral envelope glycoproteins (Lawson *et al*., 1996; Kikkert *et al*., 1999; Kitajima *et al*., 1992; Mohamed *et al*., 1973; Prins & Golbach, 1998; Tas *et al*., 1977).

The function of the gene products is still not completely understood (de Assis Filho *et al*., 2002; Bandla *et al*., 1998; Nagata *et al*., 2000; Whitfield *et al*., 2005). The NSs protein functions in the suppression of RNA silencing during plant-infection (Bucher *et al*., 2003; Takeda *et al*., 2002). The nucleocapsid protein (N) assists in viral replication in a structural and regulatory manner via its role in the formation of ribonucleocapsid proteins (RNPs), which are structural features of TSWV (Kainz *et al*., 2004; Whitfield *et al*., 2005). These serve as templates for viral gene transcription and genomic replication (Elliot, 1996; Schmaljohn, 1996). The viral membrane glycoproteins play a role in virus binding and entry and also viron assembly. Current research indicates that virus acquisition by thrips occurs as a result of a thrips mid-gut receptor binding to the glycoproteins (Whitfield *et al*., 2005). The NSm protein is involved in cell-to-cell movement in plants but appears to have no corresponding function in the thrips phase of replication (Gunasinghe & Buck, 2003; Whitfield *et al*., 2005).

TSWV exists as a heterogeneous population of multiple strains, enabling adaptation and evolution of the virus (Adkins, 2003; de Avila *et al*., 1990; Moyer *et al*., 2003a). Many strains have been identified based on the characterisation of symptoms on indicator plants, as well as on commercial crops such as capsicum and potato (Best & Gallus, 1955; Norris 1951a; Thomas-Carroll & Jones, 2003). Molecular methods have also been

used to more accurately determine strain differences (Aramburu & Martí, 2003; Bucher *et al*., 2003; Pappu *et al*., 1996; Qiu *et al*., 1998; Qiu & Moyer, 1999). TSWV isolates appear to vary greatly, depending on geographic source, and due to high intraspecific-polymorphism and genetic differentiation between sub-populations (Adkins, 2003; Kainz *et al*., 2004; Moyer *et al*., 2003a, 2003b). Infection of plants with multiple strains has resulted in genomic reassortment to create new variants, sometimes with increased virulence, enabling the virus to overcome nearly all host resistance genes (Bucher *et al*., 2003; Qiu *et al*., 1998; Qiu & Moyer, 1999), leading to epidemics (Moury *et al*., 1997; Roggero *et al*., 2002).

Genome reassortment may, conversely, reduce the level of virulence or the ability of vector thrips to transmit the new strain, or both (Fraser, 1990; Nagata *et al*., 2000; Naidu *et al*., 2003; Sin *et al*., 2003). The spread of new strains has been postulated as one possible reason for the loss of fitness in vector thrips transmission by *T. tabaci* in Western Europe (Chatzivassiliou *et al*., 1998a, 1999, 2001; Jones 1959; McPherson *et al*., 1999; Paliwal 1974, 1976; Wijkamp *et al*., 1995), and South America (Nagata *et al*., 2002). No significant molecular differences have been observed among TSWV strains in Australia (Dietzgen, 2003; Talty & Dietzgen, 2001), although resistance-breaking strains have been reported (Latham & Jones, 1998). A strain, originally obtained from peanut, that is not able to be transmitted by thrips, has been characterised (Naidu *et al*., 2008).

Host range of TSWV

Well over 1000 plant species worldwide in at least 92 families have been recorded as *Tospovirus* hosts (Peters, 1998), but new hosts continue to be identified, such that there are now over 1100 species identified as hosts of TSWV (Nischwitz *et al*., 2006a, 2006b). New hosts are usually identified as a result of vector-induced field infections and outbreaks (Chatzivassiliou *et al*., 2000a, 2000b, 2001; Cho *et al*., 1986; Groves *et al*., 2001, 2002; Hobbs *et al*., 1993; Kaminska & Korbin 1994; Johnson *et al*., 1995; Latham & Jones, 1997; Mertelík *et al*., 1996; Stobbs *et al*., 1992), but also through laboratory inoculations (Adkins & Rosskopf, 2002; Bautista *et al*., 1995; Mertelík *et al*., 1996; Stobbs *et al*., 1992). The host range has been described and reviewed by Cho *et al*. (1987), German *et al*. (1992), Mumford *et al*. (1996), Peters (1998), and Ullman *et al*. (1997). The principal food and industrial host crops susceptible to TSWV are listed in Table 1.2.

Table 1.2 Important food and commercial plant species susceptible to TSWV.

Food and industrial plant hosts	References
Tomato	Allen & Aramburu *et al*., 1997; Azeri, 1994; Broadbent, 1986; Bald, 1937; Brittlebank, 1919; Gitaitis *et al*., 1998; Sakimura, 1940; Wangai *et al*., 2001; Williams *et al*., 2001
Capsicum	Gitaitis *et al*., 1998; Hobbs et al., 1993; Smith, 1931, 1932; Yurtmen *et al*., 1998
Eggplant	Feguson, 1951; Sakimura, 1940; Smith, 1932
Zucchini	Gardner & Whipple, 1934
Tobacco	Azeri, 1981; Chatzivassiliou *et al*., 1998, 2001; Fromme *et al*., 1927; McPherson *et al*., 1999; Norris, 1946; Smith, 1931; Wingard, 1928
Lettuce	Cho *et al*., 1986, 1987, 1988; Gardner & Whipple, 1934, Sakimura, 1940; Wilson 1998
Peanut	Al -Saleh *et al*., 2007; Amin, 1985; Camann *et al*., 1995; Helms *et al*., 1961; Hoffmann *et al*., 1998; Mandal *et al*., 2001
Broad bean	Gardner & Whipple, 1934
Chick pea	Thomas *et al*., 2004
Chicory	Sakimura, 1940
Potato	Al-Shahwan *et al*., 1997; Hutton & Peak, 1952; Norris, 1946, 1951a; Smith, 1931, 1937; Wilson 2001
Papaya	Cook, 1972; Gonsalves & Trujillo, 1986
Soybean	Golnaraghi *et al*., 2001
Artichoke	Garcia & Feldman, 1978

The principal ornamental hosts are: *Alstroemeria, Anemone, Antirrhinum, Araceae, Aster, Begonia, Bouvardia Calceolaria, Callistephus, Celosia, Cestrum, Columnea, Cyclamen, Dahlia, Dendranthema x grandiflorum, Eustoma, Fatsia japonica, Gazania, Gerbera, Gladiolus, Hydrangea, Impatiens, Iris, Kalanchoe, Leucanthemum, Limonium, Pelargonium, Ranunculus, Saintpaulia, Senecio cruentus, Sinningia, Tagetes, Verbena, Vinca* and *Zinnia* (listed by Chatzivassiliou *et al*., 2000b; EPPO/CABI, 1997; EPPO, 1999; Ochoa *et al*., 1999;). Many weeds are also hosts and are important as inoculum reservoirs (Cho *et al*., 1986; Groves *et al*., 2002; Hobbs *et al*., 1993; Latham & Jones 1997; Pappu *et al*., 2009; Stobbs *et al*., 1992; Wilson, 1998). Nearly all greenhouse crops appear to be susceptible to TSWV, with the possible exception of roses and poinsettias (Edmunds & Pottorof, 2011).

Most host species of TSWV are annual or biennial, however a number of perennial hosts have been identified (Chatzivassiliou *et al*., 2001; Groves *et al*., 2002; Mertelík *et al*., 1996). Locally abundant perennial species may serve as important, long-lasting TSWV inoculum sources for vector thrips (Jericho, 2005). Weed hosts in Australia acting as major sources of inoculum are capeweed (*Arctotheca calendula*) and sowthistle (*Sonchus oleraceus*) (Cooke *et al*., 2009). The extreme polyphagy of vector thrips is an important factor that contributes to the wide host range of TSWV.

Symptoms of TSWV

The symptoms of TSWV are highly variable across plant species (German *et al*., 1992; Goldbach & Peters, 1996; Latham & Jones, 1996; Mandal *et al*., 2006; Roselló *et al*., 1996), within species under different environmental conditions (Díaz-Pérez *et al*., 2007; Llamas-Llamas *et al*., 1998; Jericho, 2005; Soler *et al*., 1998), and particularly depending on plant age at the time of infection (Mandal *et al*., 2007; Moriones *et al*., 1998; Soler *et al*., 1998; Wilson, 2001). TSWV symptoms differ in type, severity and extent, ranging from local chlorotic and necrotic lesions in hypersensitive responses, to irregular chlorotic and necrotic areas, ring spots, necrotic streaks, line patterns, stunting, mottling and wilting when the virus is translocated systemically through the plant (Jericho, 2005; Persley *et al*., 2007). Other symptoms can include bronzing, curling, dark brown streaks on leaf petioles and stems, stunting and cessation of growth (Persley *et al*., 2007). Sensitivity to TSWV can vary markedly across genotypes and cultivars. Symptoms in some genotypes can be conspicuous and result in severe damage, whereas others under similar conditions might only develop mild symptoms, affecting only some parts of the plant. This has been shown in capsicum (Hobbs *et al*., 1994; Mandal *et al*., 2006), peanut (Riniker *et al*., 2008), tobacco and tomato (Mandal *et al*., 2006), and potato (Jericho, 2005; Wilson, 2001); Symptom expression can also differ

depending on the strain of TSWV that infects the plant. This has been shown in tomato (Ciuffo *et al*., 2005), *Capsicum* (Roggero *et al*., 2002), potato (Best & Gallus 1955; Norris 1946, 1951a), tobacco (Mandal *et al*., 2006), and peanut (Mandal *et al*., 2006).

TSWV symptoms in potato

Norris & Bald (1943) and Norris (1951a, 1951b) provided early descriptions of symptoms of TSWV infection in potato. Symptoms in potato also vary according to cultivar (Wilson, 2001). On shoots in susceptible cultivars like Shepody (Wilson, 2001) and Riverina Russets (Jericho & Wilson, 2003), conspicuous brown blotches and ring spots may occur (Jericho, 2005) (Fig. 1.1). Further development may see spots develop into larger areas of necrosis, leading to early leaf death. Symptoms in other cultivars include leaf chlorosis, distortion and severe stunting of the whole plant (Jericho, 2005) (Fig. 1.2). Symptoms of TSWV in most susceptible potato cultivars tend to become less conspicuous as plants mature, in part due to a level of mature plant resistance (Jericho, 2005; Norris, 1951a; Wilson, 2001). TSWV symptoms in potato are easily mistaken for early blight, caused by *Alternaria solani* (Norris, 1951a; C. Wilson, personal communication, 2005). Misdiagnosis is common, and can lead to an underestimation of disease incidence, and consequently, inappropriate control responses (Jericho, 2005). Localised necrotic lesions are sometimes observed around areas of feeding by viruliferous thrips. As infections develop, brown streaks may appear on petioles, veins and stems (Costa & Hooker, 1983; Norris, 1951a).

Figure 1.1 Ringspots and necrosis in TSWV-infected potato leaves
(cv. Sheopdy – left, cv. Atlantic – right)

Figure 1.2 Severely stunted potato plant caused by TSWV-infection.
Most leaves on the lower parts of stems are shrivelled and desiccated following severe chlorosis/necrosis.

Symptoms in tubers vary, and are also highly dependent on the level of virus translocation from leaf to tuber, with some cultivars possessing an overall susceptibility

to infection, but good resistance to translocation of TSWV (Wilson, 2001). Russet Burbank is one potato cultivar with good translocation resistance, where foliage infections usually result in no visible effects on the tubers, particularly if the TSWV infection is late and after tuber initiation (C. Wilson, personal communication, 2005). When potato tubers are infected, symptoms range from no visual symptoms, to small spots and patches of discoloured flesh, to large orange- to dark brown necrotic patches (Wilson, 2001). As these patches expand they tend to form a ring of discoloured flesh towards the outer parts of the tuber, but as infections increase in severity, this patchy brown discolouration spreads throughout the tuber (Fig. 1.3). Cracked, pitted or distorted tubers may also be present (Jericho, 2005; Norris 1951a, 1951b), although no such symptoms were observed during this study. Wilson (2001) has stated that such symptoms of malformation may be observed following foliar TSWV, without necessarily requiring tuber infections to be present. Even minor tuber symptoms can render potatoes unsuitable for processing or consumption.

Figure 1.3 Discolouration and necrosis in TSWV-infected potato tubers cv. Atlantic.

Thrips vectors of Tomato spotted wilt virus

Description and lifecycle

Thrips are minute, slender-bodied, fast-moving hemimetabolous insects, and may be winged or wingless. They range in size from 0.5 to 15 mm in length (mostly 1-2 mm). The adults have simple or forked emergent sense cones on antennal segments III & IV, and the number of antennal segments varies from 6 to 9 (usually 7 or 8). Thrips have

two pairs of slender wings; in the Terebrantia the forewings each with two longitudinal veins in addition to the costal vein, but without veins in the Tubulifera. The wings have a ciliated fringe (Thysanoptera means fringe-winged) and are covered in microtrichia. However, in some species the adults of one or both sexes are wingless. The legs of thrips end in 1-2 tarsal segments, with an adhesive arolium (bladder) at the pretarsus. The arolium is eversible, meaning it can be turned out using haemolymph pressure, enabling thrips to grip smooth surfaces (Lewis, 1997a). The mouth parts of adult thrips are asymmetrical, with only one mandible (the right mandible being vestigial or absent), which is used to puncture the cell walls of host tissue, through which the paired maxillary stylets can be inserted to inject digestive enzymes and suck out the cell contents. General introductions to the Thysanoptera; and reviews of thrips structure, biology and phylogeny include Lewis (1973) and Mound *et al*. (1980). Of particular note is the important work on the morphology and functional anatomy of thrips by Heming (1970a, 1970b, 1972, 1975, 1978, 1980).

The Thysanoptera are divided into two suborders: the Terebrantia, and the Tubulifera. The Tubulifera are identified by their characteristic tube-shaped apical abdominal segment and three non-feeding quiescent stages (prepupa and two pupal stages). Females of the Terebrantia have a saw-like ovipositor on the ante-apical abdominal segment and have only two non-feeding stages (prepupa and pupa). Thrips deposit their eggs into plant tissue and eggs hatch after 2-3 days, depending on temperature and plant host species. There are two larval feeding stages. The life cycle takes about 20-30 days from egg to adult, again depending on temperature. The number of lifecycles per year also depends on prevailing temperatures. In the greenhouse, thrips species may sometimes be found year-round. In more variable climates, thrips overwinter as adults in weeds, grasses, plant debris on the ground and other protected places until warmer conditions return in Spring, when adults can fly to preferred host species to lay eggs (Cho *et al*., 1995; Larentzaki *et al*., 2007).

The only known vectors for all Tospoviruses are found in the family Thripidae, within the suborder Terebrantia (Best, 1965). There are about 4500 described species within the Thysanoptera (Mound *et al*., 1980), of which only 450 are known from Australia. About 1750 species are recognised in the family Thripidae, with some 200 species present in Australia (Mound & Gillespie, 1997). Thrips have been found in all parts of the world from Greenland to the Sub-Antarctic Islands. Despite the number, wide host range and geographical extent of thrips species, only nine species worldwide are known to transmit TSWV: *Thrips tabaci* Lindeman (Wijkamp *et al*., 1995), *T. setosus* Moulton (Tsuda *et al*., 1996), *Frankliniella occidentalis* Pergande (Medeiros *et al*., 2004; Nagata *et al*., 2004,

Wijkamp *et al*., 1995), *F. schultzei* Trybom (Sakimura, 1969; Wijkamp *et al*., 1995), *F. fusca* Hinds (Naidu *et al.*, 2001; Sakimura, 1963b), *F. bispinosa* Morgan (Avila *et al*., 2006), *F. intonsa* Trybom (Wijkamp *et al*., 1995), *F. cephalica* Crawford (Ohnishi *et al*., 2006) and *F. gemina* Bagnall (de Borbón *et al*., 1999). Five other thrips species (*T. palmi, Ceratothripoides claratris, F. zucchini, Dictyothrips betae* and *Scirtothrips dorsalis*) transmit tospoviruses, but not TSWV (Riley *et al*., 2011). Other important studies and reviews discussing the vector competence of these species include German *et al.* (1992), Jones (2005), Mound (1996), Mumford *et al.* (1996), Nagata and de Ávila (2000), Nagata and Peters (2001); Persley *et al*. (2006); Ullman *et al.* (1997), and Ullman *et al*. (2002).

Three species of TSWV-vector thrips, all introduced, are found in Australia: onion thrips, *Thrips tabaci* Lindeman; tomato thrips, *Frankliniella schultzei* Trybom; and western flower thrips, *Franliniella occidentalis* (Pergande) (Austin *et al*., 2004; Malipatil *et al*., 1993; Mound, 1996, 2004), but only *T. tabaci* and *F. shultzei* are usually associated with potato crops in Southern Australia. These species are also particularly important vectors of multiple plant viruses in many regions of the world besides Australia (Riley *et al*., 2011; Ullman *et al*., 1997). *T. tabaci* is the only species in this group that is present in field crop production in Tasmania (Wilson, 2001). In this study, identification of species was conducted using the descriptions of Mound & Walker (1982) and *Pest Thrips of the World* (Moritz *et al*., 2004a).

Thrips tabaci

Adults of *T. tabaci* are approximately 2 mm in length and variable in colour, ranging from pale yellow, typically seen in warmer seasons, to brown in colder climates (Fig. 1.4). The wings are pale, and when at rest, the wings are laid over the abdomen and extend slightly past it. The nymphs are similar in shape but smaller in size and pale yellow in colour. The forewings are pale with major setae brown. The head is wider than long; ocellar setae III on anterior margins of ocellar triangle; ocelli are grey in colour. Antennae are 7-segmented; antennal segments III-V are bicoloured. The pronotum has three pairs of posteromarginal setae. The metanotum has slender elongate reticles medially; median setae not at anterior margin. The forewing has four (rarely five or six) setae on the distal half of the first vein. On tergite VIII the posteromarginal comb is long and fine; tergite IX has only one pair of dorsal porers (anterior pair absent). Pleurotergal lines of sculpturing with numerous fine, ciliate microtrichia are present. Sternites are without discal setae. (Mound & Walker, 1982). The male of the species is wingless and is rarely found. To date, no males of this species have been recorded in Australia (L. Mound, CSIRO, personal communication, 2005).

Figure 1.4 *Thrips tabaci* female

from Mound *et al*. (2009)

Frankliniella occidentalis

Adults of *F. occidentalis* are usually yellowish to bicoloured, with distinctive tergal markings (brown bars) on a yellow-brown background, with darker forms also observed (Fig. 1.5). Rugman-Jones *et al*. (2010), using nuclear-mitochondrial barcoding, suggested that *F. occidentalis* may be a complex of two sympatric, cryptic species, also observing that darker specimens were more likely to be identified as one species than the other. The legs are typically yellow with brown markings. Antennal segment I is yellow, II dark, III mainly yellow, IV and V brown with a yellow base, and VI-VIII brown. The forewings are pale with major setae brown. The head is slightly wider than long; ocellar setae pair I just in front of the first ocellus; pair III long, just inside anterior margins of ocellar triangle; one pair of postocular setae long. The antennae are 8-segmented; with segments III and IV each with a forked sense cone. The pronotum has four pairs of elongate setae and five pairs of posteromarginal setae of which the submedian pair is longer than the rest. The metanotum has elongate median setae at the anterior margin. The tarsi are 2-segmented. The forewings have two complete rows of setae. Tergites IV-VIII have paired ctenidia laterally; tergite VIII with the ctenidia anterolateral to the spiracles, and posterior margin with a complete comb of fine microtrichia, each arising from a broad, triangular base. The male is similar to the female, but without a comb on tergite VIII, and with a transverse glandular area on sternites III-VII. (Mound & Walker, 1982).

Figure 1.5 *Frankliniella occidentalis* female of common pest form

from Mound *et al*. (2009)

Frankliniella schultzei

F. schultzei exists as two different, but anatomically similar, colour morphs, a dark and a pale form (Mound, 1968; Sakimura, 1969). Only the dark form is present in Australia and adults are dark brown in colour (Fig. 1.6). The antennae are 8-segmented; III and IV with forked sense cone, VIII longer than VII. The head is wider than long; three pairs of ocellar setae are present, pair III arising close together between anterior margins of posterior ocelli. The pronotum has five pairs of major setae, with anteromarginal setae slightly shorter than anteroangular setae, and one pair of minor setae present medially between posteromarginal and submedian setae. The metanotum has two pairs of setae at the anterior margin, with campaniform sensilla absent. The forewings have two complete rows of veinal setae. Tergites VI-VIII have a pair of lateral ctenidia, on VIII anterolateral of the spiracle; with posteromarginal comb on VIII not developed. Sternites III-VII are without discal setae. The male is similar to the female but smaller. *F. schultzei* is exceptional in the genus because of the close placement of ocellar setae III within the ocellar triangle.

Figure 1.6 *Frankliniella schultzei* female of dark form.

from Mound *et al*. (2009)

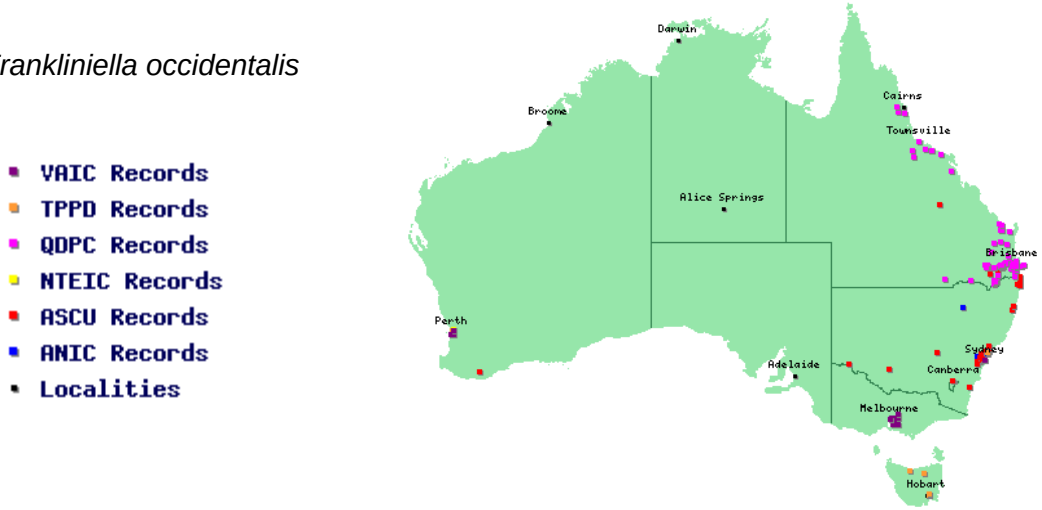
Distribution

TSWV outbreaks in tomatoes and potatoes in the first half of the 20th century in Victoria, South Australia, and New South Wales have been attributed to *T. tabaci* and *F. schultzei* (Conroy *et al.*, 1949; Magee, 1936; Norris & Bald 1943; Norris 1951a & 1951b; Pittman 1927; Samuel *et al.*, 1930). *F. occidentalis* was recorded for the first time in Australia in 1993, in *Chrysanthemum* crops south of Perth, Western Australia (Malipatil *et al.*, 1993). It was found shortly thereafter in other parts of the country, with occasional TSWV infections in potato in Western Australia associated with *F. occidentalis* (Latham & Jones, 1997). *Thrips tabaci* and *F. schultzei* were also recorded in the potato growing areas in Western Australia (Thomas & Jones, 2000), and on potato in South Australia and Victoria (Jericho & Wilson, 2003). *T. tabaci, F. schultzei* and *F. occidentalis* were found in New South Wales (Clift & Tesoriero, 2002). In Tasmania, *T. tabaci* is the only known vector trapped in open cultivation (Jericho, 2005; Jericho & Wilson, 2002; Wilson, 1998). In Tasmania, low level infestations of *F. occidentalis* in protected cultivation within cut flower operations and wholesale nurseries have existed since 1995 (Hill, 2003), and are occasionally detected outside on flowering plants that have been purchased from these nurseries, but this species has never established permanently away from these nursery sources (Davies & Westmore, DPIPWE, unpublished data, 2010).

The rapid geographic spread of TSWV in many crop systems during the 1990s has been attributed to the higher efficiency of TSWV transmission by *F. occidentalis* (German *et al.,* 1992; Goldbach & Peters 1996; Roselló *et al.,* 1996; Ullman *et al.,* 1997; Wijkamp *et al.,* 1995). In Australia, the introduction and subsequent spread of *F. occidentalis* (Malipatil *et al*., 1993) is thought to be a factor in the exacerbation of TSWV epidemics (Ullman *et al.,* 1997). In response, a national strategy for the management of *F. occidentalis* and TSWV was formed in the 1990s, along with several other projects funding research into managing the pest on specific crops, funded through the Horticultural Research and Development Corporation (HRDC). However, potato is not a preferred host of *F. occidentalis*, and *F. occidentalis* has not been found in many instances of TSWV epidemics in potato, although some outbreaks have been attributed to *F. occidentalis*. This is especially the case in Tasmania, where *F. occidentalis* has never been identified on potato. Consequently *T. tabaci and F. schultzei* are the most important vectors in potato cropping regions (Groves *et al.,* 2001, 2002; Wilson 1998, 2001). The most up-to-date (December, 2011) known distributions based on specimen records for each of these species from the Australian Plant Pest Database (Plant Health Australia, 2001), is presented in Fig. 1.7.

(a) *Thrips tabaci*

(b) *Frankliniella occidentalis*



(c) *Frankliniella schultzei*

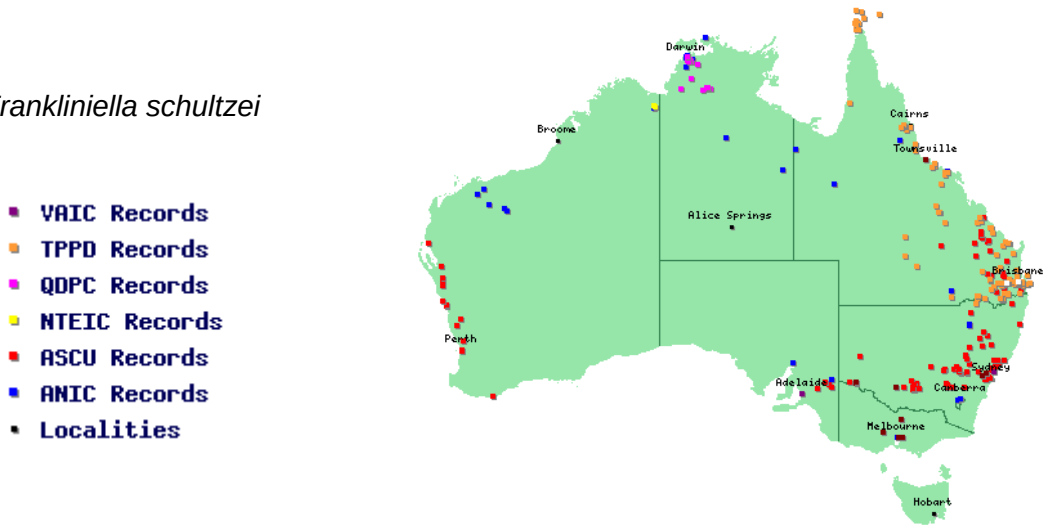


Figure 1.7 Australian distribution maps to December, 2011 (Plant Health Australia, 2001) for: (a) *T. tabaci*, (b) *F. occidentalis* and (c) *F. schultzei*.

Host range

The extreme polyphagy of thrips provides a wide host range for feeding and reproduction (Adkins & Rosskopf, 2002; Chatzivassiliou *et al*., 1996; 2000a, 2001; Cho *et al*., 1986; Cook *et al*., 2011; Groves *et al*., 2001, 2002; Hobbs *et al*., 1993; Johnson *et al*., 1995; Lewis, 1997a; Mertelík *et al.*, 1996; Mound & Teulon, 1995; Mound, 1997; Ochoa *et al.,* 1999; Stobbs *et al*., 1992; Terry, 1997; Ullman *et al*., 1997; Wijkamp *et al*., 1995; Wilson 1998a). The list of host species that act as TSWV reservoir hosts, as well as feeding and reproductive hosts for thrips, includes annual and perennial crops, weeds, flowers and ornamentals (Bautista *et al*., 1995; German *et al.*, 1992; Lewis *et al*., 1997c; Mertelík. *et al*., 1996; Mound, 2002; Ochoa *et al.*, 1999; Peters, 1998; Stobbs *et al*., 1992; Teulon *et al.,* 1993; Teulon & Penman*,* 1996; Yudin *et al*., 1986). *T. tabaci* in particular is highly polyphagous (Cook *et al*., 2011), feeding on grasses and broad-leaved plants, including many vegetable and fruit crops (Groves *et al.,* 2002; Terry, 1997; Ullman *et al*., 1997). While thrips damage plants through feeding, which is particularly important in the ornamental and cut flower industries, the focus of most host studies has been on host susceptibility to TSWV and the epidemiology of the disease in each host (Herrin & Warnock, 2002; Roselló *et al*., 1996; Ullman *et al*., 1997; van de Wetering *et al.,* 1998).

Dispersal

Thrips dispersal varies with species, host and environmental conditions (Hsu *et al*., 2010; Morsello *et al*., 2008, 2010). Thrips may move between plants within one host or between hosts in a single day; they may also spend several generations on one host. *Thrips tabaci* and *F. occidentalis* exhibit changing patterns of dispersion through the day, with aggregation on leaves during afternoons (Matteson & Terry, 1992, Sites *et al*., 1992). This has a large impact on the suitability of sampling protocols; sampling at certain times of the day may yield few thrips, while later sampling may detect much higher numbers.

Thrips are weak fliers, but have been observed dispersing over long distances between crops (Lewis, 1997b). Dispersal is particularly high during the warmest part of the season (Morsello *et al*., 2010; Teulon & Penman, 1996), which might be explained by higher activity levels and/or the need to find new hosts as crops mature and dry. Long distance dispersal on high altitude winds has also been observed (Lewis, 1997b). Most introductions of exotic species into new cropping areas and new geographical regions are predominantly as a result of unintentional human transportation (Mound, 1983). There is considerable movement of local species across the landscape in the transportation of fruit and vegetables (L. Hill, DPIPWE, personal communication, 2010).

Long distance wind-mediated dispersal is particularly important in understanding the spread of TSWV epidemics in southern Australian cropping regions, particularly with regard to the sporadic nature of outbreaks (Jericho, 2005). Many cropping areas, including potato, in southern Australia, are under pivot irrigators in otherwise dry areas. This is particularly so for potato cropping in South Australia, NSW and areas of northern Victoria, but not in Tasmania where 'green bridges' between cropping areas are usually present during the potato growing season. In drier areas, as crops mature, thrips need to disperse and travel long distances, utilising wind currents, in order to find new hosts that are still green, although in these circumstances individual thrips may have little control over their flight path and destination (Lewis, 1997b). This can lead to large influxes of viruliferous thrips into a new crop. Whereas TSWV infections in large potato crops in Tasmania tend to begin on crop borders, infections in drier areas often face large outbreaks with TSWV spread throughout the crop (C. Wilson, personal communication, 2005). This difference could be explained by greater incidence of long distance wind-mediated dispersal between 'green islands' in dry farming areas, compared to graduated movement across a green landscape in wetter farming areas.

Acquisition and transmission

The interactions between thrips and TSWV and the movement of the virus through the thrips have been extensively reviewed (de Assis Filho *et al.,* 2002; Bandla *et al.,* 1998; Chatzivassiliou *et al*., 1998a; de Assis Filho *et al.,* 2002; German *et al.,* 1992; Goldbach & Peters, 1996; Kikkert *et al.,* 1997; Kritzman *et al.,* 2002; Nagata & Peters, 2001; Reitz, 2009; Roselló *et al.,* 1996; Sakimura, 1963a; Ullman, 1996; Ullman *et al.,* 1993, 1995, 1997; Whitfield *et al*., 2005), although there is still much that is not well understood (de Assis Filho *et al.,* 2002; Nagata & Peters 2001; Ullman *et al.,* 1997). Thrips acquire TSWV from an infected host as early first instar larvae, after puncturing plant cells and feeding on sap containing virion particles. Some findings limit acquisition potential to first instar larvae (van de Wetering *et al.,* 1996), while other studies have found that some populations can acquire TSWV as early second larval instars (Ullman *et al.,* 1997; van de Wetering *et al.,* 1999). The virus can be acquired during periods of feeding as short as five minutes, but thereafter follows a latent period during which the thrips is not yet able to transmit the virus. After the virus replicates within the thrips and is transported to the salivary glands, transmission becomes possible at the second larval instar or adult stage (Sakimura 1963a; Ullman *et al.,* 1993; Wijkamp *et al.,* 1993). The virus can then be transmitted again during a similarly short feeding period. The ability to acquire TSWV is lost at the second instar stage or later (Ohnishi *et al.,* 2001; Ullman *et al.,* 1992; Whitfield *et al*., 2005).

Virion particles enter cells in the proximal mid-gut region in both *F. occidentalis* and *T. tabaci,* before spreading to adjacent mid-gut cells and the muscle cells surrounding the mid-gut (Ullman *et al*., 1993). The second and third mid-gut regions are then infected, and the virus is released into the haemocoel and secondarily infects other tissues, replicating to high titres (de Assis Filho *et al.,* 2002; Kritzman *et al*., 2002; Nagata *et al.,* 1999; Tsuda *et al.,* 1996). The virus moves to the salivary glands only while there is direct contact between mid-gut muscle cells and the salivary glands during the first and possible early second instar stage (Moritz *et al*, 2004b). After this time the salivary glands move away from the mid-gut. The virus is then transmitted to a new host via salivation during feeding (Ullman *et al.,* 1993, 1995; 1997). The virus must traverse at least six membrane barriers for transmission to occur (Whitfield *et al*., 2008). The virus is passed transtadially (i.e. persisting through moults from larval to adult stage). Consequently, viruliferous thrips remain infective for life (Wijkamp *et al.,* 1996), which may be three to six weeks depending on environmental conditions (Goldbach & Peters, 1996). TSWV is not passed transovarially to progeny (Sakimura 1963a; Wijkamp *et al.,* 1996).

The ability of different life stages of thrips to vector TSWV may be due to genetic elements both within the vector and the virus (Bandla *et al.,* 1998; Kikkert *et al.,* 1998; Nagata *et al.,* 2000; Sin *et al.,* 2003; Ullman *et al.,* 1993, 1995). While a great deal has been made of the genetic differentiation of thrips in this regard, it has also been demonstrated that genetic differences between TSWV strains are involved, as numerous studies have now shown that transmission efficiency varies with strain in a number of different thrips species (Jenser *et al*., 2002; Jones 1959; Nagata *et al*., 2000; Naidu *et al*., 2003, 2008; Paliwal 1974, 1976; Sakimura 1963a; van de Wetering *et al*., 1996; Wijkamp *et al.,* 1995). Nagata *et al*. (2000) found that TSWV may survive and even replicate in some vector thrips species, even though transmission does not occur. Differences in the envelope membrane glycoproteins, G_N and G_C may contribute to transmission variability, connected to their lectin-binding properties and glycosidase sensitivities (Naidu *et al.,* 2003, 2004; Whitfield *et al*., 2004). They may also be due to altered genome structure, arising from deletions in lipid envelope membranes, or the accumulation of defective interfering RNAs, which may affect particle stability by altering protein-protein or RNA-protein interactions (Sin *et al.,* 2003).

Changes in host virus titre can alter the chances of a vector acquiring and transmitting a virus and, thus, may influence disease epidemics (van de Wetering *et al*., 1998). Subsequent virus titre in the thrips vector also influences transmission (Rotenburg *et al*., 2009). The viral NSm protein facilitates the cell-to-cell spread of the viral genome

through structurally modified plasmodesmata (Gunasinghe & Buck, 2003; Paape *et al*., 2006). The movement of the virus through the plant is influenced by host species (Garg & Khurana, 1999; Kikkert *et al*., 1999; Llamas-Llamas *et al*., 1998), cultivar (Aramburu & Martí, 2003; Wilson, 2001) and growth stage (Soler *et al*., 1998). The rate of virus translocation may be greater in sensitive varieties compared to those that are more tolerant (Maris *et al*., 2003b; Moury *et al*., 1997; Soler *et al*., 1998, 1999; Wilson, 2001). Systemic movement is also affected by temperature (Llamas-Llamas *et al*., 1998; Moury *et al*., 1998; Soler *et al*., 1998) and water stress (Córdoba *et al*., 1991). The efficiency with which different strains of TSWV are transmitted depends in part on differences in vector competence between thrips species (Nagata *et al.,* 2002; Wijkamp *et al.,* 1995) and within populations of single thrips species (Sakurai *et al.,* 2002; van de Wetering *et al.,* 1999), and also by the quality of acquisition and inoculation hosts (Chatzivassiliou *et al*., 1999; Norris 1951a; Sakimura 1963b; Wijkamp *et al.,* 1995).

Vector competence

It was originally reported that *T. tabaci* transmitted all known isolates of TSWV worldwide (Sakimura, 1962). However, virus transmitters and non-transmitters within vector populations have been reported by many researchers over a long period of time (Cabrera-La Rosa & Kennedy, 2007; Chatzivassiliou *et al*., 1998a, 1999, 2001, 2002; Jacobson & Kennedy, 2010; Jenser *et al*., 2002; Jericho, 2005; Jones 1959; Karadjova & Krumov, 2008; McPherson *et al.,* 1999; Nagata *et al.,* 2002; Paliwal 1974, 1976; Wijkamp *et al.,* 1995). Important early studies documenting non-transmission include those of Jones (1959), Sakimura (1963a), and Paliwal (1974, 1976). Despite *T. tabaci* being considered the main vector of TSWV for a long period of time, even when other vectors, such as *F. occidentalis*, became known, its failure to transmit some TSWV isolates more recently has raised doubts about its vector competence (Chatzivassiliou *et al*., 1999, 2001; Wijkamp *et al*., 1995). Studies have shown that some populations can transmit some TSWV isolates, but the efficiency of transmission is relatively low and there is considerable variation between populations (Cabrera-La Rosa & Kennedy, 2007; Chatzivassiliou *et al*., 1999; Wijkamp *et al*., 1995).

Populations of *T. tabaci* have exhibited low efficiency and variability of TSWV transmission, and in some cases zero transmission, in regions of North America and Europe (Chatzivassiliou *et al*., 1998a, 1999, 2001, 2002; Jones 1959, Karadjova & Krumov, 2008; McPherson *et al.,* 1999; Paliwal 1974, 1976; Wijkamp *et al.,* 1995), South America (Nagata *et al.,* 2002), Australia (Jericho, 2005), and Hawaii (Mound, CSIRO, personal communication, 2005). Many possible explanations for this variability in transmission or even loss of vector competence have been presented. TSWV and/or *T.*

tabaci may have evolved to the extent that they have become incompatible (German *et al.,* 1992; Jenser *et al.,* 2002). Incompatibilities have also been correlated with the absence of males in *T. tabaci* populations (Chatzivassiliou *et al*., 1998a; Wijkamp *et al.,* 1995). In the last twenty years, with the global spread of *F. occidentalis*, a more uncontrollable pest and more efficient vector than *T. tabaci*, the displacement of TSWV isolates transmitted by *T. tabaci*, with those transmitted by *F. occidentalis* has also been suggested (Nagata & Peters 2001; Ullman *et al.,* 1997).

TSWV has spread across the world in many crops over the last two decades and this has been attributed to the efficient vectoring capacity of *F. occidentalis* (German *et al.,* 1992; Goldbach & Peters 1996; Roselló *et al.,* 1996; Ullman *et al.,* 1997; Wijkamp *et al.,* 1995). In Australia, the introduction and subsequent spread of *F. occidentalis* (Malipatil *et al*., 1993) has contributed to this (Ullman *et al.,* 1997). However, *T. tabaci* is still the dominant vector in some crops in some regions. *T. tabaci* is responsible for all TSWV outbreaks in potato and lettuce fields in southern Tasmania (Jericho, 2005; Jericho & Wilson, 2003; Wilson 1998a, 1998b, 2001) and is the main vector in tobacco in Eastern Europe when other vector species were not present (Chatzivassiliou *et al.,* 1998a, 1999; Jenser *et al*., 2002; Nagata & Peters 2001; Sakimura 1963a; Zawirska 1976). Despite *T. tabaci* being the first reported vector of TSWV, and remaining the primary vector of TSWV in tobacco crops in Eastern Europe and the Mediterranean region, its significance as a TSWV vector in other areas is now localised, with large variation among *T. tabaci* populations in their ability to transmit TSWV (Jacobson & Kennedy, 2010).

In Australia, early outbreaks of TSWV in potatoes and tomatoes in South Australia, New South Wales and Victoria, were attributed to *T. tabaci* and *F. schultzei* (Conroy *et al.*, 1949; Magee, 1936; Norris & Bald, 1943; Norris, 1951a, 1951b; Pittman, 1927; Samuel *et al.*, 1930). Sporadic infections in potato in Western Australia have been associated with *F. occidentalis* (Latham & Jones, 1997). *T. tabaci* and *F. schultzei* have also been recorded on potato in the same State (Thomas & Jones, 2000). Surveys in Victoria and South Australia recorded *T. tabaci* and *F. schultzei* on potato (Jericho & Wilson, 2003). In New South Wales, *T. tabaci, F. schultzei* and *F. occidentalis* were found (Clift & Tesoriero, 2002). Broughton & Herron (2007) reported severe outbreaks of TSWV in potato in South Australia, but did not specify the vector. In Tasmania, all TSWV outbreaks have been attributed to *T. tabaci* due to the absence of other vectors in field crops (Jericho and Wilson, 2002; Wilson, 1998). The low level infestations of *F. occidentalis* in protected cultivation and some of Tasmania's wholesale nurseries have never spread to field crops, and up to this point in time have not been associated with any TSWV infections (L. Hill, DPIPWE, personal communication, 2011).

Studies have been conducted on how aspects of thrips feeding behaviour affects vector competence (Harrewijn *et al*., 1996; van de Wetering *et al*., 1998; van de Wetering, 1999), particularly in relation to feeding differences between male and female thrips (van de Wetering *et al*., 1998). Differences in feeding behaviour between males and females of *F. occidentalis* have been exhibited on petunia leaf disks (van de Wetering *et al*., 1998). This study found that females fed more frequently and intensively than males, however TSWV was transmitted more efficiently by males. Higher virus transmission by males of *F. occidentalis*, with lower accumulation thresholds, was also found by Sakurai *et al.* (1998, 2002).

Low or non-transmissability of some TSWV strains by vector thrips has been reported (Jenser *et al*., 2002; Jones 1959; Maris *et al*., 2003a; Norris 1951a, 1951b; Paliwal 1974, 1976; Roca *et al.*, 1997; Sakimura 1963a; Wijkamp *et al.,* 1995). This specificity in transmission makes some vector species more important in some regions, although no significant molecular differences have been observed among TSWV strains in Australia (Dietzgen, 2003; Talty & Dietzgen, 2001). But some molecular differences must exist due to the discovery of resistance-breaking strains (Latham & Jones, 1998). The rate of transmission of different TSWV isolates is facilitated and affected by the distinct transmission specificity between (Nagata *et al.,* 2002; Wijkamp *et al.,* 1995) and within vector species (Sakurai *et al.,* 2002; van de Wetering *et al.,* 1999).

Other factors are also important. The level of virus titre in the host affects the chances of a vector acquiring, and therefore transmitting TSWV. Virus titre is determined by the level of viruliferous thrips feeding on the host, and host sensitivity or tolerance to TSWV (Maris *et al*., 2003b; Moury *et al*., 1997; Soler *et al*., 1998, 1999), including the extent to which the virus is systemically translocated (van de Wetering *et al*., 1998). Systemic movement of TSWV in plants is mediated by the viral NSm protein (Gunasinghe & Buck, 2003) and is influenced by host species (Garg & Khurana, 1999; Kikkert *et al*., 1999; Llamas-Llamas *et al*., 1998), variety (Aramburu & Martí, 2003; Jericho, 2005; Maris *et al*., 2003b; Moury *et al*., 1997; Soler *et al*., 1998, 1999; Wilson, 2001), growth stage (Jericho, 2005; Soler *et al*., 1998), temperature (Jericho, 2005; Llamas-Llamas *et al*., 1998; Moury *et al*., 1998; Soler *et al*., 1998), and water stress (Córdoba *et al*., 1991). Cross-interactions between these factors may also affect infection success, translocation of the virus, and therefore the efficiency with which thrips acquire the virus (Jericho, 2005).

The ability to transmit TSWV is thought to be governed by factors such as thrips preference for and performance on hosts (Allen & Broadbent, 1986; Bautista & Mau 1994; Bautista *et al.,* 1995; Chatzivassiliou *et al.,* 1998b, 1999, 2001, 2002; de Kogel, 2002; Maris *et al.,* 2003a; Sakimura 1963b; Sakurai *et al.,* 2002; Wijkamp *et al.,* 1995), thrips development stage (Inoue *et al.,* 2002; Moritz 2002), host phenological stage (Inoue *et al.,* 2002), temperature (Chatzivassiliou *et al.,* 2002; Wijkamp & Peters 1993), vector sex (Sakurai *et al.,* 1998, 2002; van de Wetering *et al.,* 1998; Wijkamp *et al.,* 1995), and geographic region (Roselló *et al.,* 1996; Sakimura 1963b). Vector sex is unlikely to be a paramount factor in Tasmania because bisexual populations of *T. tabaci* have still not been observed. However, this is not the case in mainland Australian States where *F. schultzei* and *F. occidentalis* are also vectors.

Distinct differences in host preference for, and reproductive performance on, different hosts has been demonstrated (Alimousavi *et al.*, 2007; Broadbent *et al*., 1990; de Jager *et al*., 1995a, 1995b; de Kogel *et al*., 1997; Herrin & Warnock, 2002; Leiss *et al.,* 2009; Loges *et al.*, 2004; Maris *et al*., 2003a, 2003b; Nugaliyadde & Heinrichs, 1984; Rahman *et al.,* 2010), including across potato cultivars (Jericho, 2005). Differences in transmission efficiencies in *T. tabaci* have been linked to trade-offs and performance on different hosts, for example on leek and tobacco, *Datura stramonium* and *Petunia hybrida* (Chatzivassiliou *et al*., 1999, 2002), and tomato (Nagata *et al.,* 2002). In transmission tests, Wijkamp *et al*., (1995) found distinct levels of specificity in thrips transmission of tospoviruses with *F. occidentalis* appearing to be the most efficient vector for TSWV.

Cabrera-La Rosa and Kennedy (2007) found that populations of *T. tabaci* differed significantly in their ability to transmit an isolate of TSWV collected from potato, and following reciprocal crosses between efficient and inefficient transmitting populations, determined that ability to transmit TSWV efficiently by *T. tabaci* is inherited as a recessive trait. Inoue and Sakurai (2006) suggested that long latent periods in *T. tabaci,* and the TSWV infection effect of reducing adult thrips survival, shortens the potential transmission period, which may be responsible for the low transmissibility of TSWV as well as the low transmission rate in thelytokous *T. tabaci* populations.

The factors affecting vector competency of *T. tabaci* is still an issue of debate. Contrasting findings on the ability of *T. tabaci* to transmit TSWV in different parts of the world have existed for decades and continue today. Several hypotheses have suggested that intra-species differences may explain the inconsistency of results from TSWV transmission studies. Diversity and biological variation among populations has been demonstrated (Brunner *et al*., 2004; Jenser *et al*., 2002; Mound 1997, 2004; Murai &

Toda, 2002; Zawirska, 1976). One theory put forward (Zawirska, 1976) is that the difference in *T. tabaci* transmission competencies is explained by *T. tabaci* being comprised of two taxonomically identical biotypes or subspecies; populations of *T. tabaci* subsp*. tabaci* being arrhenotokous, producing males and females, efficient vectors of TSWV and associated with tobacco (*Nicotiana tabacum*); with *T. tabaci* subsp*. communis* being associated with other hosts, such as leek, onion and potato (Harris *et al*., 2001)*. T. tabaci* subsp*. communis* is thelytokous and propagates parthenogenetically, producing females only and, it was suggested, does not vector TSWV (Chatzivassiliou *et al*., 2002; Wijkamp *et al*., 1995). However, more recently female-only populations from Australia have been shown to be capable of transmitting TSWV (Jericho, 2005), requiring some modification to this theory.

Brunner *et al*. (2004) posed three possibilities: *T. tabaci* might be (a) a single polyphagous species, (b) a complex of host races with partial genetic differentiation but ongoing gene flow, or (c) a complex of morphologically cryptic species no longer joined via gene flow. Their results present strong evidence for *T. tabaci* representing a complex of at least three taxa. Clustering analyses and haplotype networks based on sequence variation at a fragment of the mitochondrial cytochrome oxidase I gene produced three major evolutionary lineages; two associated with leek and the third with tobacco (Brunner *et al*., 2004). The findings suggested an ancient origin for the three major phylogenetic lineages, rejecting the idea that *T. tabaci* is a single cosmopolitan and polyphagous species. However, unfortunately this study was solely one of host-associated genetic differentiation, with no examination of vector competence of the different populations. More recently, Jacobson and Kennedy (2010) demonstrated that competency to transmit TSWV is associated with genetic variation among *T. tabaci* populations and among TSWV isolates.

The most extensive study of TSWV-transmission by *T. tabaci* in Australia prior to this study was conducted by Jericho (2005), upon which this study follows and builds. Jericho (2005) gave Tasmanian populations of *T. tabaci* collected from onion the opportunity to acquire TSWV from five hosts (potato, tomato, *Datura stramonium*, *Arctotheca calendula* and *Solanum nigrum*), and these thrips were presented with 10 transmission hosts (*Chenopdium album*, *A. calendula*, *S. nigrum* and seven potato cultivars). Despite virus titre in the accumulation hosts being high and feeding activity on each host confirmed, no virus transmission occurred, leading Jericho (2005) to conclude that the population had a TSWV-transmission competency of zero. Contrasting with these controlled experimental results, Jericho (2005) observed extensive TSWV-infections in potato crops in cultivar field trials in southern Tasmania, where the only

TSWV-vector is *Thrips tabaci*. Jericho (2005) discussed the possibility that the results could be due to the population biotype used in the controlled experiments, but rejected this as a possibility because of the belief that *T. tabaci* subsp*. communis* could not be a considered to be a virus vector. Other reasons put forward to explain the failure to transmit the virus were rearing and experimental temperatures, such as described by Chatzivassiliou *et al.* (2002), and fitness trade-offs due to serial feeding on certain hosts, such as was found by Chatzivassiliou *et al.* (1999) in leek and (Wijkamp *et al.,* 1995) in bean.

Thrips population dynamics

Thrips, like most phytophagous insects, locate hosts by responding to a range of stimuli, including visual, mechanical, gustatory and olfactory characteristics (Prokopy & Owens, 1983; Visser & Thiery, 1986). Colour, shape and olfactory cues are usually involved in an insect's initial orientation to a plant, whereas once an insect has alighted on the plant, acceptance or rejection, and the initiation of feeding is determined by texture as well as the presence or absence of specific chemicals stimulants or deterrents (Renwick, 1983). Differences in host preference by vector thrips at the cultivar level have been demonstrated (Herrin & Warnock, 2002; Jericho, 2005; Maris *et al*., 2003a). Many factors may be influencing host choice, such as plant chemistry, plant morphology and colour (Terry, 1997). Other factors, such as protection from predators and adverse environmental conditions, and the nutritive qualities of each plant host may also be important (Bernays & Graham 1988; Fry 1996; Joshi & Thompson 1995).

Resistance is usually divided into antibiosis and antixenosis. Antibiosis resistance refers to plant attributes, such as metabolites, which affect insect biology, such that insect pest abundance is decreased through reduced longevity, growth rates and/or reproduction, reducing subsequent damage to the host plant. Antixenosis resistance refers to the inability or reduced ability of a plant to act as a host, without affecting the biology of the insect. This is generally known as non-preference, and may be achieved through chemical, morphological, or structural means. Compounds or structures may reduce feeding through repellence, suppression or deterrence (Schoonhoven, 1982). Tolerance refers to the ability of a plant host to withstand or recover from insect feeding damage. Tolerance to thrips feeding is unlikely to be of much value in the thrips-host-virus tritrophic interaction. While tolerant biotypes that maintain strong production under high thrips feeding activity may exist, it is the transmission of TSWV that causes most damage.

Host preference and performance

Because TSWV can only be acquired by immobile first instar (and possibly early second instar) larvae, which must be able to complete their development on the host selected by the adult female, preference for and performance on TSWV-susceptible hosts is a critical aspect of TSWV disease epidemiology (Allen & Broadbent, 1986; Bautista & Mau, 1994; Chatzivassiliou *et al*., 2002; Duffus, 1971; Gray & Banerjee, 1999; Irwin & Ruesink, 1986; Jericho, 2005; Thresh, 1974; Wijkamp *et al*., 1995), yet understanding of factors affecting host plant resistance to thrips is still limited (Leiss *et al*., 2009). Host species and cultivar characteristics have been shown to influence vector population dynamics and vector competence (Wijkamp, 1995).

Once TSWV is established in susceptible commercial cultivars, virus spread within the crop, to intercrop hosts, and to new crops depends on whether the infected cultivars can support breeding colonies. Further spread of the virus to epidemic proportions, which may rely on secondary infections, will depend on the level of vector performance on the host crop (Duffus, 1971; Irwin & Ruesink, 1986; Thresh, 1974), although some studies have suggested that secondary spread is limited (Camann *et al*., 1995; Coutts *et al*., 2004; Gitaitis, 1998). Studies have shown that thrips exhibit distinct host cultivar preferences in potato (Jericho, 2005), lettuce (Yudin *et al*., 1988), capsicum (Maharijaya *et al*., 2011; Maris *et al*., 2003b), onion (Doederlein & Sites, 1993; Verma, 1966), cucumber (de Kogel *et al*., 1997a), *Chrysanthemum* (Broadbent *et al*., 1990), *Impatiens* (Herrin & Warnock, 2002) and rose (Gaum *et al*., 1994). Other studies to show variation in performance, behaviour and longevity of thrips, particularly *T. tabaci* and *F. occidentalis,* and hence ability to transmit TSWV across a range of host plant species, include Agrawal *et al*. (1999), Baez *et al*. (2011), Bautista *et al*. (1995), Bautista & Mau (1994), Chatzivassiliou *et al*. (2002); Delphia *et al*. (2007), Sakimura (1963b); Terry (1997); Ullman *et al.* (1997); and Wijkamp *et al*. (1995). Characteristics of host choice have been used to breed and select cultivars with reduced thrips preference in a range of crops, including onion (Alimousavi *et al.*, 2007; Loges *et al.*, 2004), *Chrysanthemum* (Broadbent *et al*., 1990; de Jager *et al*., 1995a, 1995b; Leiss *et al.,* 2009), cucumber (de Kogel *et al*., 1997a, 1997b); rice (Nugaliyadde & Heinrichs, 1984), strawberry (Rahman *et al.,* 2010), common bean (Frei *et al*., 2003) and *Capsicum* (pepper) (Maris *et al*., 2003b).

Plant morphology and growth habit

Morphological characters, such as leaf shape and canopy architecture have been shown to influence thrips success. Flat leaves and open plant architectures have been associated with reduced densities of *T. tabaci* (Coudriet *et al*., 1979; Patil *et al*., 1988).

Other host selection cues of thrips may include leaf waxiness (Hemmati & Benedictus, 2000; Nouri Moghaddam *et al*., 2004), leaf glossiness (Molenaar, 1984), and leaf trichome density (Scott Brown & Simmonds, 2006; Sedaratian *et al*., 2010). Plant traits may also influence thrips success indirectly, for example, trichome density may influence the abundance and effectiveness of natural enemies, such as predatory mites. Peterson (1990) found that the predation rate on thrips by *Amblyseius cucumeris* was significantly higher on smooth cucumber leaves than on hairy leaves. Gunasinghe (1988) showed that leaf trichome density needed to be above 1714/cm^2 to impede aphids on soybean so is unlikely to be a factor physically deterring thrips on potato. The leaf location on plants has also been correlated with the level of thrips resistance (de Kogel *et al*., 1997a, 1997b).

Plant nutrition

Nutritive qualities of a plant have been shown to affect host choice by and subsequent performance of thrips. Higher levels of soluble protein and other nitrogenous compounds in plants have been found to increase susceptibility to thrips (Scott Brown *et al.,* 2002), and be beneficial to thrips populations (Baez *et al*., 2011; Brodbeck *et al.*, 2001; Chen *et al*., 2004; Davies *et al*. 2005; Fennah, 1963; Hsu *et al*., 2010; Malik *et al*., 2009; Mollema & Cole, 1996; Schuch *et al*., 1998). Thrips' attraction to damaged tissue has been observed and linked to a response to the changing balance of plant nutrients (Kirk, 1997). Pollen in particular, at least from some plant species, has been found to have highly favourable effects on thrips fecundity (Brodbeck *et al.*, 2002; Tsai *et al.*, 1996).

Stressed plants can sometimes, counterintuitively, be more nutritious to thrips, due to breakdown of plant cells and the release of free amino acids (Mattson & Haack, 1987; White, 1984) and reduced synthesis of defensive chemicals (Rhoades, 1979). A relatively new and interesting area of study is the interference of plant defences against invertebrate pests due to pathogen infection. Some species of thrips have been shown to benefit from feeding on TSWV-infected plants, which has been ascribed to TSWV infection interfering with induced plant defences against insect herbivory, resulting in faster larval growth rates, and consequently reduced periods of vulnerability to some predators (Belliure *et al*, 2005, 2008; Felton *et al*., 1999; Felton & Korth, 2000).

Antibiosis

Toxins and defensive compounds may be produced by a plant as part of its normal growth process, or they may be produced as a response to insect herbivory as part of an induced defence mechanism, initiated by the recognition of insect oral secretions and

signals from injured plant cells (Howe & Jander, 2008). These compounds may target physiological processes in the insect, such as digestion and fecundity. Protease inhibitors interfere with protein digestion, causing stunted growth, increased mortality, and reduced fecundity. Protease inhibitors, such as equistatin (blocks cysteine and aspartic gut proteases of many insects) have been found to be effective against thrips, reducing the growth of larvae and fecundity of adults, and also strongly deterrent to adults (Outchkourov *et al*., 2004). Leiss *et al*. (2009) found that thrips resistance in *Chrysanthemum* was linked to higher amounts of the phenylpropanoids, chlorogenic acid and feruloyl quinic acid, which are known for their inhibitory effect on herbivores.

Epidemiology of disease outbreaks

All virus-vector-plant relationships are complex, involving multiple interacting variables, including environmental factors. For this reason the epidemiological progression of TSWV outbreaks is also highly variable, changing across time and place (Damsteegt, 1999; Gray & Banerjee, 1999; Jericho, 2005). TSWV epidemics are influenced by the availability of inoculum in the environment (Pappu *et al*., 2009), the level of pre-existing infection in the crop (for example in planted potato setts) (Jericho, 2005; Jones, 2004; Latham & Jones, 1996, 1997; Pappu *et al*., 2009; Wilson, 1998, 2001), susceptibility of the plant species (Pappu *et al*., 2009), TSWV strain (Pappu *et al*., 2009), presence of vector competent thrips and thrips performance and longevity on the host (Wijkamp, 1995), vector sex (Sakurai *et al.,* 1998, 2002; van de Wetering *et al.,* 1998; Wijkamp *et al.,* 1995), feeding behaviour (Harrewijn *et al*., 1996; Sakurai *et al.,* 2002; van de Wetering *et al*., 1998; van de Wetering, 1999), and the level of virus accumulation at different developmental stages (Inoue *et al.,* 2002). Because TSWV must be acquired by early instar larvae emerging from eggs oviposited on an infected plant, non-reproductive host plants are of little epidemiological importance, even if they are susceptible to TSWV (Bautista & Mau, 1994; Jericho, 2005; Sakimura, 1963a). Such plants are only of interest in that they may provide for adult thrips useful sources of food and protection from predators.

The speed and extent of TSWV spread within a crop is also affected by the age of plants at the time of transmission, especially because of resistance factors associated with plant age (Jericho, 2005; Thresh, 1974; Wilson, 2001). While older, larger plants in contact with neighbours facilitate greater thrips movement through the crop and greater thrips numbers (Norris 1951a, 1951b), infection rates are usually lower and fewer due to “mature plant resistance” (Beemster, 1987). Fewer virus particles are also translocated downwards to tubers (Norris 1951a, 1951b; Wilson 2001). This has been shown in other

virus-vector-host systems such as aphid-transmitted potyviruses in potato (Gibson, 1991).

Studies aimed at managing TSWV and thrips vectors are many and ongoing, but debilitating TSWV epidemics continue to arise, if sporadically, in potato and other vegetable and ornamental crops. This is in part because the ecological and epidemiological factors underpinning these outbreaks in Australia are still not well understood (Jericho, 2005). One particular problem is identifying the many sources of TSWV inoculum, which can determine the extent of an epidemic (Duffus, 1971; Gray & Banerjee, 1999; Jericho, 2005; Kranz, 1974, 1990; Plumb & Thresh, 1983; Thresh, 1974). Inoculum sources may arise from propagation of infected seed stock (Conroy *et al*., 1949; Norris & Bald, 1943; Norris, 1951b; Shepherd, 1972), infected volunteers carried over from previous crops (Horne & Wilson, 2000; Norris & Bald 1943), hibernating viruliferous thrips (Groves *et al*., 2001; Jenser *et al*., 2003), adjacent or even distant infected crops, or from annual or perennial weeds (Duffus, 1971; Norris & Bald 1943; Thresh, 1974).

The ongoing debate over the vector competence of *Thrips tabaci,* and why it appears to be so variable, is one of the key factors that needs resolving in order to better understand the epidemiology of TSWV outbreaks in Tasmania.

Management of TSWV and vector thrips

Control of TSWV and vector thrips in potato and many other vegetable and ornamental cropping systems worldwide has rarely been successful for a number of reasons. Knowledge of TSWV disease epidemiology in potato is also limited due to its sporadic nature and low incidence outside Australia. Once plant infections are noticed, it is often too late to do anything in large area field crops, such as potato, due to the cost associated with roguing large numbers of plants. However, many growers in Australia will apply insecticides if an insect-transmitted virus is identified early, in an attempt to prevent or reduce further spread of the virus to uninfected plants. Some growers apply insecticides routinely as a preventative measure against vector thrips, including soil-applied systemic insecticides at planting.

Chemical control

Because of routine screening of seed potato crops for a suite of potato viruses, thrips usually carry TSWV from external sources, often rendering insecticide applications only marginally effective. Furthermore, because thrips are small, reproduce rapidly, and congregate in places such as flower heads and leaf axils, complete insecticide coverage

is difficult. In order to control high population densities of this pest during warm, dry periods, repeated applications at 7-10 day intervals are required. For this reason systemic insecticides are often used, however, *F. occidentalis* has demonstrated an ability to rapidly develop resistance to insecticides, further limiting the effectiveness of chemical pesticides (Bielza *et al*., 2007, 2008; Broadbent & Pree, 1997; Brødsgaard, 1994; Espinosa *et al*., 2002; Herron & James, 2005, 2007; Immaraju *et al*., 1992; Jensen, 2000; Kontsedalov *et al*., 1998; Martin & Workman, 1994; Robb *et al*., 1995; Zhao *et al*., 1995). More recently, insecticide resistance has also been reported in populations of *T. tabaci* (Anon, 2008; Herron *et al*., 2008; Herron, 2006; MacIntyre *et al*., 2005; Shelton *et al*., 2006), increasing the need to develop non-chemical control methods for this pest.

Biological control

Natural enemies that have been investigated as biocontrol agents against thrips include predacious bugs, predacious mites, parasitic wasps, pathogenic fungi, and nematodes. Predacious bugs with potential include minute pirate bugs, *Orius* spp. (Heteroptera: Anthocoridae) and plant bugs, including the species *Dicyphus tamaninii* Wagner and *Macrolophus caliginosus* Wagner (Heteroptera: Miridae) (Riudavets & Castañé, 1998). Several species of *Orius* have been recorded as predators of *F. occidentalis* and some have been used in greenhouse trials to assess their efficacy, including *Orius laevigatus* (Fiever), *O. majusculus* (Reuter), *O. armatus* Gross, *O. heterorioides* Woodward & Postle, *O. tantillus* (Motschulsky), and *O. insidiosus* (Say) (Ferguson & Schmidt, 1996; Goodwin & Steiner, 1996; Riudavets & Castañé, 1998). Problems with such control agents include their short-day induced diapausing nature (Tommasini & Nicoli, 1996), and difficulty in mass producing populations (Blümel, 1996). The other drawback of predacious bugs, and biological control agents more generally, is that while they may be effective against reducing thrips populations over time, they are of little use in preventing initial TSWV infections as a result of short feeding times following an influx of thrips from an external inoculum source. Many predators of *T. tabaci* do not become abundant until relatively late in summer (Alston & Drost, 2008), after potatoes have already been exposed at their most vulnerable stages to TSWV infection.

Many species of phytoseiid mites have been recorded as eating some stages of *F. occidentalis* (Sabelis & van Rijn, 1997). From a review of over 30 years of literature, Kostiainen and Hoy (1996) identified 12 mite species that predate on *F. occidentalis*. A major problem associated with mites as biocontrol agents include their limitation to eating early instar larvae only, with older life stages immune to attack because of their larger size and more effective defensive behaviors. There is also uncertainty as to

whether these mites can successfully complete their life cycle solely on a diet of thrips (Riudavets, 1995; Sabelis & van Rijn, 1997). Consequently, the crop plant on which mites are expected to provide biological control of a pest can strongly influence their success or failure. While some species of nematode, e.g. the sphaerulariid nematode *Thripinema nicklewoodi* (Tylenchida: Allantonematidae) are being investigated for biocontrol potential, nematodes generally are unlikely to be suited to biological control of thrips as most are soil-borne, thereby being relatively ineffective on foliage. Thrips parasitoids are found in three families (Eulophidae, Trichogrammatidae, Mymaridae) and several genera. Parasitoids have shown little potential to date because their development times are longer than that of thrips, so populations are unable to keep pace with the increase in thrips numbers (Loomans & Murai, 1997; Loomans & van Lenteren, 1995).

Development of bio-pesticides based on pathogenic fungi is progressing, but is only ever likely to be applicable to glasshouse situations, as high humidity is usually required for widespread infection. *Verticillium lecanii* has been successful in controlling thrips in glasshouse cucumber and *Chrysanthemum* (Helyer *et al.*, 1992; Ravensberg *et al*., 1990; van der Schaaf *et al*., 1991). Products based on *Beauveria bassiana* have also been released commmercially, but most other released products have only been effective at killing thrips in soil.

Cultural control

Cultural control options include avoiding planting thrips-susceptible crops or cultivars following other susceptible hosts (because of the likelihood of infected volunteers as a source of inoculum), managing vegetation in the field and field edges, using coloured mulches (to repel thrips), and avoiding high nitrogen levels (Brodbeck *et al*., 2001; Malik *et al*., 2009; Mollema & Cole, 1996). Where infected volunteers are detected, these and TSWV-susceptible weeds can be removed, although this approach becomes more difficult as crop size increases. Crop rotations can be utilised to prevent successive plantings of susceptible crops. Inter-planting with non-host crops can also be effective in preventing the build up of large populations (Uvah & Coaker, 1984). In glasshouse situations, a summer fallow may be successful, in which all plants are removed and the glasshouse heated to maintain soil temperatures at 60°F (16°C) for three weeks. During this time, any thrips eggs hatch and the nymphs starve for lack of food (Willmott, 2002).

Resistance to TSWV

Breeding potato cultivars with robust and even multiple resistance mechanisms, and tolerance to TSWV infections is a more feasible option in view of the drawbacks and general failure of other control methods. Potato cultivars with different types of resistance to TSWV have been identified (Hooker, 1981; Jericho, 2005; Wilson, 2001). Some cultivars exhibit hypersensitive responses, resulting in localised infections, whereas others exhibit levels of resistance to the virus translocating from leaf to tuber (Wilson, 2001). These resistance mechanisms are being examined and bred into cultivars through conventional breeding and molecular markers (Dawson *et al.,* 2002; Isenegger *et al.,* 2001; Jansky & Rouse, 2003; Kirkham *et al.,* 2001; Williams *et al.,* 2003; Wilson, 2001; Wilson *et al*., 2006, 2009). Biotechnological approaches, such as genetic modification may also be developed in potato. Incorporation of pathogen-derived resistance against TSWV has been exhibited successfully in other crops (Cho *et al.,* 1998; Goldbach & Peters 1996; Yang *et al.,* 2004), such as post-transcription gene silencing in tomato. However, consumer resistance to transgenic crops limits the near- to medium-term commercial viability of such methods. In Tasmania, a moratorium on the deployment of all genetically modified, non-research crops currently exists. In addition, resistance to TSWV does not provide complete immunity, and is sometimes overcome by resistance-breaking strains (Aramburu & Martí, 2003; Qiu *et al.,* 1998; Qiu & Moyer, 1999; Roggero *et al.,* 2002; Thomas-Carroll & Jones, 2003; Thompson & van Zijl, 1996), and in some cases, high temperatures (Roggero *et al*., 1996). As such, deployment of resistant potato genotypes would still be accompanied by a program of thrips management.

All breeding programs must maintain or even improve yields and tuber quality characteristics desired by growers, processors and consumers. While this is not always easy, it has been achieved in the development of potato lines with resistance to common scab (Wilson *et al*., 2010).

Host resistance to thrips

Understanding the factors underpinning host choice is important for developing control methods, and in particular for guiding breeding programs for new cultivars. Characteristics of host choice have been used to breed and select cultivars with reduced thrips preference in a range of crops, including onion (Alimousavi *et al.*, 2007; Loges *et al.*, 2004), *Chrysanthemum* (Broadbent *et al*., 1990; de Jager *et al*., 1995a, 1995b; de Kogel *et al*., 1997a; Leiss *et al.,* 2009), rice (Nugaliyadde & Heinrichs, 1984), strawberry (Rahman *et al.,* 2010), common bean (Frei *et al*., 2004) and *Capsicum* (pepper) (Maris *et al*., 2003b).

Host plant resistance to many insect pests has been introduced in a variety of crop cultivars through both traditional breeding methods and deployment of genetically modified plants (Christou *et al*., 2006; Hilder & Boulter, 1999). Resistance to thrips has been observed in onion (Brar *et al*., 1993; Coudriet *et al*., 1979; Diaz-Montano *et al*., 2010; Jones *et al*., 1934; Verma, 1966), *Capsicum* (Maris *et al.* 2003a, 2003b; Sharman & Persley, 2006; Soler *et al*., 1999), tomato (Mirnezhad *et al*., 2010), *Chrysanthemum* (de Jager *et al*., 1995a, 1995b; Leiss *et al*., 2009), cowpea (Muchero *et al*., 2010), cotton (Stanton *et al*., 1992), common bean (Cardona *et al*., 2002), cabbage (Stoner *et al*., 1989), *Impatiens* (Herrin & Warnock, 2002), cucumber (de Kogel *et al*., 1997a) and potato (Jericho & Wilson, 2003), suggesting that genetic resistance to thrips can be improved through selection and breeding. Thrips resistant potato cultivars, that are non-preferred for both feeding and oviposition, would reduce feeding damage and TSWV infections. However, the resistance mechanisms in some potato cultivars are still being characterised (Jericho, 2005). As such it is uncertain whether these might be overcome by thrips under certain conditions. Screening programs for host resistance to thrips, and subsequent breeding efforts might enable the introduction of resistant mechanisms to those cultivars used for their processing and eating qualities, high yields and favourable agronomic characteristics (Jericho, 2005).

Integrated pest management

TSWV has been very difficult to control due to its sporadic nature, short feeding times for successful transmission, difficulty in controlling the thrips vector and lack of knowledge of inoculum sources (Cho *et al.,* 1989, 1998; Jericho, 2005; Jones, 2004; Plasencia & Sánchez, 1999; Ullman *et al.,* 1997). Each management option previously discussed - chemical and biological management, cultural controls, and host resistance to TSWV and thrips – should be more effective at reducing TSWV infections and epidemics, and limiting the loss of marketable tubers, when used in combination as part of an integrated pest management program. Additional management options include seed certification, pre-planting and postharvest phytosanitation, thrips monitoring, trap crops (push-pull systems), plant nutrition management, planting time, planting location, and pre- and post-emergent insecticides. The development of potato cultivars with resistance to TSWV infection and/or TSWV translocation, and/or vector thrips would greatly enhance the efficacy of these management options. While many options exist, there are of course limitations to each. Planting time, as a method of reducing exposure to vector thrips at crucial times of plant growth, is restricted by environmental factors. Planting location relative to other thrips and TSWV hosts is often restricted by small farming areas and the requirements of crop sequencing. Insecticides, in addition to their expense and their

failure to completely control thrips, can have detrimental effects on beneficial insects that help to control other pests, such as aphids, mites, bugs and lepidopteran pests. Roguing of infected plants is difficult in large scale field plantings, and often comes too late.

Trap crops are increasingly being considered as part of integrated pest management in a number of crops, as more and more growers move away from sole reliance on chemical control (Bennison *et al*., 2002; Cook *et al*., 2007; Pickett *et al*., 1997). Trap crops have several advantages. They can reduce pest occurrence in the commercial crop, enabling spraying operations to be conducted on smaller areas using less insecticide, in order to maintain populations of beneficial insects in the commercial crop, and reduce the chemical and physical impact on the crop and soil. While establishing a perimeter trap crop is an additional cost of production, providing the system worked well, it would be hoped that this cost would be offset by reduced spraying costs and increased yields. In order for trap cropping methods to be introduced, further work is needed to delineate thrips preferences for plant host species and colours.

Trap crops are more likely to work in environments where cropping fields are continuous in time and space, because thrips are more likely to travel shorter distances and encounter a trap crop before entering a commercial crop. Isolated, and irrigation-dependent, crops in dry areas that are surrounded by very little green vegetation are less likely to benefit, because any infestation by *T. tabaci* is likely to occur as a result of a long-distance flight with thrips alighting across a large area. For this reason, trap crops may be feasible alternatives throughout Tasmania and in coastal and hinterland cropping regions of the Australian mainland, however many of the cropping regions further inland in South Australia and NSW may be unsuitable.

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Chapter 2 - Field trials assessing potato cultivars in relation to resistance to *Tomato spotted wilt virus* (TSWV) and thrips vectors across two different regions of south-east Australia.

Abstract

Three comparative cultivar trials were conducted between 2005 and 2007, in Tasmania and South Australia, to evaluate cultivar differences in field resistance to TSWV and *T. tabaci* in potato (Cultivars: Atlantic, Bismark, Coliban, Desiree, Fergifry, King Edward, Russet Burbank, Russet Ranger, Shepody, Tasman, 93-6-3). Overall infection levels of *Tomato spotted wilt virus* (TSWV) were moderate in the first trials in Tasmania and South Australia, with TSWV-incidence varying from 9-26 percent across cultivars in Tasmania and 3-22 percent in South Australia. Due to high variability across replicates there were no significant differences between cultivars in foliar TSWV-infection in these trials, however cv. Bismark was scored with the highest incidence of TSWV in both cases. All cultivars in these two trials were above the two percent infection limit at which commercial seed potato crops would be rejected for certification. TSWV infection levels were much lower in the second Tasmanian trial, with only three plants in total (cv. Atlantic and cv. Fergifry) succumbing to TSWV infection.

The efficiency of TSWV translocation from field infected foliage to tubers was investigated, but there were no significant differences in tuber TSWV infection levels between cultivars in any trial. This was in part attributable to considerable variation in tuber infection levels between infected plants within cultivars. Tuber infection levels in Bismark ranged from 8-100 percent and in Russet Burbank from 0-75 percent in the South Australian trial.

Thrips counts showed the highest numbers of *T. tabaci* on Bismark, with 4.4 thrips per leaf, but this cultivar was not significantly different from Russet Burbank, Russet Ranger and King Edward, which had 3.4-3.9 thrips per leaf, bringing into question an earlier study by Jericho (2005) suggesting that cv. Bismark had field resistance to this TSWV vector. The lowest thrips numbers were found on Atlantic and Shepody, with 2.3 and 1.7 thrips per leaf respectively.

Introduction

One of the most significant factors in the epidemiology of TSWV outbreaks in potato is cultivar susceptibility to the virus (Garg & Khurana, 1999; Jericho, 2005; Pappu *et al*., 2009; Wilson, 2001). Cultivar-based resistance may vary in time and space due to plant age at time of infection (Mandal *et al*., 2007; Moriones *et al*., 1998; Norris 1951a, 1951b; Soler *et al*., 1998; Thresh, 1974; Wilson, 2001), virus strain (Best & Gallus 1955; Ciuffo *et al*., 2005; Mandal *et al*., 2006; Norris 1946, 1951a; Pappu *et al*., 2009; Roggero *et al*., 2002), inoculum pressure (Jericho, 2005; Jones, 2004; Latham & Jones, 1996, 1997; Pappu *et al*., 2009; Wilson, 1998, 2001), presence of vector-competent thrips and thrips performance and longevity on the host (Wijkamp, 1995), vector sex (Sakurai *et al.,* 1998, 2002; van de Wetering *et al.,* 1998; Wijkamp *et al.,* 1995), feeding behaviour (Harrewijn *et al*., 1996; Sakurai *et al.,* 2002; van de Wetering *et al*., 1998; van de Wetering, 1999), environmental factors (Díaz-Pérez *et al*., 2007; Llamas-Llamas *et al*., 1998; Jericho, 2005; Soler *et al*., 1998), and cultural practices (Córdoba *et al*., 1991; Jericho, 2005; Llamas-Llamas *et al*., 1998; Moury *et al*., 1998; Roca *et al.*, 1997).

Potato breeding programs have successfully developed cultivars with improved yields and processing qualities (Dawson *et al.,* 2002; Kirkham *et al.,* 2001; Williams *et al.,* 2003; Wilson *et al*., 2010). Identification of and breeding for some levels of resistance to common potato-infecting viruses, such as PVS, PVX, PVY and PLRV, has also been achieved (Salazar, 1996; Solomon-Blackburn & Barker, 2001; Wilson & Jones, 1992, 1993a, 1993b, 1995). However, selecting and breeding for resistance to TSWV in potato is at a relatively early stage. Potato cultivars with potential resistance to TSWV have been identified (Hooker, 1981; Jericho, 2005; Wilson, 2001), but further confirmation of comparative cultivar resistance levels is still required in the laboratory and field.

Cultivar-based resistance to TSWV has been observed at the foliar and tuber level in mechanical inoculation experiments in the glasshouse and from natural thrips transmission in field trials (Jericho, 2005; Wilson, 2001). Some cultivars have shown lower levels of infection in foliage following mechanical and/or thrips inoculations, enabling higher growth and yield than other cultivars that more readily succumb to infection, whereas others have exhibited levels of resistance to the virus translocating from leaf to tuber (Wilson, 2001). Characterisations of resistance from these studies are described here based on a scale of the percentage of plants with foliar infection (or percentage of tubers from infected plants) following mechanical inoculation of 0-25% (highly resistant), 25-50% (moderately susceptible/moderately resistant) and 50-100% (highly susceptible). Atlantic and Bismark are believed to be very susceptible varieties; while Russet Ranger, Shepody, Spunta are moderately susceptible. King Edward and

Tasman have shown moderate resistance to foliar infection, Russet Burbank has shown moderate resistance to tuber infections and Coliban has shown high levels of resistance to tuber infections (Wilson, 2001). These resistance mechanisms are being examined and bred into cultivars through conventional breeding and with molecular markers (Dawson *et al.,* 2002; Isenegger *et al.,* 2001; Jansky & Rouse, 2003; Kirkham *et al.,* 2001; Williams *et al.,* 2003; Wilson, 2001; Wilson *et al*., 2006, 2009). Characterisations of TSWV infection levels in commercial processing crops or field trials relying on natural thrips transmission are more subjective in nature, but are described in this study as 0-10% (low), 10-25% (moderate) and 25-100% (high), although any infection level above 2% (the maximum infection level allowable for seed crop certification), would be considered as high by many growers.

In experiments using (thrips independent) mechanical inoculation of TSWV into potato at 28 days after planting, Jericho (2005) found no significant differences between cultivars in TSWV foliar infection rates in any one trial (Table 2.1); however the differences in the range of infection levels for each cultivar across trials suggest further testing may be warranted. There were significant differences in tuber infections arising from mechanical inoculation in just one trial, which were high in Atlantic and Bismark; moderate in Shepody and Russet Ranger, and lower in Russet Burbank, Coliban, King Edward and Royal Blue. In Jericho's field trials (relying on natural thrips transmission only), there were no significant differences between cultivars in either TSWV foliar or tuber infection levels.

Table 2.1 Combined (averaged) results from selected cultivars in glasshouse and field trials conducted in 2001-2002 and 2002-2003 (from Jericho, 2005).

	TSWV incidence (%) in shoots		TSWV incidence (%) in tubers	
Cultivar	Mechanical inoculation (glasshouse)	Natural thrips inoculation (field)	Mechanical inoculation (glasshouse)	Natural thrips inoculation (field)
Atlantic	69	14	30	8
Bismark	63	4	20	7
Coliban	56	-	3	-
King Edward	31	0	3	0
Ranger Russet	44	16	6	6
Royal Blue	38	7	1	1
Russet Burbank	44	11	27	5
Shepody	38	1	12	0
Tasman	25	0	0	0

While there were no significant differences in foliar infection between cultivars within each inoculation method, there were highly significant ($p < 0.001$) differences in TSWV-infection levels within cultivars between mechanical and thrips inoculation in all trials, particularly in cv. Bismark, which led Jericho (2005) to suggest that "vector-mediated components may be responsible". This hypothesis was strengthened when plant host resistance to *T. tabaci* at the cultivar level was demonstrated in no-choice cage experiments by Jericho (2005), where cv. Bismark was found with very few adults and little feeding damage, and cv. Royal Blue was strongly preferred for feeding, but showed high resistance to oviposition. Other studies have shown that some thrips species exhibit distinct host cultivar preferences in lettuce (Yudin *et al*., 1988), *Capsicum* (Maharijaya *et al*., 2011; Maris *et al*., 2003b), onion (Doederlein & Sites, 1993; Verma, 1966), cucumber (de Kogel *et al*., 1997), *Chrysanthemum* (Broadbent *et al*., 1990), *Impatiens* (Herrin & Warnock, 2002) and rose (Gaum *et al*., 1994). Characteristics of host choice, such as leaf shape, colour, wax levels and chemical constituents, have been used to breed and select cultivars with reduced thrips preference in a range of crops, including onion (Alimousavi *et al.*, 2007; Loges *et al.*, 2004), *Chrysanthemum* (Broadbent *et al*., 1990; de Jager *et al*., 1995; de Kogel *et al*., 1997; Leiss *et al.,* 2009), rice (Nugaliyadde & Heinrichs, 1984), strawberry (Rahman *et al.,* 2010), common bean (Frei *et al*., 2004) and *Capsicum* (pepper) (Maris *et al*., 2003b).

Determining thrips preferences in laboratory choice experiments and host resistance to TSWV in glasshouse inoculation trials are important components of a program of breeding or improving potato varieties for resistance to TSWV infection. However, evaluation of potato varieties in the field is also necessary. Between 2005 and 2007, three comparative field trials were conducted: two at University of Tasmania Farm, Cambridge, Tasmania (42.802°S, 147.428°E WGS84) and one at Penola, South Australia (37.335°S, 140.844°E WGS84). The key aims of these trials were to determine potato cultivar susceptibility to field infection with TSWV and to cultivar efficiency of TSWV translocation to tubers. Secondary aims were to determine any associations between thrips populations and cultivar and TSWV infection levels. Due to the unavailability of TSWV-free tubers from some cultivars at certain times, comparisons differed slightly across the three trials. While 11 cultivars (Atlantic, Bismark, Coliban, Desiree, King Edward, Fergifry, Russet Burbank, Russet Ranger, Shepody, Tasman and 93-6-3) were tested in total, only five cultivars (Atlantic, Bismark, King Edward, Russet Burbank and Shepody) were common to all three trials. However, all of these five cultivars are important processing or fresh market cultivars that have previously been categorised for susceptibility to foliar and tuber TSWV-infections.

Field Trial 1

University of Tasmania Farm, Cambridge, Tasmania, Dec 2005 – Mar 2006

Materials and methods

The first Tasmanian trial was planted in early December of 2005. The experiment was conducted as a randomised complete block design with 16 plants for each of six cultivars (Atlantic, Bismark, King Edward, Russet Burbank, Russet Ranger and Shepody) in a 4 x 4 arrangement, in plots of 1.5 m x 8.5 m with four replications (Figure 2.1). Potato tubers were planted with 0.35 m between plants in each row, and 0.35 m between rows. Planted tubers were either sourced from certified TSWV-free stock (tested in the previous season), or were tested for TSWV infection prior to planting by DAS-ELISA. Plots were prepared following standard commercial practice, with tubers hand-planted into furrows. Buffer zones of bare earth of 2 m in width were established between replicates and surrounding the entire trial area. The trial site was sprayed with Roundup® herbicide to control weeds two weeks before planting tubers, and kept free of weeds by hand weeding during the trial. Plants were watered according to need by gun irrigator. No fungicide or insecticide was used in this trial. The trial area was surrounded by a mixture of native and improved grasses, clovers, capeweed, and other weeds. In

the year immediately prior to the trial, the area was planted to onion, and the four years prior to that the area was under permanent pasture.

Two inoculated tomato plants (TSWV isolate *An_{WA}-1* in *cv.* Grosse Lisse, Arthur Yates & Co. Ltd, Homebush, NSW, Australia), confirmed as TSWV-positive by DAS-ELISA, were transplanted at the north-facing end (predominantly wind-ward) end of each row of potatoes in replicates one and three, and at the south-facing end of each row in replicates two and four, at the same time as the potato tubers, as was done by Jericho (2005). This was done to ensure a relatively even source of inoculum across the trial. Tomato plants were chosen because of their indeterminate growth, providing a viable source of TSWV throughout the duration of the trial. During potato cultivar trials in 2002-03, Jericho (2005) reported that *Thrips tabaci* occurred naturally at this location, and that the small number of *Thrips imaginis* detected was explained by it having only been introduced recently to southern Tasmania. Wilson (1998) also reported no detections of *T. imaginis* on lettuce farms from Southern Tasmania in the Cambridge area, but plentiful *T. tabaci* and *T. australis*. Contrary to this, the Tasmanian Plant Pest Database and Invertebrate Collection holds records of *T. imaginis* from across southern Tasmania going back to the 1960s (Plant Health Australia, 2001). An analysis of specimen records held by Plant Health Australia (2001) was conducted to further investigate the likely presence of these two species within potato crops, as indicated by collection data.

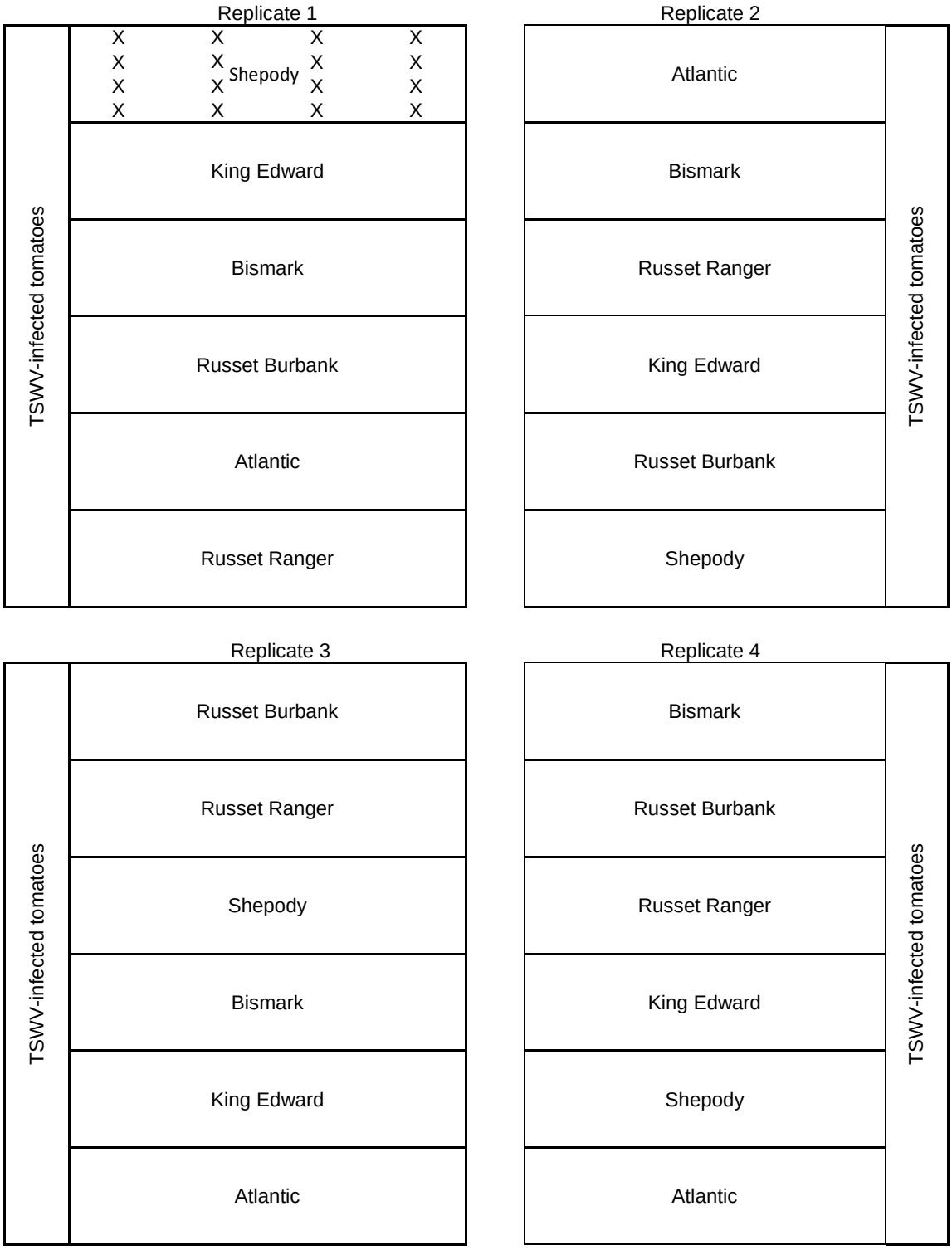


Figure 2.1 Potato cultivar trial layout conducted as a randomised complete block design with 16 plants for each cultivar in a 4 x 4 arrangement, in plots of 1.5 m x 8.5 m with four replications, at University of Tasmania Farm, Cambridge, Tasmania, Dec 2005 - Mar 2006. “X” represents plant spacing (shown for cv. Shepody replicate 1 only).

The same area was surveyed in November, prior to the 2005-2006 field trial, in order to confirm that *T. tabaci* would be present during the trial. Beatings were conducted on a range of weeds, predomoninantly in the family Asteraceae, as well as on unkempt grassland and fennel. No *T. tabaci* was detected. The majority (over 80 percent) of thrips identified were *T. imaginis*, with lesser numbers of *T. australis*, *Limothrips cerealium*, and species in the suborder Tubulifera, which were not further identified. Because prior surveys of the trial area did not detect *Thrips tabaci*, the TSWV-positive tomato plants were each exposed to 20 adults of *T. tabaci* one week before planting, in order to ensure that vector thrips would be present and relatively evenly distributed across each cultivar plot at the trial site when the potatoes emerged. However, these adults were sourced from four populations of thrips (TAS-BH, NSW-C, NSW-W, SA-M) collected from onion in 2003-2005, and reared on green bean, which were later shown to not be capable of vectoring TSWV (Chapter 5).

Beginning in mid-January, four weeks after emergence, the number of thrips on each cultivar was assessed at weekly-fortnightly intervals until early March (five sampling dates). Assessment consisted of counting the number of (adult) thrips on one leaf from the mid-level of the canopy from each of the four plants in the centre of each cultivar plot. This gave a total of sixteen leaves sampled from each cultivar on each sampling date. A snap-lock plastic bag was placed over the sampled leaf and the bag sealed as the leaf was pulled off. Leaves were returned to the laboratory for counting under a stereomicroscope, to ensure that only specimens of *T. tabaci* were counted. At the conclusion of the trial, just before plants began to senesce, leaves were taken from each plant and tested for TSWV-infection using DAS-ELISA.

Enzyme-linked immunosorbent assay (ELISA)

TSWV specific antibodies (monoclonal mixture) (Agdia, Elkhart, Indiana USA) were used in double antibody sandwich ELISA as described by Clark and Adams (1977). Sap was extracted from the leaf disks (1g/10mL) in phosphate buffered saline with Tween (PBS-T) (1.5mM potassium phosphate, 137mM sodium chloride, 8 mM disodium hydrogen phosphate, 2.7 mM potassium chloride, 10 mM sodium sulphite, 0.2% (w/v) bovine serum albumin, 15mL/L of Tween 20 and 20g/L of polyvinyl pyrrolidone, pH 7.4). All samples and known TSWV-positive and negative controls were tested in duplicate. The substrate was 0.5mg/mL *p*-nitrophenyl phosphate in 97mL/L diethanolamine, pH 9.8. Results were assessed by spectrophotometric measurement of absorbance at 405 nm using a Labsystems Multiskan RC plate reader with Genesis software (Labsystems, Helsinki, Finland). Samples with absorbance values greater than twice the mean of

negative controls were considered positive, as recommended by Clark and Adams (1977).

Seasonal thrips activity across main potato-growing Australian States

Collection records from the Australian Plant Pest Database were also interrogated to determine whether there are any potential differences in the seasonal activity of *T. tabaci* and *T. imaginis* in Tasmania, and whether any potential differences are specific to Tasmania or are common across southern Australia.

Statistical analysis

TSWV infection in foliage and tubers was analysed using ANOVA in Genstat 13 (VSN International, Hemel Hempstead, UK). Thrips counts on cultivars were transformed using a square root function, and a repeated measures analysis using an unstructured correlation matrix was conducted using *proc mixed* on SAS v9.2, with a random effect included for replicates. Pearson's correlation coefficient was used to test for spatial correlation between thrips numbers and the level of TSWV-infection.

Results

TSWV-infection levels were moderate across the first Tasmanian trial, ranging from 9-26 percent across cultivars (Fig. 2.2). Not all 16 plants of each cultivar per replicate survived and were thus unable to be scored for infection with TSWV (Table 2.2). Overall, variability was high across replicates, resulting in no statistically significant difference in TSWV foliar infection between cultivars, $F_{5,15} = 0.86$, $p = 0.53$, and no significant block effect, $F_{3,15} = 0.28$, $p = 0.84$ (Table 2.2). Twenty-six percent of all cv. Bismark plants became infected with TSWV. Infection rates in other cultivars ranged from 9 to 17 percent. All potato cultivars had average infection levels at least 4.5 times above the maximum infection level (2%) allowable for seed crop certification, with Bismark 13 times higher than the rejection level.

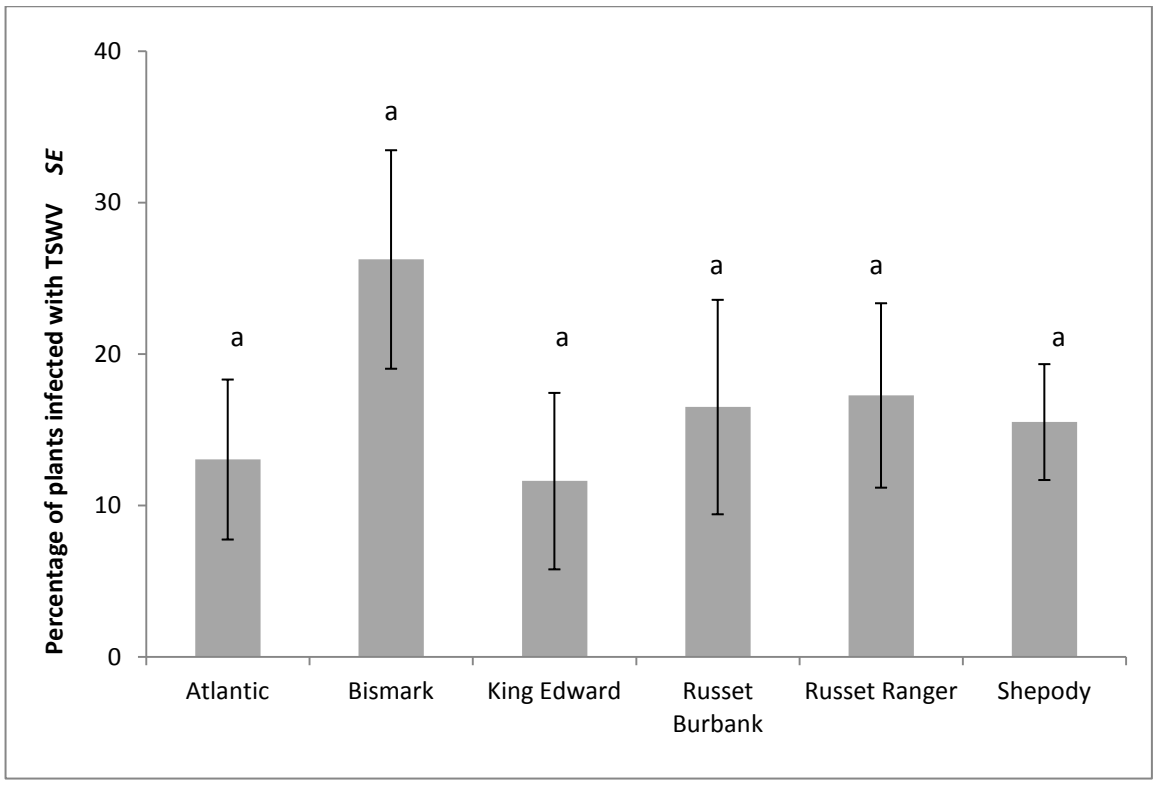


Figure 2.2 Incidence of TSWV across potato cultivars in randomised block design with 16 plants for each cultivar in a 4 x 4 arrangement in 4 replications. TSWV-positive tomato plants were placed at the beginning of each cultivar block at the time of tuber planting. Leaves were removed from each plant just prior to senescence and tested for TSWV-infection. Data are expressed as mean ± *SE*.

Table 2.2 Incidence of TSWV across potato cultivars in randomised block design with 16 plants for each of 6 cultivars in a 4 x 4 arrangement in 4 replications (384 plants).

	Number of plants infected				**Average percent infection**
Cultivar	**Replicate 1**	**Replicate 2**	**Replicate 3**	**Replicate 4**	
Atlantic	3/13	3/15	1/11	0/10	**13.0**
Bismark	4/16	6/15	3/9	1/15	**26.3**
King Edward	0/2	no emergence	2/11	1/6	**11.6**
Russet Burbank	2/16	1/12	1/13	6/16	**16.5**
Russet Ranger	2/10	1/11	1/15	5/15	**17.3**
Shepody	1/7	1/9	1/10	4/15	**15.5**
Average (%)	**15.8**	**14.8**	**14.2**	**20.1**	**16.2**

T. tabaci was found in abundance in this trial and on all potato cultivars. Thrips numbers were highest on Bismark averaging nearly 4.4 thrips per leaf, and lowest on Shepody

averaging 1.7 thrips per leaf (Fig. 2.3). There were significant differences between cultivars; $F_{5,86} = 10.40$, $p < 0.0001$; with Tukey-adjusted pair-wise comparisons indicating more onion thrips on Bismark than Atlantic ($p = 0.0003$), with only 2.3 thrips per leaf, and Shepody ($p < 0.0001$), with only 1.7 thrips per leaf. There were more thrips on Russet Ranger (3.5 thrips per leaf) than Atlantic ($p = 0.021$) and Shepody ($p < 0.0001$). King Edward (3.4 thrips per leaf) also had higher thrips counts than Shepody ($p = 0.014$).

No other TSWV-vectors were identified either before or during the trial, and *T. tabaci* strains released were subsequently shown to be non-vectors of TSWV (Chapter 5), therefore naturally occurring populations of *T. tabaci* were assumed to be responsible for all TSWV transmission (but see discussion and Chapter 5). Sex identification of randomly selected *T. tabaci* individuals during the trial detected only females, although the existence of males during the season could not be discounted.

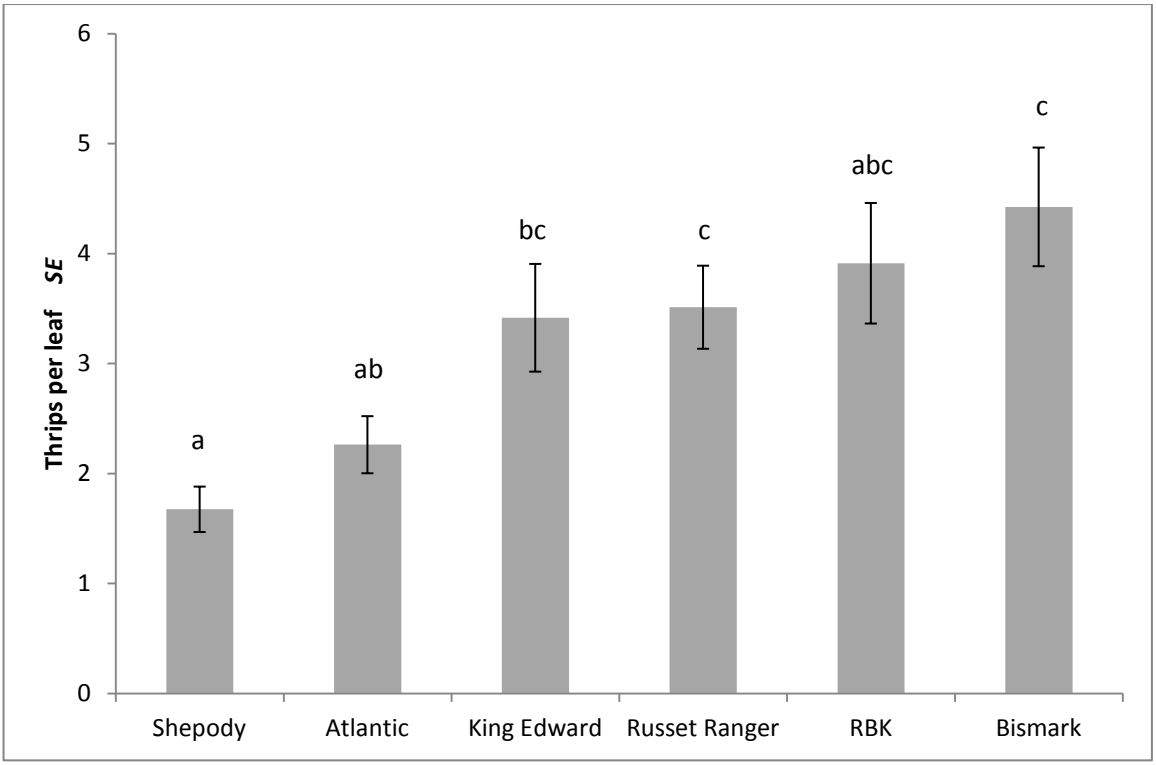


Figure 2.3 Average *T. tabaci* per leaf across potato cultivars in 80 leaves sampled per cultivar assessed at fortnightly intervals (16 leaves sampled on each of 5 sampling dates). Data are expressed as mean ± *SE*.

The number of *T. tabaci* on all cultivars rapidly increased from mid-January, averaging 3.4 thrips per leaf, to peak in late January at 5.8 thrips per leaf, before rapidly declining to 1.1 thrips per leaf in mid-February and 0.8 thrips in early March (Fig. 2.4). Average temperatures over this period were around 15°C in early to mid-January, increasing to over 25°C in late January, before declining again to around 15°C by mid-February. Maximum temperatures in late January, coinciding with peak thrips, reached 39.9°C, which was only 0.2°C below the all time high daily maximum temperature in January for this area. After mid-February, temperatures over the remainder of the trial varied but did not reach the maxima of late January. The differences between dates were significant; $F_{4,83} = 74.81$, $p < 0.0001$; with all pair-wise comparisons significantly different at the 0.05 level, except for there being no difference between 20 Jan and 27 Jan ($p = 0.86$), or between 15 Feb and 1 Mar ($p = 0.63$).

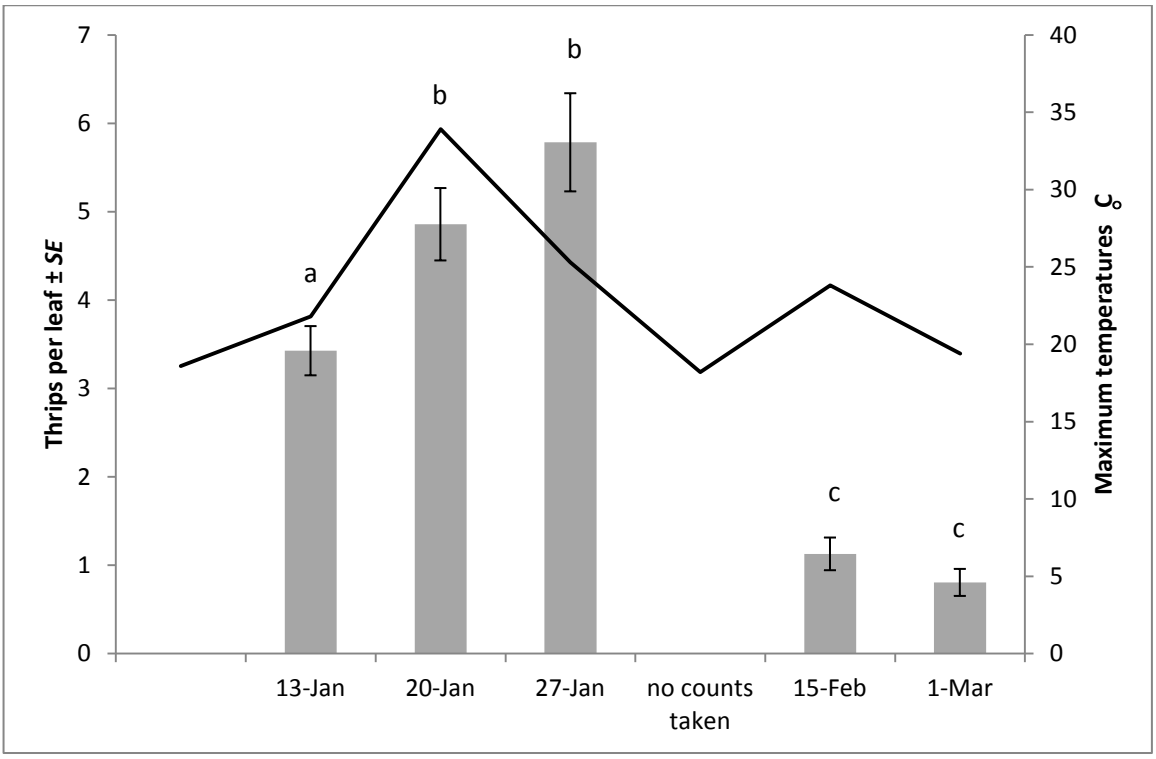


Figure 2.4 The average number of *T. tabaci* per leaf on each cultivar from 16 leaves sampled on each sampling date. Thrips count data are expressed as mean ± *SE* on the left vertical axis. Maximum daily temperatures on the day of sampling at the nearby (7.5 km) Hobart Airport (from the Australian Bureau of Meteorology) are shown for each sampling date on the right vertical axis.

In a test of fixed effects for the full model, the interaction was significant, indicating differences between the counts of thrips on cultivars between sampling dates, $F_{20,174} = 2.49$, $p = 0.0008$. Tests by date for the interaction indicated that cultivars differed significantly at the 0.05 level on all dates except for 13 Jan ($p = 0.34$) (Table 2.3). Tests by cultivar for the interaction indicated that dates differed significantly for each cultivar,

$F_{5,86} = 10.4$, $p < 0.0001$. Cultivars on 13 Jan did not differ significantly, but on other dates the cultivars differed. Tukey-adjusted pairwise comparisons showed a number of differences between cultivars on all dates except for 13 Jan (Fig. 2.5).

Table 2.3 Mixed procedure (SAS v9.2) showing tests of interaction of thrips counts (differences between cultivar tested by date) from the repeated measures analysis.

Effect	Date	Num DF	Den DF	F Value	Pr > F
Potato cultivar*Date	13 Jan	5	85	1.16	0.34
Potato cultivar*Date	20 Jan	5	85	3.50	0.006
Potato cultivar*Date	27 Jan	5	85	7.06	< .0001
Potato cultivar*Date	15 Feb	5	85	2.83	0.02
Potato cultivar*Date	1 Mar	5	85	5.42	0.0002

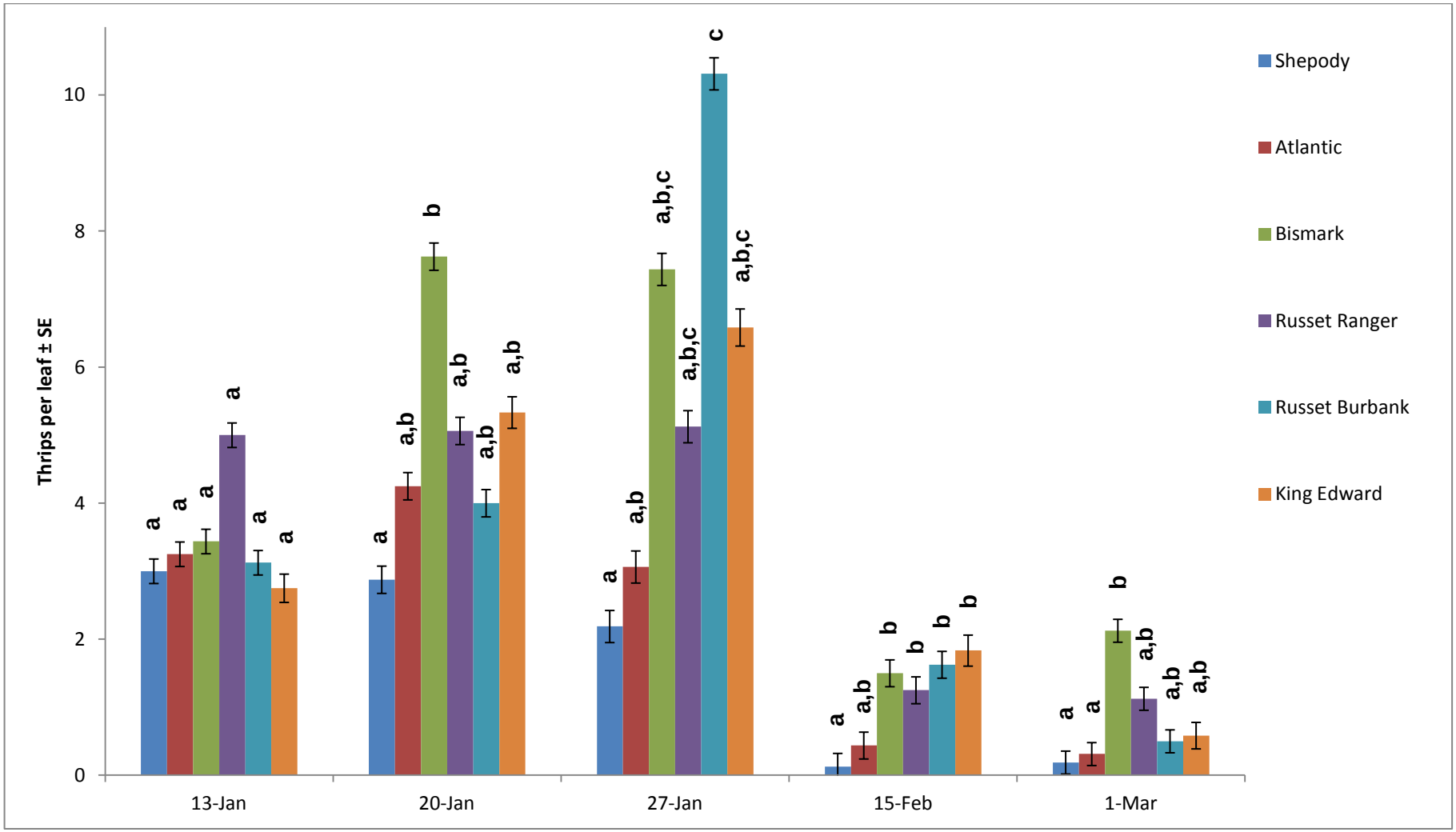
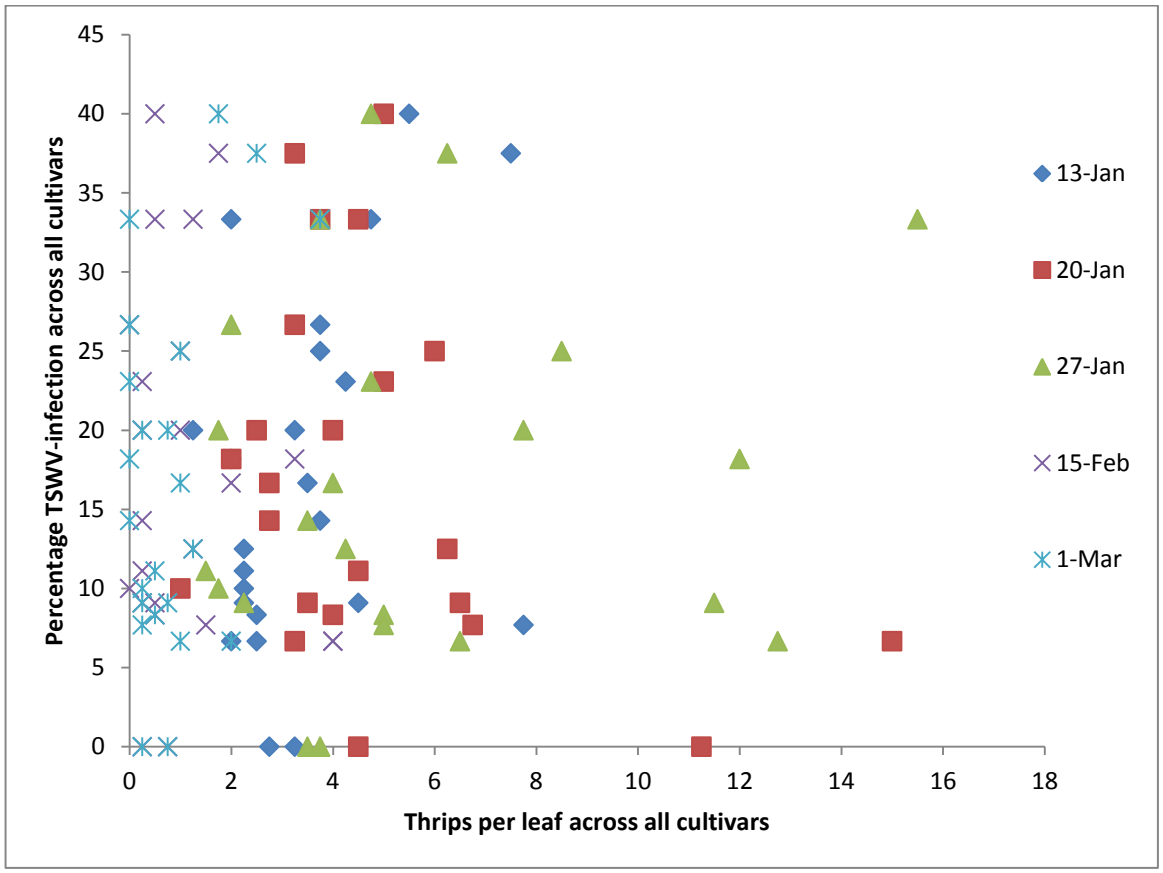


Figure 2.5 The average number of *T. tabaci* per leaf on each cultivar from 16 leaves sampled on each sampling date. Thrips count data are expressed as mean ± *SE.* Significant differences between cultivars **within** each sampling date are shown.

Combining all cultivars, there was no significant correlation between the numbers of thrips per leaf and the percentage incidence of TSWV foliar infection per replicate (r = 0.03, n = 115, p = 0.76) (Fig. 2.6).

Figure 2.6 Scatterplot of the average number of thrips per leaf across all potato cultivars, from weekly-fortnightly assessments, beginning four weeks after emergence in mid-January to mid-March (five sampling dates) versus the percentage of TSWV-infection of each cultivar per replicate scored at the end of the trial.



There were also no significant correlations between the numbers of thrips per leaf on any one sampling date, or combinations of the first three sampling dates, and the percentage incidence of TSWV foliar infection (Table 2.4).

Table 2.4 Pearson's correlation coefficients testing the correlation between numbers of thrips per leaf and incidence of TSWV foliar infection per replicate.

Sampling date	r	n	p
13 Jan	0.37	23	0.08
20 Jan	-0.32	23	0.14
27 Jan	0.15	23	0.49
15 Feb	-0.12	23	0.57
1 Mar	0.39	23	0.06
13 Jan + 20 Jan	-0.07	46	0.65
20 Jan + 27 Jan	-0.05	46	0.72
13 Jan + 20 Jan + 27 Jan	0.03	69	0.83

Seasonal thrips activity across main potato-growing Australian States

Australian Plant Pest Database records up to December, 2011 (Plant Health Australia, 2001) for New South Wales, Victoria, Tasmania, South Australia and Western Australia revealed a difference in the monthly distribution of collection records across States for both *T. tabaci* ($X^2_{44,291}$ = 89.85, p <0.0001) and *T. imaginis* ($X^2_{44,284}$ = 84.74, p = 0.0002) (Fig. 2.7). The highest number of unique collection records for *T. tabaci* in Tasmania occurs in January, whereas the highest number of records for *T. imaginis* occurs in November. In other States peak numbers for both species are recorded between September and November.

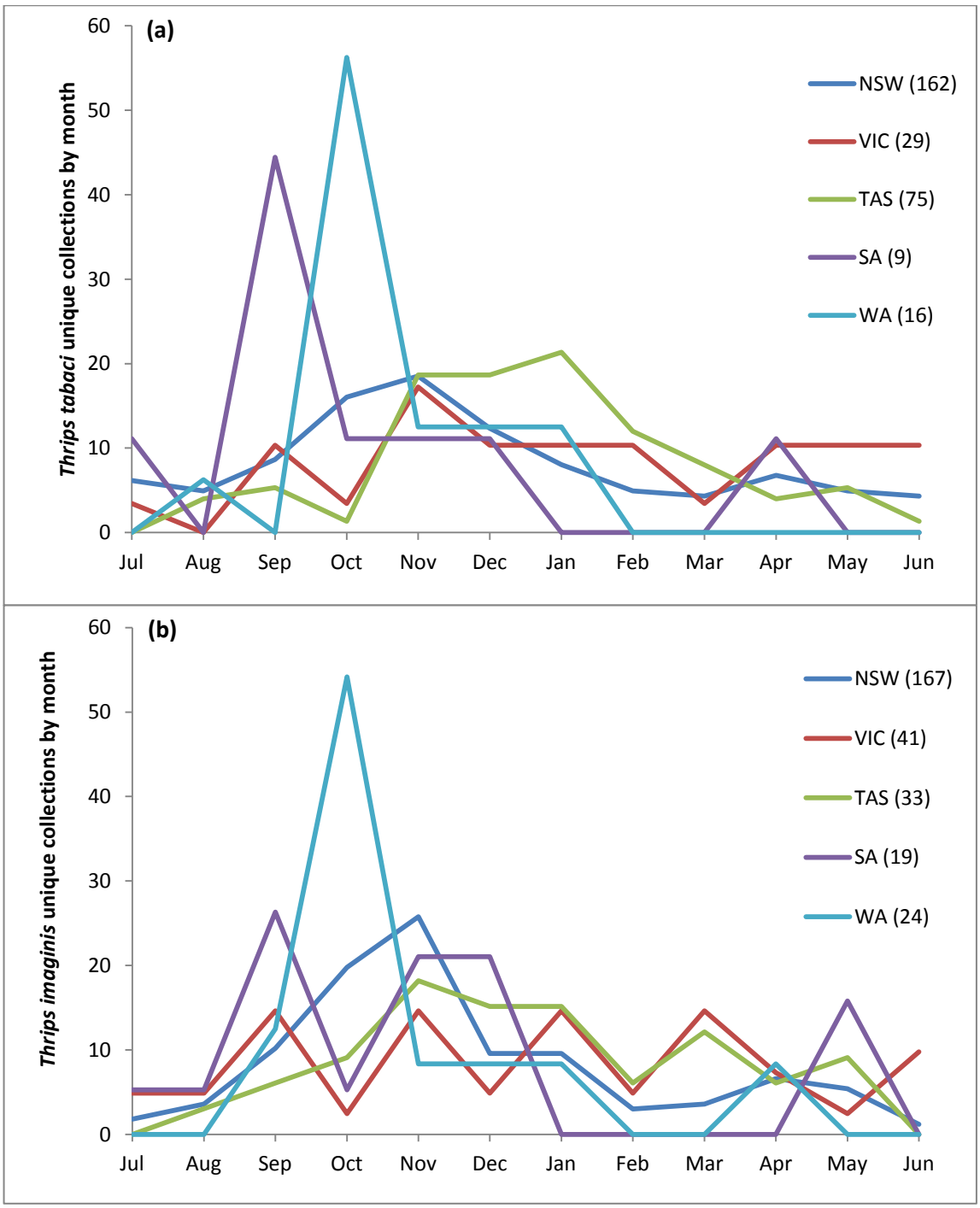


Figure 2.7 Unique collections of (a) *Thrips tabaci* and (b) *Thrips imaginis* by month (as a percentage of total) for five Australian States (New South Wales, Victoria, Tasmania, South Australia and Western Australia). The total number of unique collections for each State is indicated in parentheses in the figure legend.

Field Trial 2

University of Tasmania Farm, Cambridge, Tasmania, Dec 2006 – Mar 2007

Materials and methods

The second Tasmanian trial was planted in December, 2006. The experiment was conducted as a randomised complete block design with eight plants for each of nine cultivars (Russet Burbank, Shepody, Atlantic, Desiree, 93-6-3, Fergifry, Bismark, King Edward and Tasman), in plots of 3 m x 3 m with 4 replications (Figure 2.8). Potato tubers were planted with 0.35 m between plants in each row, and 0.35 m between rows. Planted tubers were either sourced from certified TSWV-free stock (tested in the previous season), or were tested prior to planting by DAS-ELISA. Plots were prepared following standard commercial practice, with tubers planted into furrows. Buffer zones of bare earth of 2 m in width were established between replicates and surrounding the entire trial area. The trial site was sprayed with Roundup® herbicide to control weeds two weeks before planting tubers, and kept free of weeds by hand weeding during the trial. Plants were watered according to need by gun irrigator. No fungicide or insecticide was used in this trial. The trial area was surrounded by a mixture of native and improved grasses, clovers, capeweed, and other weeds. In the five years immediately prior to the trial, the area was under permanent pasture.

In this trial a source of TSWV inoculum was provided by TSWV-infected *Chrysanthemum* plants (confirmed by DAS-ELISA) obtained from an outbreak at a local nursery. The plants were infested with *Thrips tabaci*, which were presumably competent to vector this strain of the virus, however, later vector competence trials ex-situ, using TSWV isolate An_{WA}*-1* resulted in nil transmission (see Chapter 5). Two of these *Chrysanthemum* plants were located at the beginning of each cultivar row at the westward end of replicates one and two, and at the eastern end of replicates three and four.

At fortnightly intervals, beginning four weeks after emergence, each plant was assessed for visual symptoms of TSWV. Leaf samples were taken from symptomatic plants and tested for TSWV using DAS-ELISA. Towards the end of the trial in late February, prior to senescence, all non-symptomatic plants were sampled and tested for TSWV-infection. All tubers from infected plants were harvested and tested for TSWV using DAS-ELISA. Data were analysed using ANOVA in Genstat 13.2. Thrips counts were not taken during this trial.

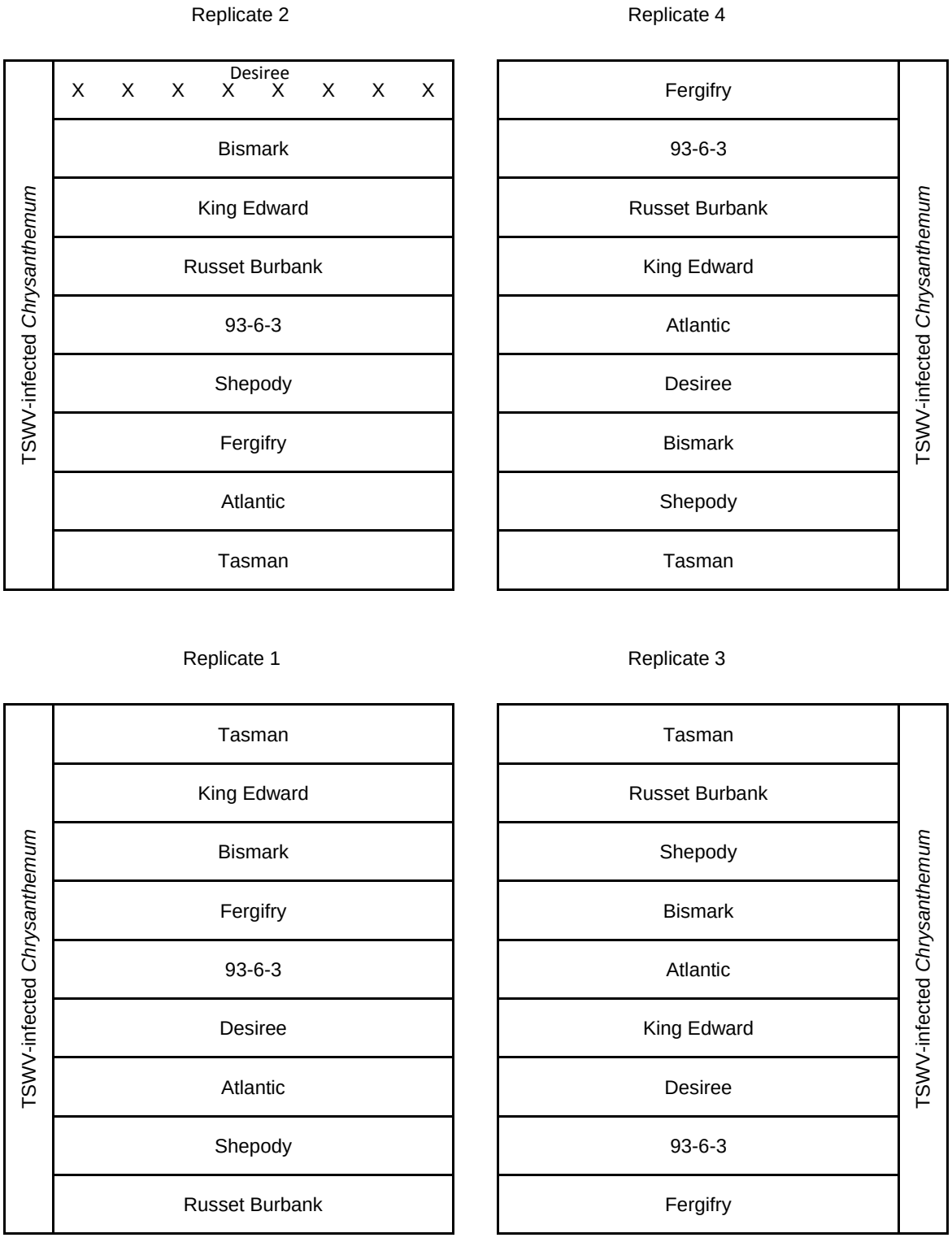


Figure 2.8 Potato cultivar trial layout conducted as a randomised complete block design with 8 plants for each of 9 cultivars in a 1 x 8 arrangement, in plots of 3 m x 3 m with four replications (288 plants), at University of Tasmania Farm, Cambridge, Tasmania, Dec 2005 - Mar 2006. "X" represents plant spacing (shown for cv. Desiree replicate 2 only).

Results

TSWV infection levels at the University of Tasmania Farm were very low in this season. Only three potato plants in the trial succumbed to TSWV infection, despite the planting of TSWV-infected and *T. tabaci*-infested *Chrysanthemum* plants within the trial. There was no significant difference in the number of TSWV infected plants between potato cultivars, $F_{8,24} = 0.87$, $p = 0.55$, and no significant block effect, $F_{3,24} = 0.71$, $p = 0.56$. There appeared to be no obvious spatial pattern between infected potato plants and TSWV-infected source plants, but this was not tested due to sparseness of the data. The three infected potato plants were located in the first and eighth rows (cv. Atlantic) of replicate 1, and in the fourth row (cv. Fergifry) of replicate 2 (relative to the *Chrysanthemum* plants).

There was no significant difference in the percentage of tubers infected from TSWV-positive plants between the two foliar infected cultivars, Atlantic and Fergifry, $F_{1,1} = 161.45$, $p=0.67$, however sample sizes were small. Cv. Atlantic had an average of 80 percent TSWV-positive tubers from two infected plants (1/1 and 5/8 infected tubers), while Fergifry had 100 percent of tubers infected (2/2 infected tubers) from one infected plant. Tubers were only tested from those plants which had positive foliar TSWV-infections.

Field Trial 3

Penola, South Australia Nov 2006 – Mar 2007

Materials and Methods

The South Australian trial was planted in October, 2006. The experiment was conducted as a randomised complete block design with eight plants for each of eight cultivars (Fergifry, Coliban, Russet Burbank, King Edward, Atlantic, Desiree, Bismark and Shepody), in plots of 3 m x 3 m with 4 replications (Fig. 2.9). Potato tubers were planted with 0.4 m between plants in each row, and 0.4 m between rows. Planted tubers were either sourced from certified TSWV-free stock (tested in the previous season), or were tested prior to planting by DAS-ELISA. Plots were prepared following standard commercial practice, with tubers planted into furrows.Buffer zones of bare earth of 2 m in width were established between replicates and surrounding the entire trial area. The trial site was situated within a larger commercial potato crop, and the management of the trial site was largely governed by decisions made by the grower according to the needs of this crop. The field was sprayed with herbicide (formulation unknown) to kill all weeds before planting tubers, and the trial site was not weeded during the trial. Plants were watered by centre pivot according to the needs of the commercial crop. No fungicide or insecticide treatments were planned, however insecticide treatments (formulations unknown) were applied early in the trial by the grower due to concerns about the level of thrips in the surrounding potato crop. The trial area was surrounded by a mixture of native and improved grasses, clovers, capeweed, and other weeds. In the five years immediately prior to the trial, the area was under permanent pasture.

No source of TSWV inoculum or *T. tabaci* was provided for this trial because the trial site was located within a commercial potato crop, however this cropping site had experienced losses from TSWV in recent years (C. Longbottom, Saffries Pty Ltd, personal communication, 2006). At fortnightly intervals, four weeks after emergence, leaf samples were taken from all plants by Field Officers from Saffries Pty Ltd, and sent to Tasmania for testing by DAS-ELSIA. At the conclusion of the trial, all tubers from infected plants were harvested and sent to Tasmania for assessment of TSWV infection. Data were analysed using ANOVA in Genstat 13.2. Thirty yellow sticky traps were placed in the commercial crop surrounding the field trial for fortnightly monitoring of thrips numbers, as leaf examinations were not possible for this interstate crop. Due to windy conditions the first two samplings of yellow sticky traps were mostly covered in debris and were impossible to score. The grower subsequently applied insecticide to the field trial (and surrounding crop) due to concerns that the presence of thrips might result in a TSWV outbreak. For these reasons thrips monitoring was abandoned.

Figure 2.9 Trial layout for potato cultivar trial conducted as a randomised complete block design with 8 plants for each of 8 cultivars in a 1 x 8 arrangement, in plots of 3 m x 3 m with four replications (256 plants), at Penola, South Australia Oct 2006 – Mar 2007. "X" represents plant spacing (shown for cv. Desiree replicate 2 only).

Results

TSWV-infection levels were moderate across the South Australian trial, ranging from 3-22 percent across cultivars, despite the fact that no TSWV-inoculum source was added, and insecticides were applied early in the trial (Table 2.5). Variability was high across replicates, resulting in no statistically significant difference between cultivars, $F_{7,21}$ = 1.73, p=0.15, with no significant block effect, $F_{3,21}$ = 0.28, p = 0.84. Because of the particularly high variability in cv. Russet Burbank, which had nearly 38 percent infection in one replicate, and no infection in the other three replicates, the analysis was repeated without this cultivar.

Table 2.5 Incidence of TSWV across potato cultivars in randomised block design with 8 plants for each of 8 cultivars in a 1 x 8 arrangement in 4 replications (256 plants).

	Number of plants infected (out of 8 per replicate)				Average percentage infection
Cultivar	**Replicate 1**	**Replicate 2**	**Replicate 3**	**Replicate 4**	
Atlantic	1	0	1	2	12.5
Bismark	1	1	3	2	21.9
Coliban	1	0	0	0	3.1
Desiree	0	1	0	0	3.1
King Edward	0	0	1	0	3.1
Fergifry	0	0	0	1	3.1
Russet Burbank	0	3	0	0	9.4
Shepody	0	1	0	0	3.1

Removing Russet Burbank from the analysis resulted in a significant difference between cultivars, $F_{6,18}$ = 3.16, p=0.026, again with no significant block effect, $F_{3,18}$ = 0.43, p = 0.73. Tukey-adjusted pair-wise comparisons in this second analysis at $p < 0.05$ showed Bismark to have higher TSWV infection levels than all other cultivars, except for Atlantic. All cultivars in this trial exhibited infections at levels greater than the maximum allowable infection level (2%) in seed crops.

A logistic regression of the proportion of infected tubers per plant with cultivar showed no statistically significant differences in tuber infection between cultivars of foliar infected plants, ($X^2_{7,123}$ = 4.90, p = 0.67) (Fig. 2.10) Because several cultivars had zero

frequencies, resulting in poor convergence, the three cultivars with zero tuber infections were removed, but the model was still not significant ($X^2_{4,123}$ = 4.90, p = 0.30). Variability in tuber infections was high in Bismark and Russet Burbank, ranging from 8-100 percent in Bismark and 0-75 percent in Russet Burbank. Atlantic on the other hand ranged only from 78-100 percent. The number of tubers per plant also varied considerably (Table 2.6).

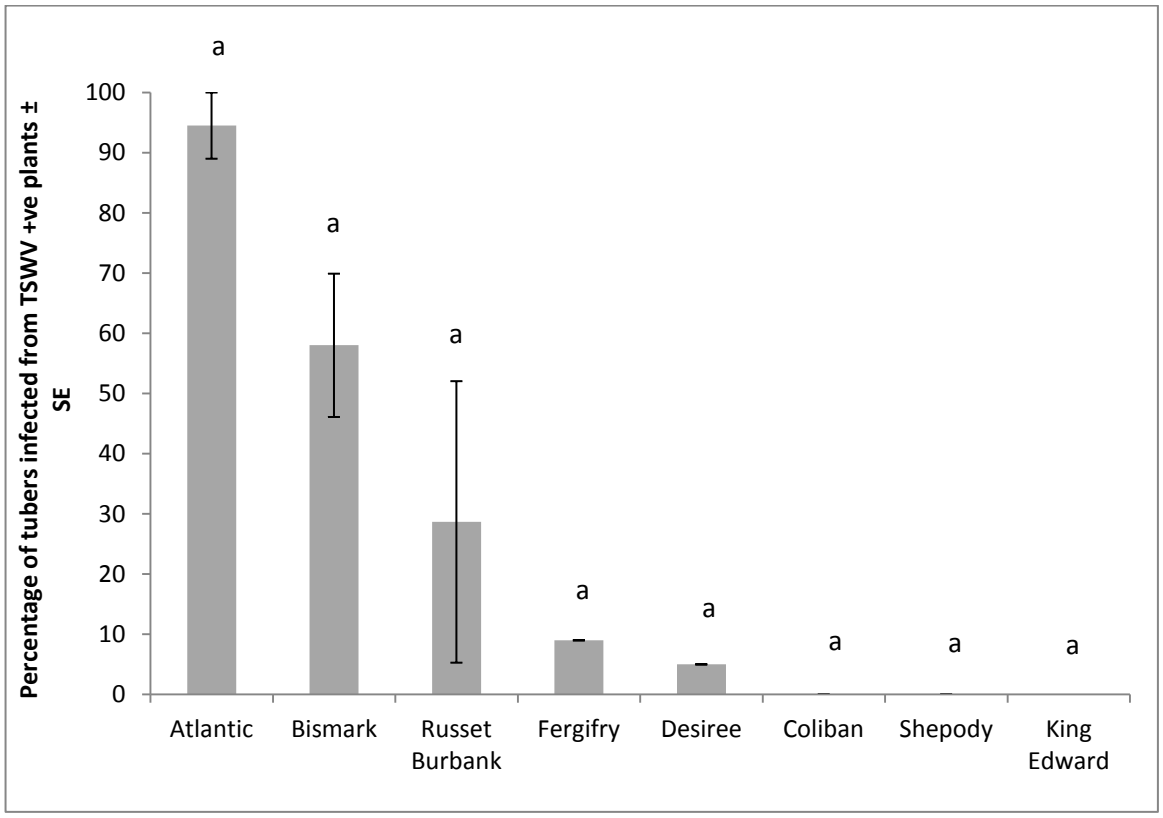


Figure 2.10 The level of TSWV translocation from infected foliage to tubers across 8 potato cultivars in randomised block design with 8 plants for each of cultivar in 1 x 8 arrangements in 4 replications (256 plants). Tubers were only tested from plants which had positive foliar TSWV-infections (see Table 2.5). Data are expressed as mean ± *SE*.

Table 2.6 Percentage of TSWV-infected tubers and total tubers per plant for each potato cultivar in the South Australian trial. Only tubers from plants testing positive for TSWV foliar infection were tested.

Cultivar	Number of plants infected	Percentage of tubers infected per plant (total tubers per plant)						
Bismark	7	45 (20)	63 (32)	100 (14)	23 (22)	72 (18)	34 (32)	8 (24)
Atlantic	4	100 (3)	100 (9)	78 (18)	100 (6)			
Russet Burbank	3	11 (18)	75 (16)	0 (20)				
Fergifry	1	9 (22)						
Desiree	1	5 (20)						
Coliban	1	0 (22)						
Shepody	1	0 (24)						
King Edward	1	0 (24)						

Discussion

The three field trials produced varying levels of TSWV infection. Significant differences between cultivars in relative TSWV infection were not seen, nor were there statistically significant differences between cultivars in translocation of TSWV to tubers. Despite this, the results are not dissimilar to those of Jericho (2005) (see Table 1), where significant differences were also few, but indicated that Atlantic and Bismark may have higher rates of TSWV translocation to tubers than other cultivars tested. Some differences to Jericho (2005) are also suggested here. Shepody is considered to have high susceptibility to virus translocation to tubers (following mechanical inoculation), while Russet Burbank is considered to have a moderate level of resistance to translocation, and Coliban a high level of resistance (Jericho, 2005; Wilson, 2001). The results here supported these previous observations for Russet Burbank and Coliban, both having 0-25 percent tuber translocation in the South Australian trial (albeit with no significant difference between these cultivars), however Shepody showed no virus translocation to tubers, which contradicts earlier findings. In the Tasmanian trial where tuber infection was measured, Atlantic (n = 2) and Fergifry (n = 1) both exhibited 80-100 percent of tubers infected, although the very low sample size (only 3 potato plants infected across the trial) was insufficient to test for differences with any confidence. These results contrast with those of the South Australian trial where Atlantic had significantly higher tuber infection (95 percent) than Fergifry, which only had nine percent of tubers infected.

A high level of resistance to thrips feeding in Bismark in both cage and field trials was reported by Jericho (2005). In the Tasmanian trial where *T. tabaci* numbers were monitored, Bismark showed no field resistance to *T. tabaci*. Bismark (along with Russet Burbank, Russet Ranger and King Edward) had higher numbers of thrips per leaf than Atlantic and Shepody. While significant differences in the number of thrips across potato cultivars were observed, there was no correlation between the percentage incidence of TSWV foliar infection with the number of thrips per leaf across the whole trial, or from single sampling dates, or from combinations of early sampling dates. This suggests that small differences in preference between cultivars may be relatively unimportant in explaining infection rates. However there are several factors to consider. An interaction between cultivar susceptibility and thrips preference may have occurred, masking the importance of thrips numbers if all cultivars were not equally susceptible to TSWV. Initial infection rates are the result of an influx of viruliferous thrips into a potato crop. If the initial influx and immediate feeding of viruliferous thrips is the dominant driver of TSWV infection, then the relative attraction of a potato cultivar over other non-potato hosts will be of critical importance. Alternatively, if the subsequent reproduction of thrips and rapid expansion of population levels is also important, then the choice of oviposition host and juvenile development will be critical in determining differences in disease incidence between crops. These are further investigated in host preference and oviposition choice tests (Chapter 4).

Jericho's hypothesis that Bismark and Royal Blue had some level of resistance to thrips because of the large difference between infection rates from mechanical inoculations and field infections, and from no-choice cage experiments is not supported by this study. The results here suggest that Bismark does not appear to have any field resistance to thrips from the measures quantified in this study (Royal Blue was not tested due to unavailability). The field results here also show Atlantic and Bismark to be the most susceptible to foliar and tuber infections. Combining high thrips numbers, high rates of foliar infection, and very high translocation of the virus to tubers, Bismark does not present well as a candidate for potato cultivar resistance to TSWV.

Pre-trial surveys at the Tasmanian site in 2005 showed high levels of *T. imaginis*, but did not detect *T. tabaci* in spring (November), however *T. tabaci* adults were found in abundance on the potato plots and surrounding weeds during the warmer summer months of the trial, suggesting a difference in seasonal influence on the life cycle of these two species. This is supported by data from the Tasmanian Plant Pest Database and Invertebrate Collection, where records show that the peak collections of *T. imaginis*

in Tasmania occur in November, whereas peak collections of *T. tabaci* occur in January (Plant Health Australia, 2001). In other Australian States records indicate that the peak collection month of both species occurs between September and November (Plant Health Australia, 2001). This may indicate that *T. tabaci* requires warmer temperatures than *T. imaginis* to emerge from its overwintering stage as either adults in weeds and crop volunteers or as pupae in the soil for development, as Tasmania has a much cooler climate than mainland Australia. However collection records must be interpreted with caution, as these may be skewed by the timing of collecting trips, the hosts being surveyed, collecting methods and the purpose of the collecting trip. The surveys conducted by Wilson (1998) on lettuce farms in southern Tasmania, which found no *T. imaginis,* used yellow sticky traps only, so detections were reliant on dispersal of this species across lettuce growing areas. Thrips surveys in this study were conducted by plant beating on a range of plant species surrounding the trial site.

There is a number of possible reasons for variation in results between these three trials, and between these trials and those of Jericho (2005). The source of TSWV inoculum was very likely different for each trial. Infected tomato plants were added to one trial, infected *Chrysanthemum* plants to another, and the third trial in South Australia relied only on natural sources. The predominant source of TSWV inoculum in the first two trials could also have come from natural sources. The two Tasmanian trials were both in close vicinity (less than 1 km) of TSWV-host crops such as pea and lucerne, and were also surrounded by weedy areas containing TSWV-host species such as: capeweed (*Arctotheca calendula*), blackberry nightshade (*Solanum nigrum*), sowthistles (*Sonchus* spp.), wild turnip (*Brassica rapa*), shepherd's purse (*Capsella bursa-pastoris*), chickweed (*Stellaria media*), fat hen (*Chenopodium album*), clovers (*Trifolium* spp.), mallows (*Malva* spp.) and *Datura* sp.. The vector competence and transmission efficiency of *T. tabaci* has been shown to vary depending on the acquisition host species (Chatzivassiliou *et al.,* 1999). Virus distribution and titre in the inoculum source plants, which affect the rate and efficiency with which *T. tabaci* acquire TSWV (German *et al*, 1992), would consequently have influenced the number of thrips transmitting the virus in the trial. Transmission efficiency has also been shown to vary with virus strain (Chatzivassiliou *et al.,* 1999; Jenser *et al*., 2002; Nagata *et al*., 2000; Naidu *et al*., 2003, 2008; van de Wetering *et al*., 1996; Wijkamp *et al.,* 1995).

Differences in vector competence and host preference, including potato cultivar preference, between genetically distinct sub-populations of *T. tabaci* could also have influenced overall infection rates, as well as infection levels between cultivars. Evidence for the existence of genetically distinct populations relating to host and vector

competence is shown and discussed in Chapter 5. Explanations for the very low rate of infection in the second Tasmanian trial could be due to the thrips population from *Chrysanthemum* being disinclined to move to neighbouring potato plants, and/or the potato plants may have shown greater resistance to this particular strain of TSWV. Given that the populations of *T. tabaci* that were added to the first Tasmanian trial were subsequently shown to be non-vectors of TSWV (Chapter 5), this and the South Australian trial were solely reliant on transmission by thrips from the natural environment.

The time at which viruliferous thrips moved into potato could have affected infection levels, as it is known that potato develops mature plant resistance (Jericho, 2005; Thresh, 1974; Wilson, 2001), in particular by reducing the efficiency of virus translocation from leaf to tuber (Wilson, 2001). It could be assumed that when viruliferous thrips move into potato at an early stage, the difference in tuber infection between cultivars would be greatest, due to the known resistance of some cultivars to virus translocation. In later infections however, as all cultivars develop some level of resistance, the difference between cultivars would be lessened. Systemic movement is also affected by temperature, with high temperatures reducing translocation of the virus (Llamas-Llamas *et al*., 1998; Moury *et al*., 1998; Soler *et al*., 1998) and water stress (Córdoba *et al*., 1991). Other effects that must be taken into consideration, that were not controlled in these trials, include growth habit and plant architecture. For example, multi-stemmed potato plants tend to have fewer tubers infected than single-stemmed plants, regardless of genotype, because thrips may have only infected a single stem.

The variation in results across these trials highlights the sporadic nature of TSWV outbreaks in potato in southern Australia. At the beginning of this study, TSWV was ranked as one of the most important issues facing the potato industry, with significant losses emerging in the 1990s and recurring almost every year up to 2005 (Jericho, 2005). Since then the incidence and importance of TSWV outbreaks have greatly declined, with only trace infection rates and no seed crops rejected on the basis of exceeding the infection threshold limits (C. Wilson, personal communication 2011). The cause of this shift remains unresolved. Despite significant work on TSWV epidemiology by Jericho (2005), the source of outbreaks and factors affecting the vector competence of *T. tabaci* in Australia are still unknown. One possible explanation could be a change in the crops and their planting dates across south-eastern Australia. Large influxes of *T. tabaci* into susceptible annual crops like potato might result fromnearby alternative host crops, such as onion, being rvested or dryland lucerne drying out in January. Changes in crop plantings and location could have large impacts on thrips numbers and flights into potato cropping areas.

Because high numbers of onion thrips were observed on cv. Bismark, contrary to expectations, further work is required to determine why this was the case. The two cultivars (Bismark and Royal Blue) put forward by Jericho (2005) as possessing resistance to thrips feeding and oviposition respectively, both have dark green foliage, so colour preference tests (Chapter 3) will examine the strength of colour preferences in *T. tabaci*, and whether differences in green hue or intensity can affect thrips preferences. Laboratory-based host preference and oviposition choice tests (Chapter 4) will further examine differences in attraction to potato cultivars by *T. tabaci*, by controlling for a range of factors that may have influenced field trial results.

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Chapter 3 - Colour preferences of the *Tomato spotted wilt virus* (TSWV) thrips vectors: onion thrips, *Thrips tabaci* Lindeman, western flower thrips, *Frankliniella occidentalis* Pergande, and tomato thrips *Frankliniella schultzei* Trybom (Thysanoptera: Thripidae).

Abstract

The colour preference of onion thrips, *Thrips tabaci* (Lindeman), western flower thrips, *Frankliniella occidentalis* (Pergande), and tomato thrips *Frankliniella schultzei* (Trybom) was tested using two-choice assays in the laboratory to determine if thrips are able to use colour cues in host location. Tests were done eliminating background contrast as a factor using individual thrips. Red, blue, yellow and white coloured cards were paired with a mid-green card. *T. tabaci* strongly preferred mid-green over blue, red, and white, with over 80 percent preferring mid-green in each pairing. There was no difference in the preference of *T. tabaci* between mid-green and yellow. Seventy-four percent of *F. occidentalis* preferred yellow over mid-green, but mid-green was preferred to all other colours. Seventy percent of *F. schultzei* chose yellow over mid-green, and mid-green was preferred over blue and white, whilst the difference in preference between mid-green and red was not significant. A comparison of the relative strength of these colour preferences between the three species only showed a significant difference in preference for yellow between species, due to the greater preference of *T. tabaci* for mid-green over yellow than the other thrips species.

In further experiments using only *T. tabaci*, this species showed a strong preference for light-green over dark green and for mid-green over dark green, and exhibited a strong preference for light green colour card over detached leaves of four potato cultivars (Shepody, Russet Burbank, Bismark, Atlantic). Spectral reflectance curves revealed that there was no significant difference across the 400-700 nm wavelength range between Shepody and Russet Burbank, but all other cultivars were different to each other. In order from highest reflectance to lowest reflectance in the range 530-650 nm, which primarily corresponds to green and yellow, were Shepody = Russet Burbank > Fergifry > 93-6-3 > Atlantic > Bismark > Spunta > Royal Blue > Tasman. Peak reflectance of all potato cultivars was at 552 nm, and a comparison of cultivars at this wavelength again showed highly significant differences, but also some similarities between certain cultivars. In order from highest reflectance to lowest reflectance at 552 nm, were Shepody = Russet Burbank > Fergifry = 93-6-3 > Atlantic = Bismark > Spunta = Royal Blue = Tasman. It is suggested that the strong preference of *T. tabaci* for light green colours could play an important role in host selection, including at the cultivar level. In areas where *T. tabaci* are the dominant vector of TSWV in potato or other crops, such as Tasmania, colour preference may offer a good basis for lessening TSWV infection via cultivar selection, crop management and push-pull trap strategies for pest control.

Introduction

Phytophagous insects locate hosts by responding to a range of stimuli, including visual, mechanical, gustatory and olfactory characteristics (Prokopy & Owens, 1983; Visser, 1986). Determination of colour preferences of an insect species, such as *T. tabaci*, is important for a number of reasons. It provides the basis for efficient sampling, monitoring and sometimes control by mass trapping using coloured sticky traps, which have been used under greenhouse and field conditions for *T. tabaci* Lindeman*, Thrips palmi* Karny, *Frankliniella occidentalis* Pergande, and other thrips species (Cho *et al*., 1995; Lu, 1990; Roditakis *et al*., 2001; Szenasi *et al*., 2001; Terry, 1997; Tsuchiya *et al*., 1995; Vernon & Gillespie, 1995). Coloured sticky traps are a rapid, cost-effective tool for monitoring thrips populations, both for estimating thrips population densities as economic indicators for control measures and for quarantine surveys. Colour preference may also provide an indication of potential host preferences for either feeding or oviposition, which could be used in cultivar selection and breeding. 'Push-pull' trap systems to draw vector thrips away from crops, and into more highly preferred non-commercial plantings, may also be developed from a better understanding of colour preference (Blumthal *et al*. 2005).

Cultivars within a number of crop species have been identified or bred for insect resistance on the basis of plant colour, in particular on the basis of foliar green hue and intensity, including poinsettia (Medina-Ortega, 2011), peanut (Ekvised *et al*., 2006), and onion (Alimousavi *et al*., 2007; Diaz-Montano *et al*., 2010; Yousefi *et al*., 2011). Thrips counts in field trials (Chapter 2) showed differences in the number of onion thrips on potato leaves between cultivars. The highest numbers of thrips were found on the dark green cv. Bismark and the fewest thrips on the lightest green cv. Shepody. However the results across other cultivars suggested that other factors besides intensity or brightness of green hue might be influencing preference. Further testing of preference between colours and between different intensitities of green hue is warranted to help delineate whether leaf colour is an important host finding cue for thrips in potato. An evaluation of spectral reflectance of potato cultivars is also necessary, because insects have a fundamentally different visual system to humans, with sensitivity to different wavelength ranges (Arnold, 2010). Differences or similarities between leaf or flower colours as perceived by humans may be very different to those perceived by *T. tabaci*.

The mechanisms behind vector thrips preferences are still largely uncertain, but visual ecological cues, including colour, play an important role in thrips preference for hosts (Bernays & Chapman, 1994; Reitz, 2009; Terry, 1997). Reeves (2010) has pointed out that despite the general trend in recent times of studies and reviews ignoring or downplaying the importance of insect vision in host plant location in favour of chemical

cues, perception of colour and shape can be as important, or in some cases more important, than chemical cues (Bullas-Appleton *et al*. 2004; Doring & Chittka 2007; Gish & Inbar 2006; Reeves & Lorch, 2009; Stenberg & Ericson 2007; Wenninger *et al*. 2009). Reeves (2010) also gave several examples to dispel the idea that insects cannot visually differentiate between plant species. Visual discrimination between host species in the absence of chemical cues has been demonstrated by the weevil, *Euhrychiopsis lecontei* (Reeves & Lorch, 2009), and aphid, *Hyalopterus pruni* (Moericke, 1969), and between host plant cultivars by the cabbage root fly, *Delia radicum* (Prokopy *et al*., 1983).

Studies have shown that most insects possess three photoreceptors, sensitive to UV (345 to 360 nm), blue (400-450 nm) and green (515-540) (Natwick *et al*., 2007), while some species within the Hymenoptera and Lepidoptera have a much greater spectral sensitivity derived from four, five or even six different photoreceptors, extending their visual range into the far red (above 620 nm) (Briscoe & Chittka, 2001). Vernon and Gillespie (1990) suggested that *F. occidentalis* had trichromatic vision (three different photoreceptors) sensitive to 350 to 360 nm in UV, 440 to 450 nm in blue, and 540 to 570 nm in yellow, because blue was the most attractive colour to this species. However, electroretinograms of *F. occidentalis* conducted by Matteson & Terry (1992), showed only two peaks of photo efficiency at 365 nm and 540 nm suggesting only two photoreceptors. Terry (1997) has further argued that flower thrips have only two types of photoreceptor, one being sensitive to UV and the other sensitive to green and yellow wavelengths. Within the Thysanoptera, gladiolus thrips (*Taenothrips simplex*) and tomato thrips (*F. schultzei*) have been reported to be attracted to red (Walker, 1974; Yaku *et al*., 2007), which corresponds to colours of their primary hosts, although no physiological evidence exists for red-sensitive photoreceptors in *F. schultzei* (Yaku *et al*., 2007). Other thrips species are believed to be red colour-blind (Matteson & Terry, 1992; Walker, 1974).

Different colours are preferred by different insect families, summarised by Hoback *et al*. (1999), but colour preferences may differ within families, (Cross *et al*., 1976), within genera (Hoddle *et al*., 2002), and even between instars and sexes within species (Leong & Thorp, 1999; Kühnle & Müller, 2011). Colour preferences may also differ within species depending on life stage (Jenkins & Roques, 1993; Kring, 1970). Most insect species are attracted to colours that resemble the flowers or foliage of their hosts or food. Yellow is a commonly preferred colour across the insect class (Borror *et al*., 1989), perhaps because the peak colour reflectance of plants is in the yellow band at 560-580 nm, which Prokopy and Owens (1983) have suggested acts as super-normal foliage stimulant to herbivorous insects. Green, being the dominant colour of plant foliage, has

also been shown to attract a number of insect species, particularly aphids (Archetti and Leather, 2005; Hagen *et al*., 2003, 2004; Karageorgou & Manetas, 2006).

Colour and cultivar preferences by thrips have been demonstrated (Herrin & Warnock, 2002; Maris *et al*., 2003). Trap attractiveness and thrips capture rates have been shown to vary according to trap colour (Beckham, 1969; Childers and Brecht, 1996; Cho *et al*., 1995; Gillespie and Vernon, 1990; Walker, 1974; Yudin *et al*., 1987). The most preferred colours for *T. tabaci, F. occidentalis,* and *F. schultzei* demonstrated in choice tests or field observations are summarised in Table 3.1, although these studies have often conflicted with each other and few have been done in the laboratory or with host plants. Some researchers have even found different colour preferences across years, for example, Demirel & Yeldirim (2008) found yellow to be highly preferred by *T. tabaci* over other colours in 2006, but in 2007, blue was the most preferred colour.

Green has been shown to be one of the least attractive colours for *T. tabaci* (Demirel & Yeldirim, 2008; Teulon & Penman, 1992), and *F. occidentalis* (Matteson & Terry, 1992; Vernon & Gillespie, 1990). Only a few studies on these thrips species have looked at differences in preference based on green hue. Gillespie and Vernon (1990) observed no difference between light and dark green in attracting thrips. Ranamukhaarachchi and Wickramarachi (2007) found slightly higher numbers of thrips (*Ceratothripoides claratris)* on light green traps compared to dark green, but about forty percent more thrips on tomato plants with dark green traps compared to those plants with light green traps. Other studies have tended to show that light green is preferred by various thrips species to dark green (Culliney, 1990; Yamamoto, 1984). If one or more thrips vectors of *Tomato spotted wilt virus* (TSWV) demonstrates differences in preference based on leaf colour, then this might offer potential for selection and breeding in potato, as some potato cultivars show distinct differences in foliar green hue and intensity.

The purpose of this laboratory study was firstly to determine the colour preference of *T. tabaci, F. occidentalis,* and *F. schultzei* between white, yellow, red, blue and green. Secondly, because *Thrips tabaci* is the only known vector of TSWV in Tasmania, this species was tested for any differences in preference between different shades of green (light, medium, dark). In-vitro choice experiments were chosen to delineate these preferences in order to exclude effects of colour contrast that occurs with sticky traps placed in field situations, and to exclude other confounding variables, such as environmental factors, predation and plant volatiles. Nine processing cultivars (Shepody, Russet Burbank, Fergifry, 93-6-3, Atlantic, Bismark, Spunta, Royal Blue, Tasman) were subjected to spectral analysis in order to quantify differences in hue and intensity,

represented by reflectance at different wavelengths. Among these nine cultivars four were chosen for choice testing with *T. tabaci. C*ultivars Shepody and Russet Burbank were chosen because they have noticeably light green foliage, while Atlantic and Bismark were chosen because they have have mid- to dark green leaves. Finally, preference tests pairing a light green card against these cultivars were conducted. Light green card was chosen for this experiment in order to provide a very strong contrast in green intensity between the choices. The light green card also showed peak reflectance at 540 nm, which has been cited as the wavelength with most sensitivity in photoreceptors of some thrips species.

Table 3.1 Highly preferred colours of *T. tabaci, F. occidentalis,* and *F. schultzei* demonstrated in choice tests or field observations.

Thrips species	Colour preference	Test method F = field/glasshouse, L = laboratory T = trap, P = leaf or flower	References
Thrips tabaci	Blue	F, T F, T F, T F, T F, T F, T	Brødsgaard (1993) Czenz (1987) Demirel & Yeldirim (2008) Liu & Chu (2004) Lu (1990) Terry (1997)
	Yellow	F, T F, T F, T F, T F, T F, T F, T	Al-Ayedh & Al-Doghairi (2004) Brødsgaard (1993) Cho *et al*. (1995) Czenz (1987) Demirel & Yeldirim (2008) Teulon & Penman (1992)
	White	F, T F, T F, T F, T	Czcenz (1987) Kirk (1984) MacIntyre-Allen *et al*. (2005) Teulon & Penman (1992)

F. occidentalis	Blue	F, T	Brødsgaard (1989)
		F, T	Chu *et al*. (2000)
		F, T	Chu *et al*. (2006)
		F, P	Chyzik *et al*. (1995)
		F, T	Guam & Giliomee (1994)
		F, T	Matteson & Terry (1992)
		F, T	Natwick *et al*. (2007)
		F, T	Roditakis *et al*. (2001)
		F, T	Vernon & Gillespie (1990)
		F, T	Gillespie & Vernon (1990)
	Yellow	L, P	Blumthal *et al*. (2005)
		F, T	Chen *et al*. (2004)
		F, T	Cho *et al*. (1995)
		F, T	Gillespie & Vernon (1990)
		F, P	Guam & Pringle, 1994.
		F, T	Robb (1989)
		F, T	Vernon & Gillespie (1990)
			Yudin *et al.* (1987)
	White	F, T	Beavers *et al*. (1971)
		F, T	Hoddle *et al*. (2002)
		F, T	Matteson & Terry (1992)
		F, T	Moffitt (1964)
		F, T	Yudin *et al*. (1987)
	Violet	F, T	Matteson & Terry (1992)
		F, T	Vernon & Gillespie (1990)
F. schultzei	Red	F, T	Yaku *et al*. (2007)

Materials and methods

Thrips colonies

A colony of thelytokous TSWV-competent onion thrips, *Thrips tabaci (Lindeman*), was collected from a Tasmanian potato field trial in 2006 (Tas-FT, see Chapter 5). The thrips were reared on common bean pods (*Phaseolus vulgaris*) according to a protocol modified from van de Wetering (1999), in 7cm x 9cm containers, at 25°C ± 1°C, 65 ± 5% RH, with a photoperiod of L16:D8 in a climate-control chamber, using cool white fluorescent light under 450μmol-m^{-2}.s^{-1} photosyntethically active radiation (PAR). Thrips were transferred twice-weekly on to fresh pods. These thrips were sent to Western Australia to be reared at the end of January 2008, in order to conduct colour preference experiments simultaneously with *F. occidentalis* and *F. schultzei*, which are unable to be imported in to Tasmania for biosecurity reasons. *F. occidentalis* and *F. schultzei* were obtained in Perth, Western Australia, from glasshouse cultures of flowering pot marigold, *Calendula officinalis*, and were not reared on green bean prior to testing as was *T. tabaci*. The experiments were conducted at the end of March 2008, so that *T. tabaci* had progressed through approximately two complete generations in Western Australia before colour preferences were assessed.

Rearing of potato plants

Potato cultivars (Shepody, Russet Burbank, Atlantic, Bismark, Spunta, Royal Blue, Tasman) were grown from tissue culture samples obtained from the Vegetable and Associated Industries Branch of the Tasmanian Department of Primary Industries and Water (now incorporated into the Tasmanian Institute of Agriculture), Devonport, in April 2005. Two additional cultivars (Fergifry and 93-6-3) were obtained from the National Potato Variety Tissue Culture Collection, Department of Primary Industry, Victoria. Tissue culture plants were grown in Potato Multiplication media (4.3 g Murashige-Skoog salts, 30 g sucrose, 0.5 g casein hydrolysate, 0.04 g ascorbic acid made up to 1 L with dH_20, and 8 g/L agar type A added before autoclaving) in 7cm x 9cm containers, at 22°C, near saturation RH, 16-hour light and 8-hour dark photoperiod, under cool white fluorescent light. All tissue culture samples tested negative for TSWV in double antibody sandwich enzyme-linked immunosorbent assay (DAS-ELISA) (Clark & Adams, 1977). Tissue culture plants were transplanted to soil in 10x10cm pots when about 5cm tall and grown for a further six weeks in a glasshouse under variable conditions, but with additional lighting to ensure 16-hour light and 8-hour dark photoperiod, and approximate temperature of 25°C ± 1°C and 65 percent relative humidity.

Colour preference

Thrips preferences for different colours were determined using two-choice tests. The tests were conducted in a choice chamber consisting of a clear plastic tube (20cm length, 2.5cm diameter) with openings at both ends and a small hole in the middle in which to place each thrips. A cream-coloured paper towel cover was placed over the chamber to block other colours from the room. The chamber was suspended about 5 cm above a cream-coloured laboratory bench. Coloured squares (20 cm x 20 cm) were cut from Prismacolor® card (white 906 = white, yellow 935 = yellow, scarlet 921 = red, cobalt 909 = blue, pistachio 939 = light green, pine green 932 = dark green) and Quill® card (emerald 90056 = mid-green) (Fig. 3.1). Adult thrips of variable age and sex were collected from rearing containers with a soft-bristled paintbrush and starved for 1 h before being placed in choice chambers. Experiments took place at room temperature (21-26°C) under indirect natural light.

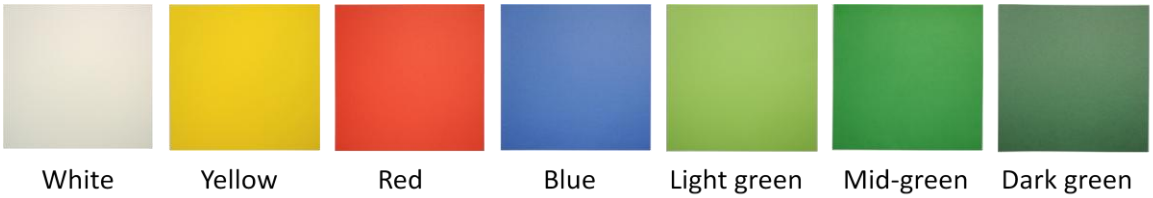

Figure 3.1 Coloured cards used in two-choice experiments.

In the first group of experiments, for each species, mid-green was paired with red, blue, yellow, and white. Mid-green was also paired with the same mid-green in order to test whether any bias existed in the choice chamber. The second group of experiments, using only *T. tabaci,* paired (i) the same mid-green with light green and dark green, (ii) dark green with light green and (iii) light green with yellow.

For each choice combination and each species, 25 thrips were used and each thrips placed singly per trial in the centre of the choice chamber, and given three minutes to reach either end, with colours rotated between each end after every five thrips. Choice chambers were cleaned between colour pairings (every 25 thrips) with 70 percent ethanol, but were not cleaned between runs of five thrips within colour pairings. Visual observation of the experiments suggested that thrips choices did not appear to be influenced by chemical cues of previous thrips, which was confirmed in the results with no obvious sequences or patterns of choices detected. Thrips were scored as preferring a colour if they made it to the very edge of one end of the choice chamber within the time period. The percentage of thrips making no choice was lower than 15 percent for all species, and these were excluded from statistical analyses. Once a thrips reached the

edge of one end, the experiment was stopped, regardless of how much allocated time still remained, and the thrips were not returned to the colony. Thrips were not individually sexed for any of the three species, however random samples from the *T. tabaci* population culture had been sexed on several occasions during the course of the study, and no male *T. tabaci* were found at any time. Experiments on each species were repeated the following day, using different thrips from the same population.

A third group of experiments was also conducted in Tasmania with *T. tabaci* using just the light green colour card against foliage (detached leaves) of four potato cultivars, Shepody, Russet Burbank, Bismark and Atlantic. These cultivars were selected because Shepody and Russet Burbank appear visually to have light green foliage, while Atlantic and Bismark appear to have medium to dark green leaves. The plants were approximately six weeks old (from transplanted tissue culture plants) at the time of the experiments. The leaves used in the choice tests were from plants grown at the same time, in the same place, and under the same conditions as the plants used for taking the reflectance measurements. They were however not the same plants as those used for the reflectance measurements.

Spectral assessment of potato cultivars and colour cards

Spectral reflectance curves of all nine potato cultivars and the seven coloured cards were obtained using a dual-channel spectroradiometer (UniSpec-DC, PP Systems, Hammerhill, MA, USA) recording across the range of 300 to 1100 nm with a 3.1-3.4 nm sampling interval (dependent on wavelength), 3.7 nm resolution and 0.1 nm repeatability. The useful sampling range was between 400 nm and 1100 nm due to the transmittance properties of the foreoptics. The dual channel system uses 2.1 mm diameter glass foreoptics; one channel is used as a cosine receptor the other has a 100 mm stainless steel ferrule covering a polished fiber tip for the target probe (25˚ field of view). Integration time was set to 200 ms and 20 scans were averaged for each recorded spectrum. A Spectralon™ panel (PP Systems) was used as a white reference for spectrometer calibration. Data was collected on an integral PC using UniWin-DC V1.5 software (PP Systems).

Two halogen light globes (150 w) were the only source of light used when taking measurements. Whole leaves, upper surface of the leaf facing upwards, were placed on black velvet, as suggested by O'Neill *et al* (1990), with the spectroradiometer probe suspended approximately 15 cm above the leaf being measured. Three plants of each cultivar, and five leaves from each plant, were measured. The reflectance of each leaf was measured and adjusted by dividing by the reflectance of a calibrated white

reference tile. Reflectances are reported graphically as the average of the fifteen leaves, with standard errors shown for each wavelength measured. In a few cases, because leaves of sufficient size were limited in number, 15 leaves for each cultivar were not available, so some cultivars had averages taken from only 12-14 separate leaf measurements.

Statistical analysis

Using SAS/STAT v9.2, contingency tables were used to test for associations between colour preference and thrips species. Following a significant overall association, five one way sub-tables were constructed to test if there was a preference for each colour. The mid-green versus mid-green pairing was always present to provide a common reference between the colour choices. Because this meant the tables were not independent of each other (Everitt, 1992), the P values of the sub-tables were adjusted using Holm's method (Holm, 1979) to achieve an experiment-wise P value of 0.05. To compare the colour preference relative to mid-green for each species, 2x3 contingency tables for each colour were constructed and tested with an overall chi-square statistic. The null hypothesis for the first two groups of experiments was that there is no preference for one colour over another for each of the thrips species tested. The null hypothesis for third group was that *T. tabaci* has no preference for light green card over any potato cultivar.

Spectral reflectance curves of the potato cultivars across the 400-700 nm wavelength range were analysed with two-way Kolmogorov-Smirnov tests in Genstat v13.0, with a null hypothesis that the two samples follow the same distribution. ANOVA was also performed to compare the reflectance of cultivars at the peak reflectance wavelength in the green region of 552 nm, using 12-15 leaves per cultivar.

Results

Spectral assessment of potato cultivars and colour cards

The spectral analysis of the nine cultivars showed distinct differences between cultivars that generally coincided with visual observations (Fig. 3.2). Only two cultivars were not significantly different to each other across the spectral range tested (400-700 nm), namely Shepody and Russet Burbank, (D = 0.152, N = 92, p = 0.218). In order from highest reflectance to lowest reflectance, were Shepody = Russet Burbank > Fergifry > 93-6-3 > Atlantic > Bismark > Spunta > Royal Blue > Tasman.

An ANOVA was also performed on peak leaf reflectance at 552 nm (threshold of green and yellow-green), which was the wavelength at which the greatest differences in reflectance between cultivars was observed. There were highly significant differences between cultivars at 552 nm, $F_{8,119}$ = 47.58, p < 0.0001. (Fig. 3.3), however these were not as apparent as comparisons across the 400-700nm range. In order from highest reflectance to lowest reflectance at 552 nm, were Shepody = Russet Burbank > Fergifry = 93-6-3 > Atlantic = Bismark > Spunta = Royal Blue = Tasman.

The visual appearances of the four potato cultivars used in preference tests against a light green card were also reflected in the spectral analysis, which showed that there was no difference in reflectance between Shepody and Russet Burbank across the 400-700 nm wavelength, but Atlantic and Bismark were significantly different to each other, reflecting the slightly lighter green hue of Atlantic in glasshouse observations (D = 0.207, N = 92, p = 0.034). Across most wavelengths, particularly in the range 530-650 nm, which primarily correspond to green, yellow-green and yellow, Shepody displayed higher reflectances than Atlantic (D = 0.348, N = 92, p < 0.0001), and Bismark (D = 0.391 N = 92, p < 0.0001). Russet Burbank also displayed higher reflectances than Atlantic (D = 0.315, N = 92, p < 0.001), and Bismark (D = 0.370, N = 92, p < 0.0001).

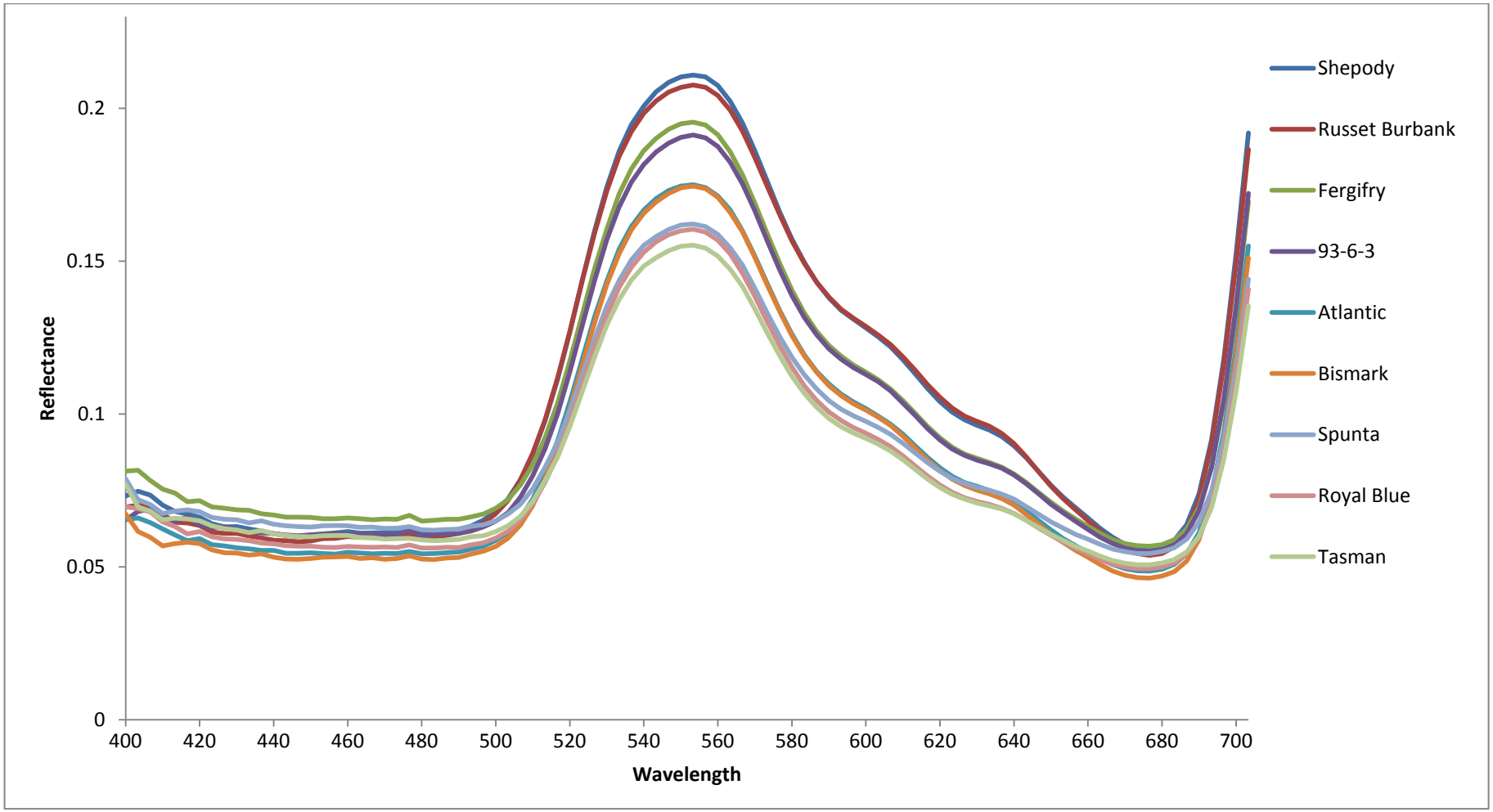

Figure 3.2 Spectral reflectance curves of nine potato cultivars showing reflectance at wavelengths 400-700 nm, with a 3.1-3.4 nm sampling interval. Two halogen light globes (150 w) were the only source of light used when taking measurements. Whole leaves, upper surface of the leaf facing upwards, were placed on black velvet with the spectroradiometer probe suspended approximately 15 cm above the leaf being measured. Three plants of each cultivar, and five leaves from each plant, were measured and adjusted by dividing by the reflectance of a calibrated white reference tile.

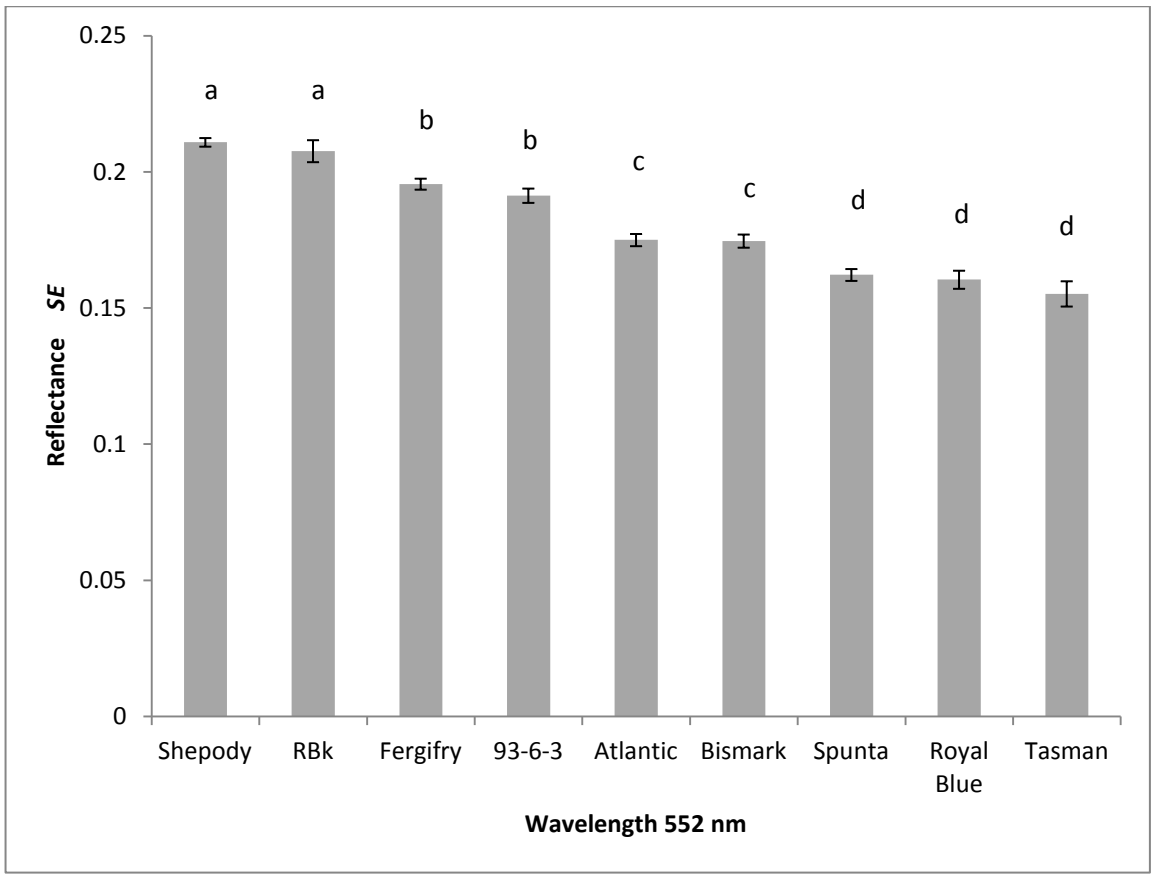

Figure 3.3 Reflectance values of nine potato cultivars at wavelength 552 nm. Data are expressed as the mean of 12-15 potato leaves per cultivar ± *SE*.

The spectral reflectance curves showing the reflectance of the seven colour cards (white, yellow, red, blue, light green, mid-green and dark green) were mainly as expected (Fig. 3.4). There was considerable difference in reflectance between the light green (55%), mid-green (34%) and dark green (18%) colour cards, but all peaked between 520-540 nm, within the green range. The spectrums of potato cv. Atlantic (and other potato cultivars not shown) were closest to that of the dark green colour card, except that the spectral reflectance curves of potato leaves peaked at 550-560 nm, which is the threshold separating green from yellow-green. Between 400-450 nm there was little difference between the reflectance of potato cultivars and that of the yellow, light green and mid-green cards. However, across 450-500 nm (blue), 500-520 nm (blue-green), 520-550 nm (green), 550-570 nm (yellow-green) and 570-600 nm (yellow) these colour cards displayed higher reflectances than potato leaves.

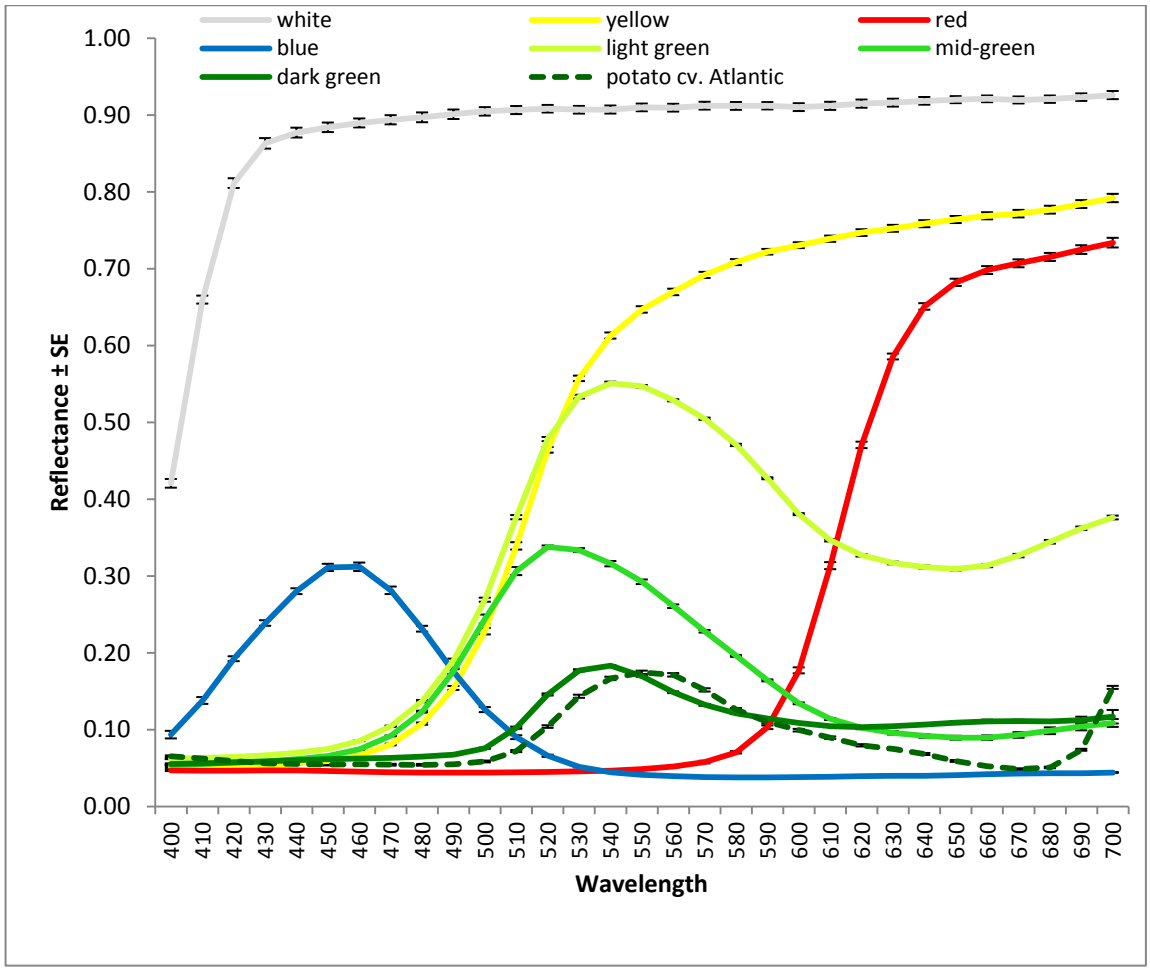

Figure 3.4 Spectral reflectance curves showing reflectance at wavelengths 400-700 nm of seven colour cards (white, yellow, red, blue, light green, mid-green and dark green) and of potato cv. Atlantic. Data are expressed as mean ± *SE*.

Broad colour preferences of the three thrips species

Colour preferences relative to the mid-green control were highly significant for *T. tabaci*, ($X^2_{4,229}$ = 36.69, p <0.0001); *F. occidentalis* ($X^2_{4,220}$ = 39.53, p <0.0001), and *F. schultzei* ($X^2_{4,226}$ = 32.3, p < 0.0001) (Fig. 3.5).

Yellow was highly preferred over mid-green by *F. occidentalis*, with 74 percent of individual thrips in this species moving to the yellow card, ($X^2_{1,43}$ = 10.3, adjusted p = 0.004). Seventy percent of *F. schultzei* also chose yellow over mid-green, ($X^2_{1,46}$ = 7.0, adjusted p = 0.024). However, for *T. tabaci* there was no significant difference in preference within the mid-green and yellow pairing ($X^2_{1,44}$ = 1.46, adjusted p = 0.46).

Only 15 percent of *T. tabaci* chose red over mid-green, ($X^2_{1,47}$ = 23.2, adjusted p <0.0001); and red was also not preferred by *F. occidentalis,* with only 25 percent moving to this colour, ($X^2_{1,44}$ = 11.0, adjusted p = 0.004). However for *F. schultzei* there was no difference in preference between mid-green and red ($X^2_{1,45}$ = 5.0, adjusted p = 0.051).

Mid-green was preferred over blue by all species, with only 13 percent of *T. tabaci* choosing blue ($X^2_{1,46}$ = 25.1, adjusted p <0.0001); 26 percent of *F. occidentalis* choosing blue ($X^2_{1,43}$ = 10.3, adjusted p = 0.004); and 25 percent of *F. schultzei* choosing blue ($X^2_{1,44}$ = 11.0, adjusted p = 0.004). Mid-green was also preferred over white by all species. The white card was chosen by only 12 percent of *T. tabaci* ($X^2_{1,43}$ = 25.3, adjusted p <0.0001); 18 percent of *F. occidentalis* ($X^2_{1,45}$ = 18.7, adjusted p < 0.0001); and 18 percent of *F. schultzei* ($X^2_{1,45}$) = 18.7, adjusted p < 0.0001). There was no significant difference in the mid-green versus mid-green control pairings for *T. tabaci* ($X^2_{1,49}$ = 0.51, adjusted p = 0.48); *F. occidentalis* ($X^2_{1,45}$ = 0.20, adjusted p = 0.65); and *F. schultzei* ($X^2_{1,46}$ = 0.09, adjusted p = 0.77).

A comparison of the relative strength of colour preferences between species showed a significant difference in preference for yellow between species, due to the greater preference of *T. tabaci* for green over yellow than the other thrips species ($X^2_{2,133}$ = 12.19, p = 0.0023). There were no significant differences across species for any of the other colours.

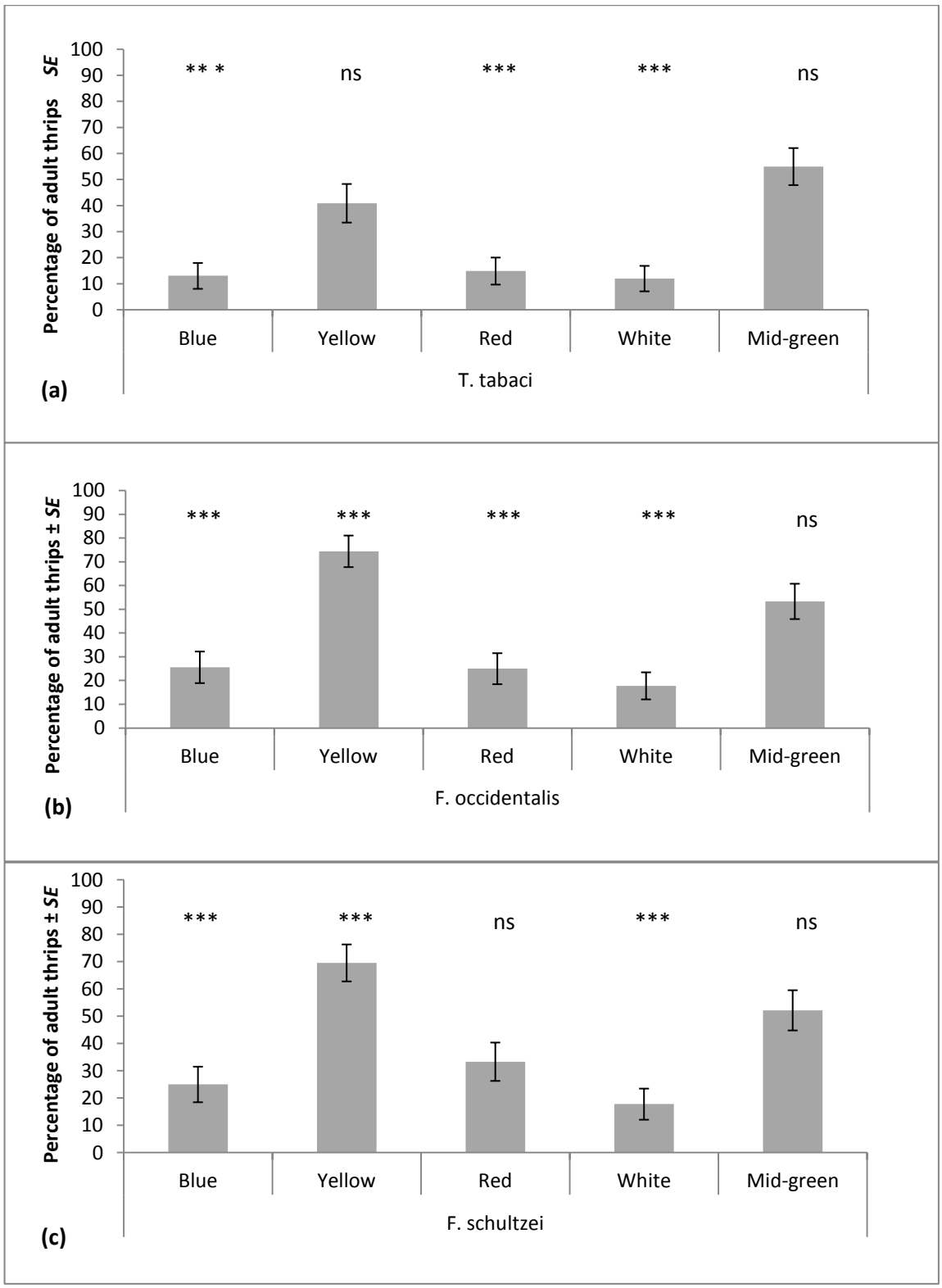

Figure 3.5 Percentage of adult thrips choosing colour card in two choice tests (control mid-green versus blue, yellow, red, white and mid-green) for (a) *T. tabaci,* (b) *F. occidentalis* and (c) *F. schultzei*. For each choice combination 50 onion thrips were used and each thrips placed singly in the centre of the choice chamber, and given three minutes to reach either end. Data are expressed as mean ± SE. (*** = $p < 0.001$, **= $p<0.01$, ns = not significant in relation to mid-green choice)

Green hue and intensity preferences of T. tabaci

Light green was highly preferred by *T. tabaci* over dark green ($X^2_{1,70}$ = 41.66, p < 0.0001); with 90 percent of individual thrips choosing light green (Fig. 3.6). Mid-green was also highly preferred over dark green ($X^2_{1,48}$ = 30.08, p < 0.0001); with 90 percent of individual thrips choosing the mid-green. There was no significant difference in preference between light green and mid-green ($X^2_{1,47}$ = 0.53, p = 0.47). Light green and mid-green were therefore equally preferred and both preferred over dark green. There was a highly significant difference between light green and yellow ($X^2_{1,47}$ = 13.30, p = 0.0003); with 76 percent of *T. tabaci* choosing light green over yellow.

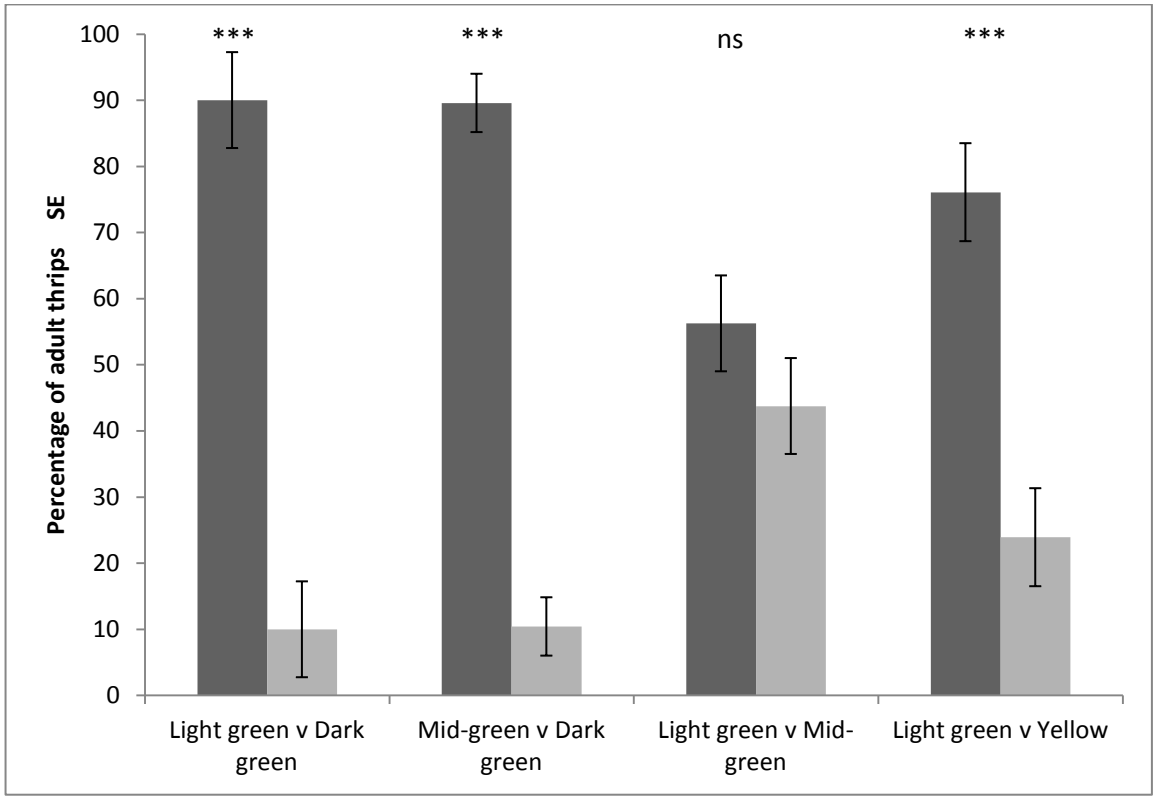

Figure 3.6 Percentage of adult *T. tabaci* choosing colour card in two choice tests (dark green versus light green; mid-green versus dark green, light green and yellow; and light green versus yellow). The tests were conducted in a choice chamber as for Figure 3.5. The first mentioned colour of each pairing is that of the left-most column. Data are expressed as mean ± *SE*. *** = p < 0.001, ns = not significant.

T. tabaci demonstrated a highly significant preference for the light green card over all potato cultivars ($X^2_{1,191}$ = 89.85, p < 0.0001) (Fig. 3.7). Specifically, when offered a choice between light green card and potato cv. Shepody, 80 percent of *T. tabaci* moved to the light green card, 81 percent chose light green over cv. Russet Burbank, 85 percent chose light green over cv. Bismark, and 93 percent chose light green over cv. Atlantic. There was no tendency for the relative response to any cultivar to differ from the rest ($X^2_{3,191}$ = 3.12, p = 0.37).

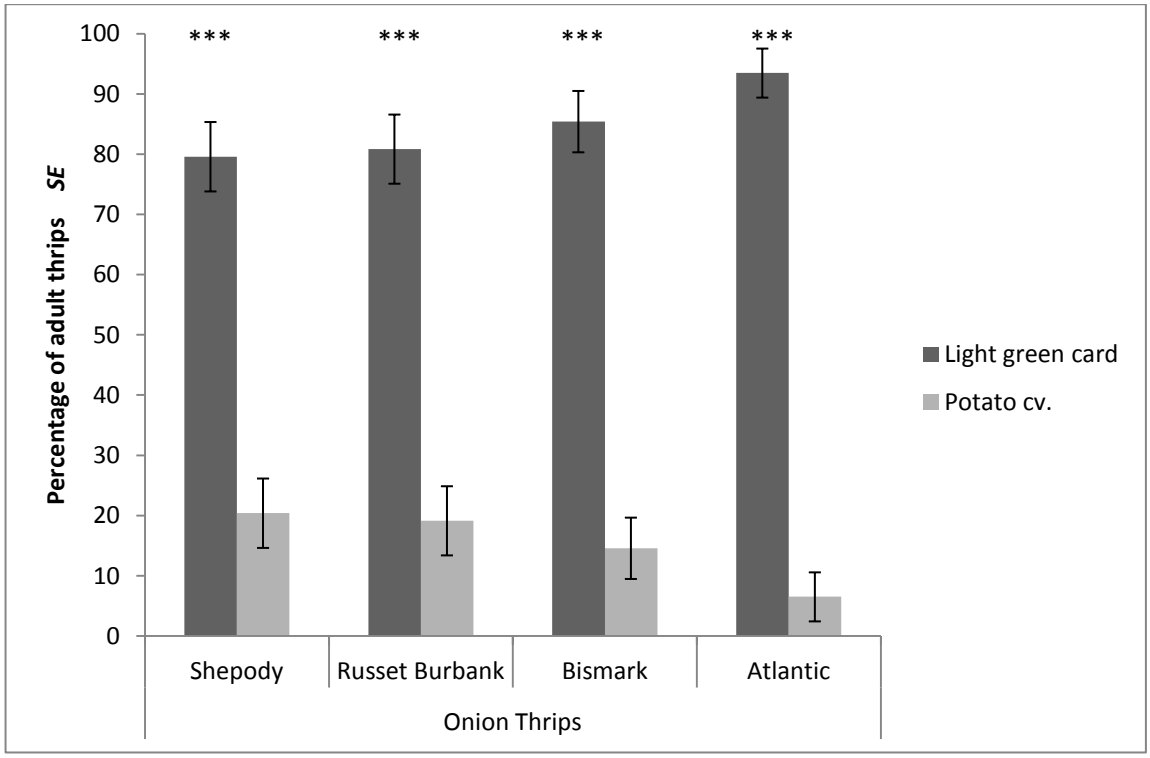

Figure 3.7 Percentage of adult *T. tabaci* choosing colour card in two choice tests (light green colour card versus potato leaf cv. Shepody, Russet Burbank, Bismark and Atlantic). The tests were conducted in a choice chamber as for Figure 3.5. Data are expressed as mean ± *SE*. *** = p < 0.001.

Discussion

Other studies of vector thrips have generally suggested blue, white and yellow to be the most preferred colours of thrips, particularly for *F. occidentalis*, and these colours are often recommended for sticky trap surveys (Cho *et al*., 1995; Hoddle *et al*., 2002; Lu, 1990; Roditakis *et al*., 2001; Szenasi *et al*., 2001; Terry, 1997; Tsuchiya *et al*., 1995; Vernon & Gillespie, 1995). Paired colour preference trials here indicate that yellow is likely to be the more highly preferred colour for *F. occidentalis* and *F. shultzei*. Blue and white were much less preferred than mid-green for these species. These results are not in agreement with those studies that have shown that *F. occidentalis* has a strong preference for blue (Brødsgaard, 1989; Chu *et al*., 2000; Chu *et al*., 2006; Gaum & Giliomee, 1994; Gillespie & Vernon, 1990Matteson & Terry, 1992; Natwick *et al*., 2007; Roditakis *et al*., 2001; Vernon & Gillespie, 1990) or white (Beavers *et al*., 1971; Hoddle *et al*., 2002; Matteson & Terry, 1992; Moffitt, 1964; Yudin *et al*., 1987), and they contradict those studies which have found that green is one of the least preferred colours of *F. occidentalis* (Matteson & Terry, 1992; Vernon & Gillespie, 1990). However, other studies have found that *F. occidentalis* is highly attracted to yellow (Atakan & Canhilal, 2004; Blumthal *et al*., 2005; Chen *et al*., 2000; 2004; Cho *et al*., 1995; Gillespie & Vernon, 1990; Robb, 1989; Vernon & Gillespie, 1990; Yudin *et al.,* 1987). The results presented here are not inconsistent with the flower-feeding life history strategy of *F. occidentalis*, which are found in large numbers in yellow flowers, with preferences for yellow flowers over leaves (Kirk, 1997; Yudin *et al*., 1988).

One possible reason for differences between results here and in other studies is the test methodology. Most colour preferences studies on thrips are conducted using coloured sticky traps in the field (see Table 1), which introduces other influences such as trap shape and contrast effects against a different colour background. These can substantially change the attractiveness of colour traps to phytophagous insects (Prokopy & Owens, 1983) and specifically to thrips (Mainali & Lim, 2010; Vernon & Gillespie, 1995). The crop within which sticky traps are placed may also affect colour preference, as colour preferences have been shown to be habitat dependent in thrips (Kirk, 1984) and other insect species (Blackmer *et al*., 2008). Colour preference in thrips can also change depending on plant host growth stage (Czenz, 1987). The methodology of a choice chamber used here was chosen to exclude these variables. Spectral differences between similar colours could also explain differences between studies. For example, Roditakis *et al*. (2001) demonstrated very large differences in preference shown by *F. occidentalis* between four different hues of blue. Differences in reflectance in the UV range between colours of the same hue can also change thrips colour preference (Matteson & Terry, 1992).

The mid-green card in these experiments showed peak reflectance at 520-530 nm. Studies have suggested that in addition to a UV-sensitive photoreceptor, *F. occidentalis* has photoreceptor sensitivity at 540-570 nm in green and yellow with a maximum efficiency at 540 nm (Matteson *et al*. 1992; Matteson & Terry 1992), and possibly 440-450 nm in blue (Vernon & Gillespie, 1990). The mid-green card used here could therefore have been less preferred than a different green hue with peak reflectance closer to 540 nm, because its peak reflectance falls outside of the peak photoreceptor sensitivity of this species. The very low preference for blue colour card by all species of thrips here favours the view of Harris *et al*. (2001) and Terry (1997) that only two types of photoreceptors, sensitive to UV and green-yellow wavelengths, exist in flower thrips. Red was also not preferred by *F. occidentalis*, however for *F. shultzei* the difference between mid-green and red was not significant. This is an interesting result because Yaku *et al*. (2007) found that red was the most highly preferred colour of *F. schulztei*, including over yellow, even though thrips were mostly thought to be red colour-blind. While this study suggests yellow is more highly preferred than red when compared to mid-green, it also shows that red is not less preferred than mid-green, as it is for the other thrips species tested here. One factor that was not controlled in these experiments was potential sex-based differences in colour preferences. While all *T. tabaci* tested were females, *F. occidentalis* and *F. schultzei* were not sexed prior to being placed in the choice chamber. *F. schultzei* has been shown to have sex-specific differences in colour recognition (Yaku *et al*., 2007), as have insects in other orders (Briscoe & Chittka, 2001).

T. tabaci preferred mid-green and yellow equally, but strongly preferred the light green card over yellow in one of the experiments.. *T. tabaci* showed no preference for any other non-green colour above that of mid-green. This contradicts those studies that have found green to be of low preference for *T. tabaci* (Demirel & Yeldirim, 2008; Teulon & Penman, 1992). However, in contrast to *F. occidentalis* and *F. schultzei,* which are anthophilous (flower-feeding) species, *T. tabaci* is phyllophilus, being a generalist and feeding predominantly on non-grass leaves and shoots (Watson, 1926). It is therefore not surprising that *T. tabaci* is less attracted to flower colours than the flower-feeding thrips species. *T. tabaci* in these experiments showed a clear ability to differentiate between green cards with differences in reflection within the same green hue, with both light green and mid-green strongly preferred over dark green. In contrast, Gillespie and Vernon (1990) found that there was no difference between dark and light green traps in attracting thrips in glasshouse cucumber crops. Lewis (1959) also found that certain *Taeniothrips* spp., *Thrips* spp., and *Aeolothrips* spp. were strongly attracted to white but not to green. However in many other thrips species light green has been shown to be

preferred more highly than dark green (Culliney, 1990; Yamamoto, 1984). While Ranamukhaarachchi & Wickramarachi (2007) found that white and blue were the most highly preferred colour traps for *Ceratothripoides claratris,* light green traps were also slightly more attractive than dark green traps. The types of photoreceptors in *T. tabaci* have not been identified, but the results here suggest as they do for *F. occidentalis*, that photosensitivity is most efficient in the green-yellow spectrum.

Reflectance values within a spectral range have been correlated with spectral ranges corresponding to attractive hues, usually with higher reflectances attracting higher numbers of thrips (Brodsgaard, 1989; Vernon & Gillespie, 1990; Walker, 1974). Matteson & Terry (1992) observed this for *F. occidentalis* in the violet-blue range, but not in the wavelength ranges that were less preferred, including those corresponding to green, yellow and red. In this study, *T. tabaci* was most attracted to green, and the same correlation with greater preference for more highly reflective colours within this attractive hue was observed. Matteson and Terry (1992) also found that differences in reflectance within the UV range can also affect thrips attraction, with very high UV reflectance acting as a deterrent, forming the basis for the use of UV-reflective mulches to deter a range of thrips species (Momol *et al*., 2004; Reitz *et al*., 2003). Due to the measuring equipment used in this study, wavelengths below 400 nm were unable to be examined with confidence, and so the influence of potential differences in UV reflectance cannot be ruled out, although Matteson and Terry (1992) suggested that differences in preference were not obvious when colours had less than 35% UV reflectance.

Leaf colour is often associated with other plant attributes, and so may be acting as an indirect cue for one or more factors that affect thrips survival and fecundity. Medina-Ortega (2011) found that *Bemisia tabaci* had a strong preference for light green cultivars of poinsettia over dark green, and that light green cultivars, while having less chlorophyll, had a higher concentration of amino acids. Light and dark green cultivars appeared to have different compositions of amino acids that did not correspond to thrips resistance, but light green cultivars also had lower levels of phenolics known as anti-feedants and toxins to herbivores, thereby resulting in higher fertility on light green cultivars. In peanut, antixenosis-based thrips resistance has been associated with dark green leaf colour (Ekvised *et al*., 2006). Conversely, Alimousavi *et al*. (2007) and Yousefi *et al*. (2011) showed that light green onion cultivars were associated with fewer numbers of *T. tabaci* than mid-green and dark green cultivars, and that light green cultivars had lower leaf wax levels. Diaz-Montano *et al*. (2010) produced a similar result, finding that *T. tabaci*-resistant onion cultivars had yellow-green foliage, while non-resistant cultivars had blue-green coloured foliage.

The strong attraction to a light green colour by *T. tabaci* may be a strategy employed by thrips to target stressed plants. Thrips' attraction to damaged tissue has been linked to a response to the changing balance of plant nutrients (Kirk, 1997). In particular, high levels of nitrogen have been shown to be beneficial to thrips populations (Baez *et al*., 2011; Brodbeck *et al.*, 2001; Davies *et al*. 2005; Fennah, 1963; Hsu *et al*., 2010; Malik *et al*., 2009; Mollema and Cole, 1996; Schuch *et al*. 1998). While high nitrogen levels are associated with healthy plants and darker green leaves, and might be expected to be a greater nutritive source for insects (plant vigour hypothesis; Price, 1991), the plant stress hypothesis (White, 1984) suggests the opposite, that availability of soluble nitrogen to insect herbivores is actually increased under plant stress. Nutritional quality is increased due to reduced protein synthesis and increased free amino acids in plant tissues (Mattson & Haack, 1987; White, 1984) and reduced synthesis of defensive chemicals (Rhoades, 1979).

Stressed plants experience a decline in leaf water content, which increases the relative concentration of α-amino acids in a given amount of leaf tissue (Fennah, 1963). Such leaves could be more nutritious to thrips, requiring reduced feeding effort to extract the same amount of amino acids and soluble nitrogen. Leaf colours associated by thrips with stressed plants may also indicate a preference for TSWV-infected plants, which often develop light-green to yellow mottling and areas of chlorosis (Naidu *et al*., 2008; Persley *et al*., 2007). Some species of thrips have been shown to prefer feeding on TSWV-infected plants and benefit from doing so (Belliure *et al*, 2008; Yudin *et al*., 1987). This may be due to TSWV infection interfering with induced plant defences against insect herbivory (Belliure *et al*., 2005; Felton *et al*., 1999; Felton & Korth, 2000).

The particular light green used in these experiments was preferred over not just all other colours and a dark shade of green, but was also preferred to four different cultivars of potato, which were accessible to the onion thrips. As expected, based on visual assessment of these cultivars in the glasshouse and field, spectral reflectance curves showed Shepody and Russet Burbank to be a lighter green than Atlantic and Bismark. As well as lower overall reflectance, there were also differences in peak wavelengths between the potato cultivars and the light green colour card. Potato leaves of all cultivars showed peak reflectance at 552 nm (green-yellow to yellow), while the light green card peaked at 540 nm. If the peak sensitivity of *T. tabaci* photoreceptors is the same as that cited for *F. occidentalis* (540 nm), then this could perhaps partially explain the preference for the light green card, which had peak reflectance at this wavelength.

Putting to one side the possibility that the light green colour cards used in these tests emitted a volatile attractant, which was not tested, there are at least two other possible explanations for such a strong preference compared to actual potato hosts. The first is that this light green colour was so attractive, that it overwhelmed any attraction and feeding cues from the potato, such as green leaf and terpenoid volatiles. The alternative explanation is that potato is not a preferred host for *T. tabaci*, and may provide negative feeding cues through the production of deterrent volatile compounds. The latter theory is not well supported by anecdotal observation in field trials conducted as part of this study (Chapter 2) and by Jericho (2005), where *T. tabaci* were found on potato leaves in abundance, despite the nearby presence of highly preferred hosts such as capeweed. Numerous allelochemicals that attract or deter different thrips species have been identified across many studies. These were reviewed extensively by Koschier (2006). Other studies of potato have detected further compounds, including a large number of sesquiterpenes (Dickens, 2000; Eigenbrode *et al*., 2002; Khalilov *et al*., 1999; Vancanneyt *et al*., 2001). The results suggest that if one or more volatile compounds were acting as a deterrent, then it is more likely to be a compound common to all potato cultivars, with only minimal variation between the cultivars used here. Cultivar differences did not greatly affect the strong preference of *T. tabaci* for light green, with no statistical difference detected. If this experiment were to be repeated, a clear barrier in front of both the colour card and the potato leaf could be used to exclude attractant or deterrent effect of volatiles, in order to isolate the effect of the colour preference.

The spectral analyses of potato foliage generally agreed with visual observations, with some exceptions. Royal Blue appeared visually darker than both Spunta and Tasman, while the measured reflectance of this cultivar sat between Spunta and Tasman. BIsmark also appeared visually to be one of the darker green cultivars, but reflectance curves placed this only just slightly lower in green intensity than Atlantic, and with higher reflectances than Spunta, Royal Blue and Tasman. While attempts were made to produce a representative result through random sampling of five leaves from three plants, leaf-to-leaf and plant-to-plant variation may not have been totally controlled. The relative differences in green hue between potato cultivars grown under controlled conditions in the field may also differ to those observed in the glasshouse due to a range of factors, such as response to cooler and more variable temperatures, more direct light, different soil characteristics and other environmental factors.

The field trials (Chapter 2) showed the lowest numbers of thrips on Shepody and higher numbers on Russet Burbank and Bismark. Given the spectral reflectance values for these cultivars, these field results do not accord well with the theory that onion thrips are

more attracted to lighter green potato foliage, despite the very strong attraction to a very light green colour card over all others tested. Further testing of host preference across potato cultivars is therefore warranted, as well as oviposition choice, because field numbers could be a product of both the initial attraction to a cultivar combined with the subsequent rate of reproduction on the cultivar. These are examined in Chapter 4. Nevertheless, the fact that *T. tabaci* showed a very strong preference for the light green card over both the dark green card and potato leaves, suggests that leaf colour could still be worthy of consideration in cultivar development, for the selection of thrips resistance, with darker green cultivars potentially being less attractive to thrips. Greater protection for potato crops against *T. tabaci* and TSWV-infection might also be achieved by utilising a push-pull strategy, by surrounding a commercial potato crop of dark green hue, with a perimeter trap of a light green potato cultivar. Trap crops may be feasible alternatives throughout Tasmania and in coastal and hinterland cropping regions of the Australian mainland, where cropping fields are continuous in time and space, because thrips are more likely to travel shorter distances and encounter a trap crop before entering a commercial crop.

One speculative reason why results may differ so much between colour preference studies of thrips is the possibility of intra-specific population differences. In Chapter 5, vector competence experiments and mtDNA analysis of fifteen populations of *T. tabaci* collected from potato, onion and other hosts in different locations around Australia, showed that some populations were vector competent and some were not, and that populations clustered into different sub-groups in a maximum likelihood tree, supported by high bootstrap values. The subgroups clustered according to the host from which they were collected, which was also linked to vector competence. Differences in feeding and oviposition preferences have been demonstrated within a number of species, usually associated with geographical separation (Schoonhoven *et al*., 2005). However, because comparative studies of insect colour preference are usually conducted between species, population differences have not been widely reported. One exception is the demonstration of clear differences in colour preference between populations of *Bombus terrestris* (Chittka *et al*., 2004; Ings *et al*., 2009).

In the colour card versus potato cultivar experiments, light green card was used in order to provide a very strong contrast between the choices. Because these experiments suggested that differences in the intensity of green hue may be as important or more important than chemical cues in host choice, future experiments should look at a greater variation of green hues and intensity approaching those of a range of potato varieties, in order to determine when the influence of colour on host preference breaks down. Colour

cards were used in experiments and then tested for reflectance across the wavelength spectrum. A more targeted approach could be employed by first selecting specific colours with peak reflectance at targeted wavelengths, and use these to help delineate the peak sensitivity of thrips photoreceptors. Electroretinography could also be used to clarify the types of photoreceptors possessed by thrips and whether this can explain the differences in colour preference between thrips species. The strength of colour preference over other host-finding cues also needs to be tested by comparing colour cards in field trials. Further studies in *T. tabaci* preference and behaviour would also benefit from conducting colour preference experiments on different thrips populations collected from different plant hosts, and in particular on vector and non-vector competent populations.

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Chapter 4 - Host preference of onion thrips, *Thrips tabaci* Lindeman, western flower thrips, *Frankliniella occidentalis* Pergande, and tomato thrips *Frankliniella schultzei* Trybom and oviposition preference of *T. tabaci* (Thysanoptera: Thripidae).

Abstract

The host preference of *Thrips tabaci* (Lindeman) for nine different potato cultivars (Atlantic, Bismark, Fergifry, Royal Blue, Russet Burbank, Shepody, Spunta, Tasman and 93-6-3) was tested using a two-choice chamber with intact leaves. The *T. tabaci* population tested showed a very strong preference for the lightest green cultivars, Shepody and Russet Burbank, over a darker green control cultivar Atlantic. No significant difference in preference was found between cv. Atlantic and the remaining cultivars, which ranged from a slightly higher intensity of green hue (lighter green) to much lower intensity green (darker green) than the control.

In further preference experiments on three species of thrips, pairing potato cv. Atlantic with blackberry nightshade *(Solanum nigrum),* tomato cv. Grosse lisse (*Solanum lycopersicum*), Datura (*Datura stramonium*), tobacco (*Nicotiana tabacum*), canola (*Brassica napus*), marigold (*Calendula officinalis*) and brown onion *(Allium cepa); F. schultzei* preferred yellow *Calendula* flowers to detached leaves of potato cv. Atlantic, but *F. occidentalis* and *T. tabaci* preferred other hosts equally with potato. All species of thrips were strongly attracted to potato when leaves were paired with a blank white card (no alternative plant host).

Oviposition choice was assessed by counting the number of larvae hatching from leaf disks exposed to *T. tabaci* in petri dishes, under both choice and no-choice conditions. In no-choice tests, juvenile performance was significantly lower on those cultivars of the brightest green hue (Shepody, Russet Burbank, Fergifry, 93-6-3) and higher on those cultivars with lower reflectance at the peak wavelength of 552 nm in the green range (Atlantic, Bismark, Royal Blue, Spunta) as determined in Chapter 3. Oviposition was highest on Atlantic, with 10.2 juvenile thrips per disk, which was three times higher than cv. Shepody, which had the lowest oviposition with only 3.4 juveniles per leaf disk. In two-choice tests, Shepody leaf disks had 72 percent fewer larvae emerging when paired with a Bismark control. Tasman, Russet Burbank, Atlantic and Royal Blue were not significantly different to Bismark. Spunta, Fergifry and 93-6-3 were not tested against Bismark in a two-choice combination.

Possible explanations for the marked differences between adult preferences in the choice chamber and oviposition choices on leaf disks are explored.

Introduction

T. tabaci is highly polyphagous, feeding on grasses and broad-leaved plants, including many vegetable and fruit crops (Groves *et al.,* 2002; Terry, 1997; Ullman *et al*., 1997). Wide host ranges for feeding and oviposition are also evident in the anthophilous *F. occidentalis* (Kirk & Terry, 2003; Reitz, 2009) and *F. schultzei* (Milne & Walter, 2000). This opportunism, including the ability to reproduce on a broad range of host plants, enables these vector thrips species to exploit temporary or intermittently occurring environments such as annual crops (Groves *et al.,* 2002; Mound & Teulon, 1995; Mound, 1997; Terry, 1997; Ullman *et al*., 1997), exacerbating the rate of spread and distribution of *Tomato spotted wilt virus* (TSWV). Polyphagy in herbivorous invertebrates can be restricted by trade-offs in performance on different hosts (Fox & Morrow, 1981; Futuyma & Moreno, 1988; Jaenike, 1990; Terry, 1997; Thompson, 1988, 1996). This has been demonstrated in ecological studies of thrips preference, association and performance (Agrawal & Colfer 2000; Bautista & Mau, 1994; Chatzivassiliou *et al*., 1999, 2001; Kirk, 1985; Teulon *et al*., 1993). Generalist herbivores, having a wide host diet, are often associated with a reduced ability to distinguish between hosts, unlike specialists, which must be able to locate and distinguish specific plant species (Bernays, 1998, 2001; Janz & Nylin, 1997). However, studies in various crops have shown distinct levels of host preference by thrips, including at the cultivar level (Herrin & Warnock, 2002; Maris *et al*., 2003a, 2003b; Yudin *et al*., 1988).

TSWV can only be acquired by first, and sometimes second, instar larvae of vector thrips (Lindorf, 1931, 1932; van de Wetering *et al.,* 1996), which must be able to complete their development on the host chosen by the ovipositing female (Bautista & Mau, 1994; Hobbs *et al.,* 1993; Terry, 1997). Oviposition choice on plant hosts is therefore critical for survival of the progeny, and plays a critical role in TSWV disease epidemiology (Allen & Broadbent, 1986; Bautista & Mau, 1994; Chatzivassiliou *et al*., 2002; Gray & Banerjee, 1999; Wijkamp *et al*., 1995). Host species and cultivar characteristics can influence host choice, population dynamics and vector competence. Studies have shown variation in performance, behaviour and longevity of thrips on different plant hosts, which can influence the ability and extent to which TSWV is transmitted (Bautista *et al*., 1995; Bautista & Mau, 1994; Chatzivassiliou *et al*., 2002; Sakimura, 1963; Terry, 1997; Ullman *et al.,* 1997; Wijkamp *et al*., 1995).

Once TSWV is established in a susceptible commercial planting as a result of a primary infection event, further virus spread within the crop depends on whether host plants can support larval development to adult stage. Secondary infection events, to epidemic proportions, may occur with high vector reproductive performance (Duffus, 1971; Irwin &

Ruesink, 1986; Jericho, 2005; Thresh, 1974). The total level of TSWV-infection in a crop is therefore determined by the sum of primary and secondary infections. Primary infections may occur at any time, whereas secondary infections can only occur some 4-6 weeks later, after thrips have completed a life cycle and TSWV has translocated through the plant. The relative importance of each type of infection depends on host developmental stage, and whether susceptibility to TSWV changes through time, as well as the suitability of the host for oviposition selection and larval development. Primary infection events will be more important than secondary infection if a crop is only susceptible to TSWV at an early stage, or if mature plants are not preferred hosts, or if larval survival is low. Host preference and oviposition testing may help to determine whether some potato cultivars are more likely than others to promote either primary or secondary infections, and hence TSWV epidemics.

Phytophagous insects locate hosts by responding to a range of stimuli, including visual, mechanical, gustatory and olfactory characteristics (Prokopy & Owens, 1983; Visser, 1986). Colour, shape and olfactory cues are usually involved in an insect's initial orientation to a plant, whereas once an insect has alighted on the plant, acceptance or rejection, and the initiation of feeding is determined by texture as well as the presence or absence of specific chemical stimulants or deterrents (Renwick, 1983). The mechanisms behind vector thrips preferences and trade-offs in different hosts and ecosystems are still largely unknown, but visual ecological cues (colour, host shape and size) and plant chemistry play a central role in thrips specialisation (Terry, 1997). Factors other than chemistry and visual ecological cues may also be important (Bernays & Graham 1988; Joshi & Thompson 1995; Fry 1996). These include morphological characters, such as leaf shape and canopy architecture, which have been shown to influence thrips success. Flat leaves and open plant architectures have been associated with reduced densities of *T. tabaci* (Coudriet *et al*., 1979; Patil *et al*., 1988). Other host selection cues of thrips may include leaf waxiness (Hemmati & Benedictus, 2000; Nouri Moghaddam *et al*., 2004), leaf glossiness (Molenaar, 1984), and leaf trichome density (Sedaratian *et al*., 2010). Plant traits may also influence thrips success indirectly, for example, trichome density may influence the abundance and effectiveness of natural enemies, such as predatory mites (Peterson, 1984).

A number of generalised theories have been formulated to explain host and oviposition choices. Optimal oviposition theory (preference-performance/'mother knows best' hypothesis) (Jaenike, 1978), states that females should oviposit on host plants that enhance the performance of their offspring. More specifically, the plant vigour hypothesis (Price, 1991) predicts that females should prefer large, healthy and vigorously growing

host plants for oviposition, and that larvae should perform best on these plants, and consequently maximise adult fecundity (Awmack & Leather, 2002; Obermaier & Zwölfer, 1999; Strong *et al*., 1984). Faster growth also reduces exposure time to predators, disease and abiotic mortality factors (Benrey & Denno, 1997; Grossmueller & Lederhouse, 1985; Häggström & Larsson, 1995; Loader & Damman, 1991; Price *et al*., 1980; Rhoades, 1983), as explained by the slow growth-high mortality hypothesis (Feeny, 1976; Williams, 1999). However, some insect species are known to oviposit on nutritionally inferior hosts for the same reason, to avoid or reduce exposure to predators (Ballabeni *et al*., 2001; Björkman *et al*., 1997; Hawkins *et al*., 1993; Obermaier *et al*., 2001). Optimal foraging theory on the other hand predicts that phytophagous adults should prefer to feed (and lay eggs) on hosts that give the highest adult performance (Scheirs *et al*., 2000; Stephens & Krebs, 1986). While these theories have generally been discussed as competing explanations, the ongoing and unexplained variation in results, with both good and poor correlations shown in both theories (Berdegue *et al.*, 1998; Cronin & Abrahamson, 2001; Mayhew, 1997, 2001; Pires *et al.,* 2000; Price *et al.,* 1999), suggests that the two concepts could be integrated (Scheirs & De Bruyn, 2002).

In many insect-plant interactions, plants with prior feeding damage are often avoided by females seeking to oviposit, in order to maximise food resources for larvae, reduce exposure to induced plant defences and reduce exposure to predators and parasitoids attracted either directly to the pest, or to visual symptoms of plant damage or to plant signals induced by herbivory (Chen, 2008; Dicke *et al*., 2003; Frost *et al*., 2007, 2008; Karban & Baldwin, 1997; Karban *et al*., 1997; Price *et al*., 1980; Walling, 2000). This avoidance has also been shown arising from direct contact with conspecific females and/or larval residues, regardless of the level of plant damage, in aphids (Michaud & Jyoti, 2007), green lacewings (Růžička, 1994), coccinellids (Růžička, 1997; Yasuda *et al*., 2000) and syrphids (Scholz & Poehling, 2000).

Understanding the factors underpinning host choice is important for developing control methods, and in particular for guiding breeding programs for new cultivars. Characteristics of host choice have been used to breed and select cultivars with reduced thrips preference in a range of crops, including onion (Alimousavi *et al.*, 2007; Loges *et al.*, 2004), chrysanthemum (Broadbent *et al*., 1990; de Jager *et al*., 1995; Leiss *et al.,* 2009), cucumber (de Kogel *et al*., 1997); rice (Nugaliyadde & Heinrichs, 1984), strawberry (Rahman *et al.,* 2010), common bean (Frei *et al*., 2003) and *Capsicum* (pepper) (Maris *et al*., 2003b),. Selection experiments provide a unique tool to study these traits and are routinely used to establish the preferences, performances and trade-offs in different crops and ecosystems.

The merits of using choice tests versus no-choice tests has been discussed by Blossey (1995), Cullen (1990) and Withers *et al*. (2000). Essentially, choice tests are considered to more realistically represent field conditions, but might generate false negatives, whereas no-choice tests are more likely to generate false positives (van Klinken, 2000). Contrary results are often obtained across these two test types (Marohasy, 1998), and so a combination of the two is often conducted. Other studies show differences between host ranges measured in the field compared to the laboratory, and can be positive (host chosen in a test which is unlikely in the field), or negative (non preference in a test, when the host is preferred in the field (Balciunas *et al*., 1996; Marohasy, 1998; van Klinken, 2000). Preferences in two choice tests can be affected by sensitisation or priming, when an insect is motivated to feed or oviposit due to the presence of a preferred host, and this motivation increases the chance of feeding or ovipositing on an adjacently-located less-preferred host (Heard, 1999). Another factor that may confuse preference in choice tests is the mixing of volatile compounds from hosts in close proximity in small test cages.

TSWV incidence in potato is determined by the influx of viruliferous thrips choosing to alight and feed on potato over other hosts in the landscape, combined with the subsequent reproduction of thrips on infected potato plants and movement of the resulting adults to other plants. Whether or not one is more important than the other is not clear, and may vary across time and place. It is also possible that non-viruliferous thrips vectors may enter potato crops and spread TSWV through reproduction on already infected plants (from infected tuber stock) or reproduce on adjacent weeds before moving to potato plants to feed. Consequently if there are differences in the relative attractiveness of potato cultivars and suitability as reproductive hosts to *T. tabaci,* then these attributes could be manipulated to reduce overall infection rates by selecting or breeding cultivars that attract fewer numbers of vector thrips and support lower reproduction. The purpose of these experiments was to determine the host preference and oviposition choice of *T. tabaci* for and on various potato cultivars. Further experiments were conducted with *T. tabaci* and two additional thrips species (*F. occidentalis* and *F. schultzei*) to determine preference for potato versus a selection of other plant species. Although *F. occidentalis* and *F. schultzei* are not present in Tasmania, they are present in mainland Australian States. These two species both vector TSWV and have been found in and around potato crops, but whether potato is a preferred host has not been tested. The paired preference trials here on detached leaves or leaf disks of different hosts, to a large degree ignore the host cue of plant architecture, focusing more on the effects of host colour and plant chemistry.

Materials and methods

Thrips colonies

A colony of thelytokous TSWV-competent onion thrips, *Thrips tabaci (Lindeman*), was collected from a Tasmanian potato field trial in 2006 (Tas-FT, see Chapter 5). The thrips were reared on common bean pods (*Phaseolus vulgaris*) according to a protocol modified from van de Wetering (1999), in 7cm x 9cm containers, at 25°C ± 1°C, 65 ± 5% RH, with a photoperiod of L16:D8 in a climate-control chamber, using cool white fluorescent light under 450μmol-m^{-2}.s^{-1} photosyntethically active radiation (PAR). Thrips were transferred twice-weekly on to fresh bean pods. These thrips were sent to Western Australia to be reared at the end of January 2008, in order to conduct preference experiments simultaneously with *F. occidentalis* and *F. schultzei*, which are unable to be imported in to Tasmania for biosecurity reasons. *F. occidentalis* and *F. schultzei* were obtained in Perth, Western Australia, from glasshouse cultures of flowering pot marigold, *Calendula officinalis*, and were not reared on common bean prior to testing as was *T. tabaci*. The experiments were conducted at the end of March 2008, so that the *T. tabaci* had progressed through approximately two complete generations in Western Australia before host preferences were assessed.

Rearing of plant hosts

Potato cultivars (Bismark, Russet Burbank, Shepody, Royal Blue, Tasman, and Spunta) were grown from tissue culture samples obtained from the Vegetable and Associated Industries Section of the Tasmanian Department of Primary Industries and Water (now incorporated into the Tasmanian Institute of Agricultural Research), Devonport, in April 2005. Two additional cultivars (Fergifry and 93-6-3) were obtained from the National Potato Variety Tissue Culture Collection, Department of Primary Industry, Victoria. Tissue culture plants were grown in Potato Multiplication media (4.3 g Murashige-Skoog salts, 30 g sucrose, 0.5 g casein hydrolysate, 0.04 g ascorbic acid made up to 1 L with dH_20, and 8 g/L agar type A added before autoclaving) in 7cm x 9cm containers, at 22°C, near saturation RH, 16-hour light and 8-hour dark photoperiod, under cool white fluorescent light. All tissue culture samples tested negative for TSWV in double antibody sandwich enzyme-linked immunosorbent assay (DAS-ELISA) (Clark & Adams, 1977). Tissue culture plants were transplanted to soil in 10x10cm pots when about 5cm tall and grown for a further six weeks in a glasshouse under variable conditions, but with additional lighting to ensure 16-hour light and 8-hour dark photoperiod, and approximate temperature of 25°C ± 1°C and 65 percent relative humidity. Other plants used were blackberry nightshade *(Solanum nigrum),* tomato cv. Grosse lisse (*Solanum lycopersicum*), Datura (*Datura stramonium*), tobacco (*Nicotiana tabacum*), canola

(*Brassica napus*), marigold (*Calendula officinalis*) and brown onion *(Allium cepa).* These were grown under the same conditions from locally obtained seed.

Potato cultivar choice of T. tabaci

T. tabaci preferences for potato cultivars (Bismark, Russet Burbank, Shepody, Royal Blue, Tasman, Fergifry, 93-6-3 and Spunta) were determined in two-choice tests paired with potato cv. Atlantic, using detached leaves. The tests were conducted in a choice chamber consisting of a plastic tube (20cm length, 2.5cm diameter), with openings at both ends, and a small hole in the middle through which thrips were introduced. A cream-coloured paper towel cover was placed over the chamber to block other colours from the room. The chamber was suspended about 5 cm above a cream-coloured laboratory bench. Adult female thrips of indeterminate age were taken from common bean pods in rearing containers with a soft-bristled paintbrush and starved for 1 h before being placed in choice chambers. Experiments took place at room temperature (21-26°C) under indirect natural light. Relative humidity was not measured. For each choice combination, a single onion thrips was placed in the centre of the choice chamber, and given three minutes to reach either end. This was repeated with 25 thrips, with hosts rotated between each end after every five thrips. This experiment was repeated the following day with another 25 thrips, giving a total of 50 replicates per cultivar. Controls were (i) potato cv. Atlantic paired with potato cv. Atlantic, and (ii) potato paired with a blank sheet of white card. The first control was used to detect any bias inherent in the choice chamber. The second control was used to determine whether any deterrent volatiles were driving thrips away from potato as a choice. In all cases there was no difference in preference in the potato versus potato pairings, indicating no directional bias in the choice chamber.

Host plant choice for all three thrips species

Host preferences of *T. tabaci*, *F. occidentalis* and *F. schultzei* for six alternative hosts (blackberry nightshade, tomato, *Datura*, tobacco, yellow marigold flowers and brown onion leaves) were determined in two-choice tests pairing these hosts with potato cv. Atlantic. The tests were conducted in the same way as choice tests between potato cultivars. Blackberry nightshade was chosen because it is a weed species commonly encountered within or near potato crops in Tasmania. Tomato was chosen because, like potato, it is a Solanaceous species, and because it was available in abundance at the time. Canola leaves and marigold flowers were paired with potato for *F. occidentalis* and *F. schultzei* in the tests conducted in Western Australia, but these were replaced with *Datura* and onion leaves for *T. tabaci* in tests conducted in Tasmania due to differences in availability of these species. Marigold flowers are a known host of western flower

thrips and tomato thrips (the populations used in these tests were originally collected from marigold), and onion is a known host of onion thrips. The final host paired with potato was tobacco because it is also an important crop affected by onion thrips. For each choice combination, a single onion thrips was placed in the centre of the choice chamber, and given three minutes to reach either end. This was repeated with 25 thrips, with hosts rotated between each end after every five thrips. Controls were again (i) potato cv. Atlantic paired with potato cv. Atlantic, and (ii) potato cv. Atlantic paired with a blank sheet of white card.

Oviposition choice of T. tabaci

Oviposition choice of *T. tabaci* on potato cultivars were determined in choice and no-choice experiments conducted on leaf disks (2 cm diameter). In the no-choice experiment, 5 adult (female) *T. tabaci* of indeterminate age were taken from common bean pods and placed on each leaf disk of potato cultivars (Bismark, Russet Burbank, Shepody, Royal Blue, Tasman, Fergifry, 93-6-3 and Spunta) in Petri dishes (9cm diameter) on a sheet of moistened paper towel, and sealed with parafilm. Adults were removed after 24 h and leaf disks were incubated for 5 days at room temperature, at which time the number of emerged juveniles and unhatched eggs was scored. In order to distinguish unhatched eggs from surrounding leaf structures, the criterion for identification was the presence of red eye-spots. This experiment consisted of ten replicates per cultivar, and the experiment was conducted three times (totalling 30 replicates per cultivar) with approximately four weeks between experiments.

In the choice experiment, 10 adult (female) thrips of indeterminate age were taken from common bean pods and placed in the centre of a Petri dish, between a leaf disk of potato cv. Bismark paired with one of five other cultivars, Atlantic, Tasman, Royal Blue, Russet Burbank, and Shepody. Sufficient leaf material was not available in three cultivars, Fergifry, 93-6-3 and Spunta, so these were not tested. Petri dishes were prepared in the same manner as the no-choice experiment. Leaf disks were placed close together but did not touch each other. Adults were removed after 24 h and leaf disks were placed separately in sterile 1.5mL microcentrifuge tubes with a strip of paper towel to absorb free moisture, and incubated for 5 days at room temperature, at which time the number of emerged juveniles on each leaf disk was scored. Unhatched eggs were also counted in the total providing they were developing, as indicated by the presence of red eye spots. This experiment consisted of fifteen replicates per choice combination. No-choice and choice tests were conducted under the same conditions as those of the thrips being reared.

Statistical analyses

Using SAS/STAT v9.2, contingency tables were used to test for associations between plant host preference and thrips species. In the first group of experiments, following a significant overall association; seven one way sub-tables were constructed to test if there was a preference for each potato cultivar. In the second group of experiments, eight one way sub-tables were constructed to test if there was a preference for each plant host species. The cv. Atlantic versus cv. Atlantic pairing was always present to provide a common reference between the host species choices. Because this meant the tables were not independent of each other (Everitt, 1992), the P values of the sub-tables were adjusted using Holm's method (Holm, 1979) to achieve an experiment-wise P value of 0.05.

For oviposition choice tests, because a Gaussian distribution is inappropriate as applied to data consisting of counts, a Generalised Linear Model (GLM) was used in SAS/ STAT v9.2, which allows for alternative distributions such as the Poisson (Nelder & Wedderburn, 1972). Where fitted models showed signs of over-dispersion when using the Poisson distribution, the negative-binomial distribution was used. Type 3 chi-square tests were applied to detect significant differences due to host. In the no-choice tests, three experiments conducted on different days were combined to perform an overall test for statistical significance. Where statistical differences ($P < 0.05$) were apparent, differences between cultivars are reported. In the two-choice experiments, Bismark was used as the control cultivar due to insufficient leaf material of Atlantic at the time. The thrips were offered a choice of two disks consisting of Bismark and another cultivar, this pairing corresponding to a single experimental unit. To accommodate this, Generalised Estimating Equations (GEE) were used to include the possible correlation resulting from the experimental structure and assume an unstructured correlation structure (Liang & Zeger, 1986). This is the same as Generalised Linear Models but allows for the possibility of correlated units. Hosts with P values less than 0.05 were considered to have a different number of larvae hatched than Bismark within each experiment.

Results

Potato cultivar choice of T. tabaci

When given the choice between each of the eight potato cultivars and Atlantic there were only two potato cultivars that were significantly preferred over Atlantic (Figure 4.1). These were Shepody, chosen by seventy-five percent of *T. tabaci* ($X^2_{1,48}$ = 12.00, adjusted p = 0.004); and Russet Burbank, chosen by 69 percent of thrips ($X^2_{1,49}$ = 7.37, adjusted p = 0.047) (Fig. 1). There were no significant differences for any of the other cultivars: Bismark ($X^2_{1,46}$ = 0.87, adjusted p = 1.00); Royal Blue ($X^2_{1,47}$ = 0.02, adjusted p = 1.00); Tasman ($X^2_{1,47}$ = 0.02, adjusted p = 1.00); Fergifry ($X^2_{1,48}$ = 0.75, adjusted p = 1.00); 93-6-3 ($X^2_{1,45}$ = 1.80, adjusted p = 1.00); and Spunta ($X^2_{1,45}$ = 0.02, adjusted p = 1.00). A one-way ANOVA comparing strength of preference across cultivars was also significant, $F_{7,8}$ = 4.83, p = 0.02. There was no difference between Russet Burbank and Shepody, but these cultivars had more thrips than all others. No differences between other cultivars were evident.

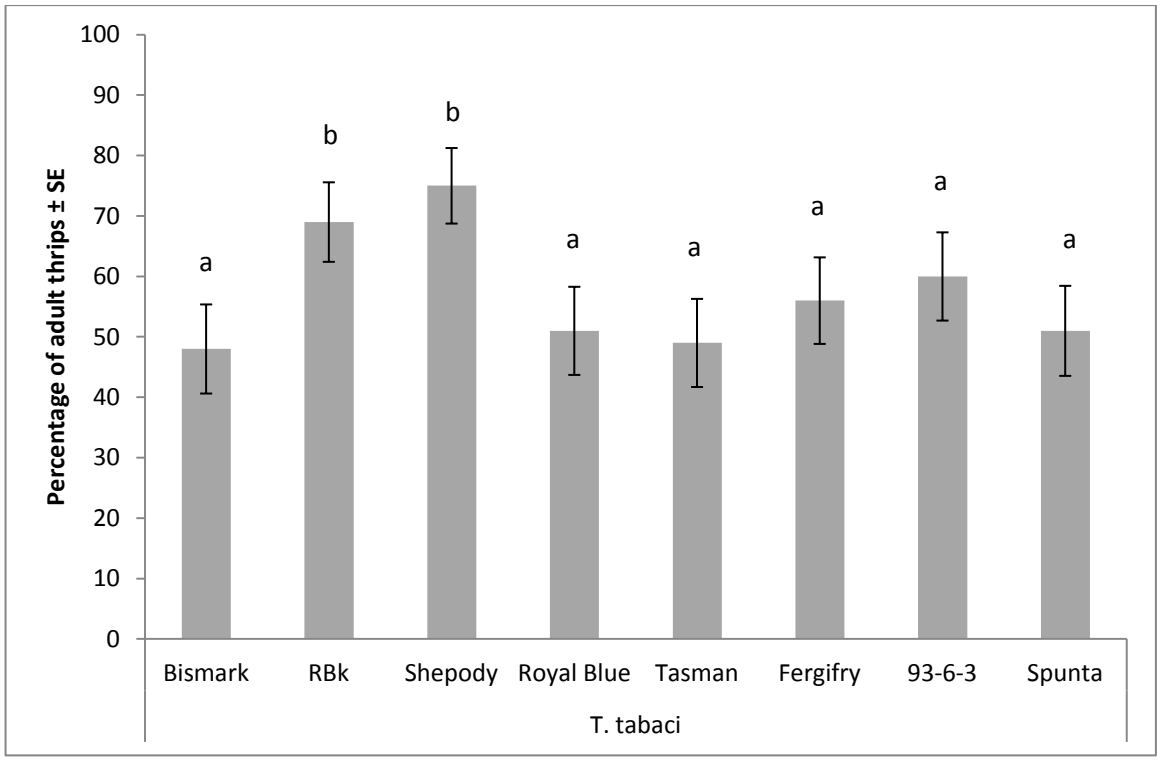

Figure 4.1 *T. tabaci* given two choice access between potato cv. Atlantic and eight other potato cultivars (Bismark, Russet Burbank, Shepody, Royal Blue, Tasman, Fergifry, 93-6-3 and Spunta). For each choice combination, 50 onion thrips were each placed singly in the centre of the choice chamber, and given three minutes to reach either end. Data are expressed as mean ± *SE*. Significant differences are shown relative to cv. Atlantic

Host plant choice for all three thrips species

The host plant species preferences of *T. tabaci* relative to the cv. Atlantic control were significant ($X^2_{6,161}$ = 20.53, p = 0.002), but only due to the potato versus blank pairing in which ninety-one percent of *T. tabaci* individuals moved to potato ($X^2_{1,23}$ = 15.70, adjusted p = 0.0005) (Fig. 4.2). There were no significant differences in preference between potato and tomato ($X^2_{1,22}$ = 0.73, adjusted p = 1.00); blackberry nightshade ($X^2_{1,25}$ = 0.36, adjusted p = 1.00); *Datura* ($X^2_{1,24}$ = 0.17, adjusted p = 1.00); tobacco ($X^2_{1,24}$ = 1.50, adjusted p = 1.00); and onion leaves ($X^2_{1,23}$ = 2.13, adjusted p = 1.00).

The host preferences of *F. occidentalis* relative to the cv. Atlantic control were significant ($X^2_{6,150}$ = 15.25, p = 0.0184); but again only because of the potato versus blank pairing in which eighty-three percent of *F. occidentalis* individuals preferred potato when offered 'blank' as an alternative choice ($X^2_{1,23}$ = 9.78, adjusted p = 0.012). There were no significant differences in preference between potato and tomato ($X^2_{1,21}$ = 1.19, adjusted p = 1.00); *Datura* ($X^2_{1,21}$ = 1.19, adjusted p = 1.00); yellow marigold flowers ($X^2_{1,23}$ = 2.13, adjusted p = 1.00); tobacco ($X^2_{1,21}$ = 0.43, adjusted p = 1.00); and canola ($X^2_{1,21}$ = 1.19, adjusted p = 1.00).

The host preferences of *F. schultzei* relative to the cv. Atlantic control were significant ($X^2_{6,145}$ = 26.99, p < 0.0001). *F. schultzei* showed a strong preference for yellow marigold flowers with 91 percent of individuals moving to *Calendula* when paired with potato ($X^2_{1,21}$ = 1.19, adjusted p = 0.0009). Eighty-five percent of *F. schultzei* individuals preferred potato when offered 'blank' as an alternative choice ($X^2_{1,20}$ = 9.80, adjusted p = 0.01). There were no significant differences in preference between potato and tomato ($X^2_{1,22}$ = 0.73, adjusted p = 1.00); *Datura* ($X^2_{1,20}$ = 0, adjusted p = 1.00); tobacco ($X^2_{1,20}$ = 0.50, adjusted p = 1.00); and canola ($X^2_{1,21}$ = 1.19, adjusted p = 1.00).

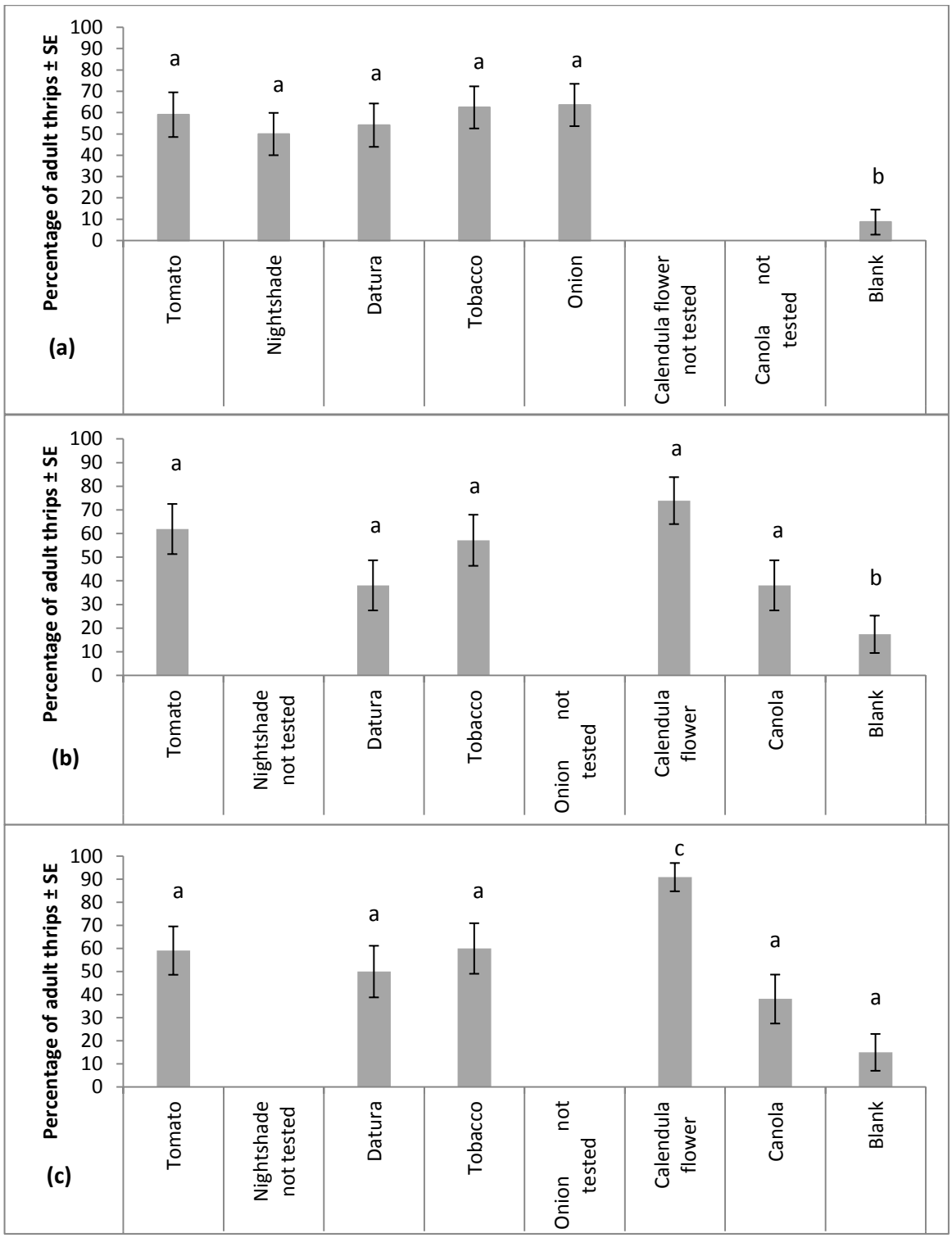

Figure 4.2 Two choice tests between potato cv. Atlantic and six other hosts (tomato, *Canola*, *Datura*, tobacco, yellow *Calendula* flowers, and onion leaves) for (a) *T. tabaci,* (b) *F. occidentalis* and (c) *F. schultzei* For each choice combination, 25 single thrips were placed in the centre of the choice chamber, and given three minutes to reach either end. Data are expressed as mean ± *SE*. Significant differences are shown relative to potato cv. Atlantic.

Oviposition choice of T. tabaci

There were significant differences in oviposition due to host ($X^2_{8,270}$ = 43.86, p < 0.0001) (Fig. 4.3). Oviposition was highest on Atlantic, with 10.2 juvenile thrips per disk, which was three times higher than cv. Shepody, which had the lowest oviposition with only 3.4 juveniles per leaf disk. Pair-wise comparisons (illustrated in Fig. 3) show that the numbers of juvenile thrips on leaf disks are lowest on those cultivars of the brightest green hue, and highest on those cultivars with lower reflectance at the peak wavelength of 552 nm in the green range, as determined in Chapter 3.

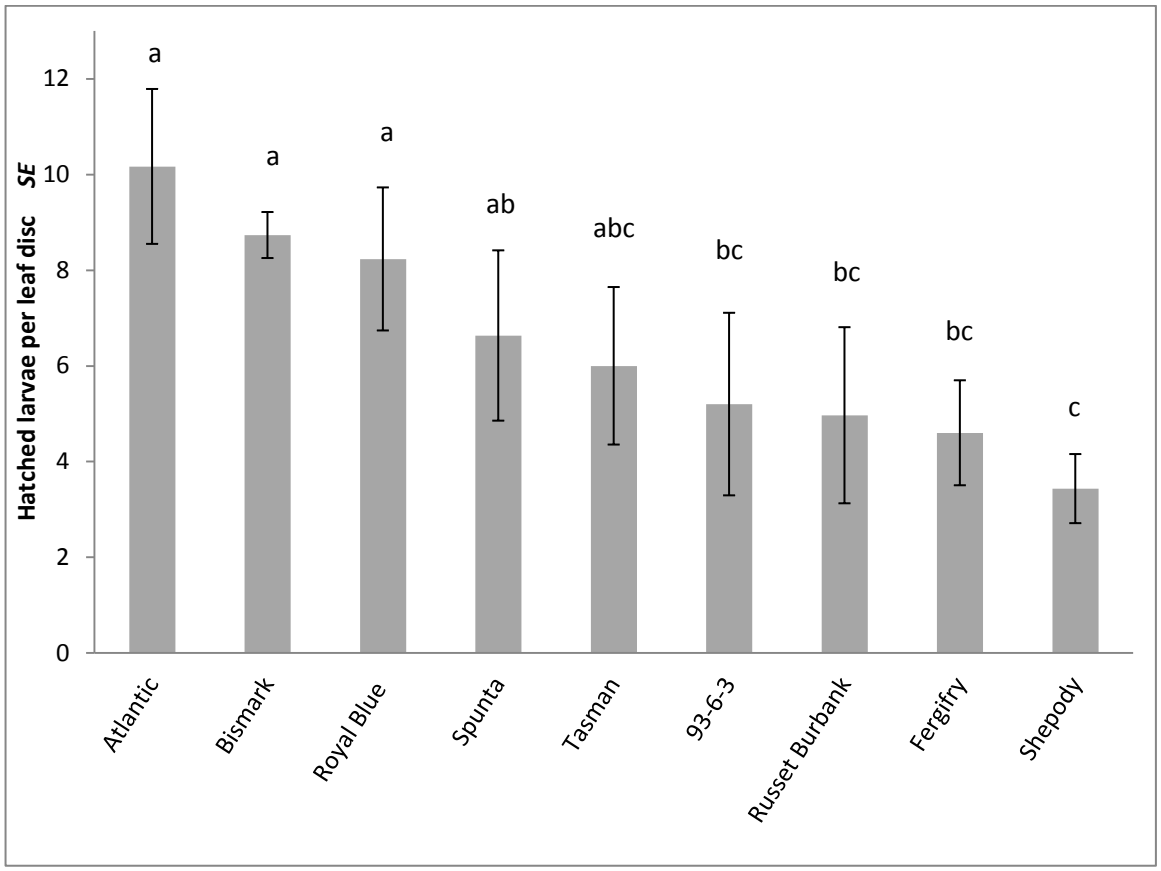

Figure 4.3 No choice oviposition (hatched first instar larvae and developing eggs per leaf disk) of *T. tabaci* on nine potato cultivars. In each of 30 replicates five adult (female) *T. tabaci* were placed on each leaf disk of potato cultivars in Petri dishes (9cm diameter) on a sheet of moistened paper towel, and sealed with parafilm. Adults were removed after 24 h and leaf disks incubated for 5 days at room temperature, at which time the number of emerged juveniles was scored. Data are expressed as mean ± *SE*.

In two-choice tests, only one cultivar showed significant differences in the number of juvenile thrips compared to Bismark (Fig. 4.4). Shepody had 72 percent fewer juvenile thrips than the control ($X^2_{1,15}$ = 5.31, p = 0.02). Tasman, Russet Burbank, Atlantic and Royal Blue were not significantly different to Bismark. Cultivars Spunta, 93-6-3 and Fergifry were not included in this experiment due to a shortage of available plant material.

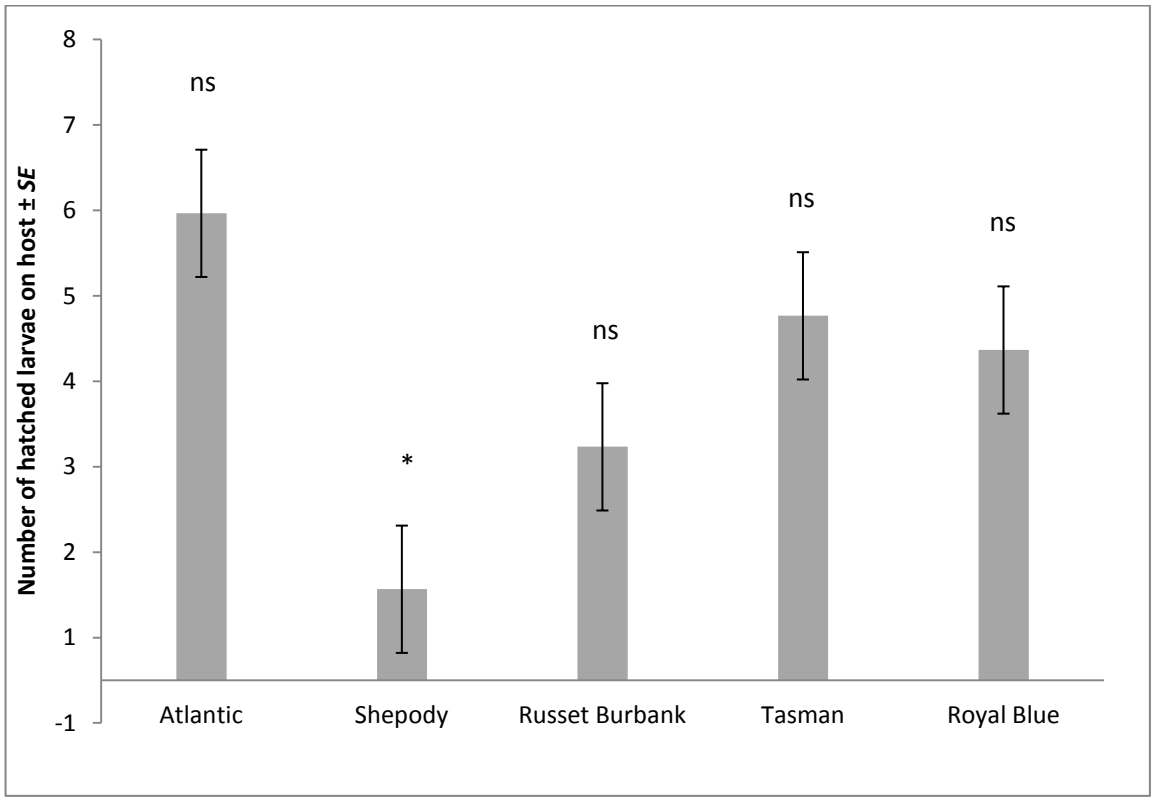

Figure 4.4 *T. tabaci* given two choice access between potato cv. Bismark and five other cultivars. In each of 15 replicates, ten adult (female) thrips were placed in the centre of a Petri dish, between a leaf disk of potato cv. Bismark paired with each of five other cultivars. Adults were removed after 24 h and leaf disks incubated for 5 days at room temperature, at which time the number of juveniles on each leaf disk was scored. Data are expressed as mean ± *SE*. * = p < 0.05. ns = not significant relative to cv. Bismark.

Discussion

Host choice experiments demonstrated clear differences in potato cultivar preference by *T. tabaci*. The preference of *T. tabaci* tested in these experiments showed increased attraction to the two cultivars with the highest intensity green hue. These results are particularly interesting in light of the results from colour card preference experiments (Chapter 3), in which *T. tabaci* preferred light-green and mid-green colour cards over dark green. Possible explanations for why thrips might be attracted to light green cultivars were explored in Chapter 3. Another explanation for preference or non-preference of *T. tabaci* for certain potato cultivars over others, is the potential effect of one or more of the numerous allelochemicals that attract or deter different thrips species, which have been identified across many studies (Koschier, 2006; Teulon *et al*., 2007). Headspace sampling and GCMS analysis of potato volatiles by Wilson *et al*. (unpublished data) have suggested that there are distinct cultivar differences in the amount and ratio of compounds emitted by potato. Such differences offer a possible explanation for the preference of one cultivar over another. While the intensity of green hue could correlate to a volatile attractant or deterrent, the strength of the attraction to a very light green colour card over four potato cultivars (Chapter 3), suggests that colour may be the dominant factor. Other studies have shown that colour, not odour, is more important in determining host preferences in some thrips species. De Kogel and Koschier (2002) shielded *Chrysanthemum* flowers and buds from *F. occidentalis* with a visual barrier, and found no difference in preference, but without the barrier found a strong choice for open flowers as opposed to buds.

The results of experiments testing preference for potato over other hosts were mixed for all species. The strong preference for yellow pot marigold (*Calendula*) flowers by *F. shultzei* is not surprising given the flower-feeding strategy of this species. Most insect species are attracted to colours that resemble the flowers or foliage of their hosts or food. Yellow is a commonly preferred colour across the insect class (Borror *et al*., 1989), and *F. occidentalis* has been shown to be attracted to yellow-coloured flowers (Blumthal, *et al.*, 2005). It was expected that *F. occidentalis* would also show a strong preference for *Calendula* flowers over potato foliage, but results were not significant. Colour preference experiments (Chapter 3) also support a strong preference for yellow over green for these two species (but not for *T. tabaci*). It should however be emphasised that these two species were taken from *Calendula* and reared on green bean for only a very short time before preference testing, whereas *T. tabaci* had been reared on green bean for many generations. Unfortunately the same pairing was not able to be conducted on *T. tabaci*.

In oviposition choice experiments, the results contradicted those of host preference tests, with overall juvenile performance significantly lower on those cultivars of the brightest green hue (Shepody, Russet Burbank, Fergifry, 93-6-3) and higher on those cultivars with lower reflectance at the peak wavelength of 552 nm in the green range (Atlantic, Bismark, Royal Blue, Spunta). While the lightest green potato cultivar, Shepody, was the most preferred in paired tests in a choice chamber, it yielded the lowest number of hatched juvenile larvae in both choice and no-choice tests. Differentiation of oviposition and feeding preferences has been widely studied among insects, particularly in the Lepidoptera (Thompson & Pellymer, 1991) and Hymenoptera (Almohamad *et al*., 2009), where adults and juveniles feed on different food types, but this is less common in species where adults and larvae feed on the same type of host. A strong relationship between preference and larval performance is the prevailing assumption for most insect-host interactions (Jaenike, 1978), although many studies have reported poor correlations (reviewed by Mayhew, 1997). Oviposition site preference has been positively correlated with larval performance in sawfly (Craig *et al*., 1989), water lily beetle (Kouki, 1993), leaf miner (Preszler & Price, 1995); leaf beetles (Heisswolf *et al*., 2005; Howlett *et al*., 2001), spittle bug (Craig & Ohgushi, 2002), leaf mining fly (De Bruyn *et al*., 2002) and lycaenid butterflies (Forister, 2004). Examples of negative correlations, where females oviposited on sites that were not best for larval performance, have also been shown in butterflies (Rausher, 1979; Underwood, 1994; van Nouhuys *et al*., 2003), holly leaf miner (Valladares & Lawton, 1991), beet armyworm (Berdegué *et al*., 1998), sawfly (Fritz *et al*., 2000), grass miner (Scheirs *et al*., 2000), leaf miner (Scheirs *et al*., 2004), psyllid (Faria & Fernandes, 2001); hessian fly (Harris *et al*., 2001) and diamondback moth (Shiojiri & Takabayashi, 2003).

Divergence of feeding and oviposition choice may also occur within plant species due to genotypic and phenotypic variation, and even within individual plants between young and old leaves. Jones & Coleman (1988) found that the beetle *Plagiodera versicolora* preferred to feed on stressed cottonwood foliage, but females preferred to oviposit on unstressed foliage. The difference in preference between feeding and oviposition was maintained using leaf disks, detached leaves, and whole plants across experiments over three years. Other species that have shown differences between feeding and oviposition hosts include the cicadellid *Homalodisca vitripennis* (Lauziere & Setamou, 2009). Another explanation of variation in results may be due to the fact that preference tests were conducted on whole leaves while oviposition choice tests were conducted on leaf disks. Differences in volatile profiles may emerge between cultivars with leaf damage, which may result in differences in preference between the two types of test.

One of the most important aspects of the preference-performance and plant-vigour hypotheses is the choice of a healthy host that will survive for a sufficiently long time for the insect to complete its lifecycle, and provide for the fastest possible growth to minimise exposure to predators. *T. tabaci* may prefer to oviposit on darker green potato cultivars because darker green foliage may be indicative of healthier plants. Healthier plants are more likely to survive the length of time needed for oviposited eggs to complete a life cycle. As well as providing sufficient resources to complete the life cycle, ovipositing females must also minimise exposure of their eggs to predictable sources of mortality (Michaud & Jyoti, 2007). Clean plants with no prior thrips feeding are more likely to have lower levels of induced plant defences, as well as lower numbers of predators. *T. tabaci* may be associating darker green plants with a lower level of thrips feeding than light green plants, which might be associated with etiolation, senescence, or disease. The opposite has also been found in some cases; with experiments by de Vries *et al*. (2006) showing that *F. occidentalis* preferred to feed and lay eggs on leaves that had previously been grazed by other thrips. However it was noted that this was an unusual result, as earlier studies have shown that thrips larval fitness is lower on plants that have been damaged due to thrips feeding.

In a meta-analysis of preference-performance relationships in phytophagous insects, Gripenberg *et al*. (2010) made a number of predictions to explain a strengthened coupling between female preference and offspring performance due to modification by ecological and/or life history factors. These were narrower diet, sessile offspring, gregarious offspring, non-feeding adults, as well as tighter coupling on woody compared to herbaceous plants, and across rather than within plant species. Thrips species in particular have limited offspring mobility, which has been shown as an important factor promoting female preference for good quality hosts (Craig & Itami, 2008; Thompson, 1988). Given that oviposition choice tests here were conducted within one plant species, potato, differences could also be expected to be lower than if they were between plant host species. Nevertheless, the only prediction that was supported in this meta-analysis was that the relationship between female preference and offspring performance was stronger for oligophagous than for polyphagous insects. Gripenberg *et al*. (2010) also pointed out that most studies in this field assess bitrophic interactions between insect and host in isolation, when ecological contexts are in fact far more complex due to the unequal distribution of host plants, microclimatic conditions, mutualists, competitors and/or natural enemies, which may have profound impacts on both female preference and offspring performance (Heisswolf *et al*., 2005; Lima & Dill, 1990; Nomikou *et al*., 2003; Van Mele *et al*., 2009).

Some insects may benefit from feeding on lower quality hosts and ovipositing on higher quality hosts, thereby reducing competition for food resources between adults and juveniles. However, the theory that *T. tabaci* prefer to oviposit on darker green potato cultivars because of their association with healthier plants does not link well with the theory that TSWV-infected plants, which are more likely to be etiolated and yellow, are preferred for oviposition by thrips as found by Belliure *et al*. (2005). While more eggs were laid on the darker green cultivars in these experiments, the paler green cultivars in each pairing appeared to suffer considerable feeding damage by the thrips, though this was not quantified (Westmore, pers. obs.). The host preference and oviposition choice tests might also be showing that *T. tabaci* are utilising both optimal foraging and optimal oviposition strategies, by feeding on lighter green leaves and ovipositing on darker green leaves where available. If adults are attracted to some cultivars for optimal feeding but to other cultivars for oviposition, then this could help explain the field trial results. Field trials showed thrips numbers were highest on Bismark and Russet Burbank, and lowest on Shepody and Atlantic, whereas in choice tests, Bismark and Atlantic were least attractive but had the highest oviposition and Shepody and Russet Burbank were most attractive but had the lowest oviposition. Thrips numbers on leaves at any one time could be a combination of those thrips that have been attracted to the plant for feeding as well as those thrips that are on the plant to lay eggs. Whether migratory influx of thrips or subsequent reproduction is the most important factor in the level of TSWV incidence will determine whether cultivar attractiveness to thrips for feeding or oviposition is most important in thrips-mediated TSWV resistance.

Another result of interest is the number of juvenile thrips found on Royal Blue in both choice and no-choice tests, because Jericho (2005) found no *T. tabaci* larvae on cv. Royal Blue in laboratory cage trials, only adults, leading him to suggest that Royal Blue is preferred for feeding, but not for oviposition. One possible explanation for the difference in results here with those of Jericho (2005) is intra-specific population differences. In Chapter 5 it is shown that genetic differentiation between populations is linked to both the host from which the populations were collected, and also to the TSWV-vector competence of those populations. Populations from potato were found to be vector competent while those from onion were not. Host preference and oviposition tests here were conducted on *T. tabaci* collected from potato, whereas Jericho's tests were conducted on *T. tabaci* collected from onion. Differences in cultivar preference may exist between genetically distinct populations collected from different hosts.

One aspect of these choice and no-choice tests that could be further modified is the effect of time-dependent changes in responsiveness. Withers *et al*. (2000) showed that

feeding and oviposition choices between preferred and less-preferred species can change depending on the time since an insect last fed (level of deprivation) and the type of host that the insect last fed upon. These factors can also affect no-choice tests, because insects that have had unlimited access to an acceptable host (such as the common bean pods used for rearing thrips in this study) prior to testing may be in a state of low responsiveness (Withers *et al*., 2000). Longer or shorter periods of starvation prior to tests might produce different results, and these could be important if long-distance flight into potato crops is shown to be the most important factor in determining the incidence of thrips-vectored TSWV. All laboratory preference tests interfere to some degree with the normal process of host plant selection, which involves a sequence of steps beginning at habitat location, then location of suitable hosts, host acceptance, and host use (Kennedy, 1965). By interfering with this cascade of decisions by only testing a specific component out of context, the results from choice tests may not reflect what would occur in the field. Host preferences of each individual thrips could be influenced by the presence of multiple thrips used in oviposition tests and also by egg load (Minkenberg *et al*., 1992).

This study would have been improved by measuring the rate of juvenile development and survival, as well as measuring the nutritive qualities of the leaves from each potato cultivar. Further parameters that could be tested in future are total development times and reproductive capacities of *T. tabaci* on different potato cultivars. Also, plant age, whole plant tests, different cage types, longer times allowed for oviposition, and multiple generations rather than single egg-laying events could all be investigated to shed further light on female preference and offspring performance. Additional experiments to compare these parameters on TSWV-infected leaves with healthy leaves would have further enhanced this work. Choice chamber experiments could also be expanded by repeating the same cultivar pairings, first with clear barriers to remove any effects of volatile attractants/deterrents, and secondly with opaque barriers to remove the effects of colour on choice. This could provide a clearer picture of whether volatile cues or colour cues are the dominant factor in the potato cultivar preferences of *T. tabaci*.

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Chapter 5 - Genetic and host-associated differentiation within *Thrips tabaci* Lindeman (Thysanoptera: Thripidae) and its links to TSWV-vector competence.

Abstract

The ability of eight thelytokous (parthenogenetically reproducing female-only) populations of onion thrips (*Thrips tabaci)* collected from potato, onion or *Chrysanthemum* host plants from various regions of Australia to vector *Tomato spotted wilt virus* (TSWV), was examined in a series of trials. Of the populations tested it was found that all three populations from potato, from two Australian states, were capable of transmitting TSWV, while no TSWV transmission was observed with four different populations of *T. tabaci* collected from onion across three Australian states, despite repeated attempts. A further population collected from *Chrysanthemum* also failed to vector TSWV. The efficiency of vector competence of the *T. tabaci* populations collected from potato was highly variable across trials, ranging from 0-100 percent, and averaging 20-35 percent. The high variability between trials prevented sufficient data from being collected to compare the relative efficiencies of each population as a TSWV-vector, however, host-associated differentiation in vector competence was clearly observed.

The genetic differentiation of seven of these eight populations of *T. tabaci*, and five others not tested for TSWV vector competence, were examined by comparison of the DNA sequences of the mitochondrial gene cytochrome c oxidase subunit 1 (COI). All Australian populations of *T. tabaci* from different hosts and from different geographical areas clustered within the European 'L2' clade of Brunner *et al*. (2004). Phylogenetic analysis of DNA sequences showed all three vector competent populations from potato, as well as four additional populations from potato that had not been tested for vector competence, clustered together in the same sub-group, while the three populations of *T. tabaci,* from onion, clustered in a different sub-group. Four populations from other hosts (*Chrysanthemum*, *Impatiens*, lucerne, blackberry nightshade) clustered in a distinct sub-group. These results link genetic differentiation to source host and to TSWV vector capacity in Australian populations of *T. tabaci* for the first time. The scope of this study was not sufficient to identify any causative link within this apparent association. It does however present a credible explanation for the marked differences in observed vector competence of this species, and the sporadic nature of TSWV outbreaks in potato crops in Australia, despite the ever-presence of *T. tabaci*.

Introduction

Thrips exhibit distinct inter- and intra-specific variation in competence to vector TSWV (Inoue *et al.,* 2002; Nagata *et al.,* 2002; Paliwal 1976; Sakurai *et al.,* 2002; Wijkamp *et al.,* 1995). Since Pittman (1927) demonstrated that *Thrips tabaci* could transmit *Tomato spotted wilt virus* (TSWV), the occurrence of vector competent and incompetent populations have been reported (Jenser *et al*., 2002; Jones 1959; Paliwal 1974, 1976; Sakimura 1963a; Wijkamp *et al.,* 1995). Many populations of *T. tabaci* have been observed to transmit TSWV poorly or not at all in some parts of North America and Western Europe (Chatzivassiliou *et al*., 1998a, 1999, 2001; Jones 1959, McPherson *et al.,* 1999; Paliwal 1974, 1976; Wijkamp *et al.,* 1995) and South America (Nagata *et al.,* 2002).

There are several extant hypotheses to explain this variation, such as evolution of either the virus or *T. tabaci* or both, making them incompatible (German *et al.,* 1992; Jenser *et al.,* 2002). Incompatibilities have also been correlated with the absence of males in *T. tabaci* populations (Chatzivassiliou *et al*., 1998a; Wijkamp *et al.,* 1995). It has also been suggested that in the last twenty years, with the global spread of *F. occidentalis*, a less controllable pest generally recognised as a more efficient TSWV vector than *T. tabaci*, TSWV isolates that were transmitted by *T. tabaci* have been displaced by those transmitted by *F. occidentalis* (Nagata & Peters 2001; Ullman *et al.,* 1997).

Reports of TSWV outbreaks attributed to *T. tabaci* still occur. *T. tabaci* has been implicated in the spread of TSWV in California (Sakimura, 1961), potato and lettuce fields in southern Tasmania (Jericho & Wilson, 2003; Jericho, 2005; Wilson 1998a, 1998b, 2001), *Chrysanthemum* and *Impatiens* in southern Tasmania (P. Cross, personal communication, 2007) and tobacco fields in Eastern Europe when other vector species were not present (Chatzivassiliou *et al.,* 1998a, 1999; Jenser *et al*., 2002; Nagata & Peters 2001; Sakimura 1963a; Zawirska 1976). Despite *T. tabaci* being the first reported vector of TSWV, and remaining the primary vector of TSWV in tobacco crops in Eastern Europe and the Mediterranean region, its significance as a TSWV vector in other areas is now localised, with large variation among *T. tabaci* populations in their ability to transmit TSWV (Jacobson & Kennedy, 2010).

T. tabaci and *F. schultzei* are the main vectors associated with TSWV in potato in Australia (Thomas & Jones, 2000). In the first half of the 20th Century, TSWV outbreaks in potato in the southern and eastern States of South Australia, Victoria and New South Wales, were attributed to *T. tabaci* and *F. schultzei* (Conroy *et al.*, 1949; Magee, 1936; Norris & Bald, 1943; Norris, 1951a, 1951b; Pittman, 1927; Samuel *et al.*, 1930). Very few reports of TSWV were made until the 1990s, some forty years later. It was at this time

that *F. occidentalis* was first recorded in Australia, appearing in a *Chrysanthemum* crop south of Perth, Western Australia (Malipatil *et al.*, 1993), and shortly thereafter in the eastern States of Australia (Tesoriero *et al.*, 1995). However, *F. occidentalis* has only been associated with a small number of TSWV infections in potato, in parts of Western Australia (Latham & Jones, 1997). More recent trapping in Victoria and South Australia detected *T. tabaci* and *F. schultzei* on potato (Jericho & Wilson, 2003). In New South Wales, *T. tabaci, F. occidentalis* and *F. schultzei* were found in a range of crops, but *F. occidentalis* was not recorded from potato (Clift & Tesoriero, 2002). *Thrips palmi* is present in certain regions of Queensland and the Northern Territory, but has not been recorded on potato in Australia (Plant Health Australia, 2001). In Tasmania, *T. tabaci* is the only known TSWV vector trapped in field crops (Jericho, 2005; Jericho and Wilson, 2002; Wilson, 1998a). Since 1995, small, isolated populations of *F. occidentalis* have existed in protected cropping environments at some cut flower businesses and wholesale nurseries (L. Hill, personal communication, 2009), but *F. occidentalis* has only ever been found outside on hosts immediately surrounding these protected growing areas, and occasionally and temporarily in other areas, on plants that have been sourced from these nurseries.

Factors influencing vector competence include thrips preference for and performance on hosts (Allen & Broadbent, 1986; Bautista & Mau 1994; Bautista *et al.,* 1995; Chatzivassiliou *et al.,* 1998b, 1999, 2001, 2002; de Kogel, 2002; Maris *et al.,* 2003a; Sakimura 1963b; Sakurai *et al.,* 2002; Wijkamp *et al.,* 1995), thrips life stage (Moritz 2002; Inoue *et al.,* 2002), vector sex (Wijkamp *et al.,* 1995), plant age (Inoue *et al.,* 2002), temperature (Wijkamp & Peters 1993; Chatzivassiliou *et al.,* 2002), and genetic differences between populations of each species across geographic region (Roselló *et al.,* 1996; Sakimura 1963b). Differences in transmission efficiencies in *T. tabaci* have been linked to trade-offs and performance on different hosts, for example on leek and tobacco, *Datura stramonium* and *Petunia hybrida* (Chatzivassiliou *et al*., 1999, 2002), and tomato (Nagata *et al.,* 2002). Distinct differences in thrips host preference for and reproductive performance on different plant hosts has been demonstrated (Alimousavi *et al.*, 2007; Broadbent *et al*., 1990; Frei *et al*., 2003; Herrin & Warnock, 2002; Leiss *et al.,* 2009; Loges *et al.*, 2004; Maris *et al*., 2003a, 2003b; Rahman *et al.,* 2010), including across potato cultivars (Jericho, 2005; Chapter 4).

Genetic differences within both the virus and the vector are believed to affect vector competence (Bandla *et al.,* 1998; Kikkert *et al.,* 1998; Nagata *et al.,* 2000; Sin *et al.,* 2003; Ullman *et al.,* 1993, 1995). Some TSWV stains are not transmissible or are poorly transmitted by some vector thrips (Jenser *et al*., 2002; Jones 1959; Maris *et al*., 2003a,

2003b; Wijkamp *et al.,* 1995). The rate of transmission of different TSWV isolates is facilitated and affected by the distinct transmission specificity between (Nagata *et al.,* 2002; Wijkamp *et al.,* 1995) and within vector species (Sakurai *et al.,* 2002; van de Wetering *et al.,* 1999). The attributes of accumulation and transmission plant hosts can also influence transmission efficiency, particularly antibiosis factors that affect thrips survivability, fecundity and feeding behaviour (Maris, 2004; Stumpf & Kennedy, 2005). No significant molecular differences have been observed among TSWV strains in Australia (Dietzgen, 2003; Talty & Dietzgen, 2001), although resistance-breaking strains have been reported (Latham & Jones, 1998).

The level of virus titre in the host affects the chances of a vector acquiring, and therefore transmitting TSWV. Virus titre is determined by the number of viruliferous thrips feeding on the host, virus strain, plant host age at time of infection, and sensitivity or tolerance to TSWV (Maris *et al*., 2003; Moury *et al*., 1997; Sela 1981; Soler *et al*., 1998, 1999), including the extent to which the virus is systemically translocated (van de Wetering *et al*., 1998). Systemic movement of TSWV in plants is mediated by the viral NSm protein (Gunasinghe & Buck, 2003) and TSWV translocation can vary according to virus strain, host plant species (Garg & Khurana, 1999; Kikkert *et al*., 1999; Llamas-Llamas *et al*., 1998), plant variety (Aramburu & Martí, 2003; Jericho, 2005; Maris *et al*., 2003b; Moury *et al*., 1997; Soler *et al*., 1998, 1999; Wilson, 2001), plant growth stage (Jericho, 2005; Soler *et al*., 1998), temperature (Jericho, 2005; Llamas-Llamas *et al*., 1998; Moury *et al*., 1998; Soler *et al*., 1998), and plant stress (Córdoba *et al*., 1991). Cross-interactions between these factors may also affect infection success, translocation of the virus, and the progression of disease (Jericho, 2005).

One theory put forward (Jenser *et al*., 2002; Zawirska, 1976) is that the difference in *T. tabaci* transmission competencies is explained by *T. tabaci* being comprised of two taxonomically identical biotypes or subspecies from among which the populations on tobacco (*Nicotiana tabacum*) are considered as *T. tabaci* subsp*. tabaci* and those living on potato and other hosts as *T. tabaci* subsp*. communis.* Populations of *T. tabaci* subsp*. communis* found on different plant populations, mainly on onion, propagate parthenogenetically and, it is suggested, are not virus vectors. However, more recently some parthenogenetically-reproducing, thelytokous populations from Australia have been shown to be capable of transmitting TSWV (Jericho, 2005), requiring some modification to this theory. It has up until recently been difficult to draw conclusions based on biotype, because morphologically, the adults of *T. tabaci* populations collected from different hosts appear to be identical, notwithstanding the observations of significant differences in colour and body size of *T. tabaci* under different temperature regimes and at different times of

the year (Murai & Toda 2002). However, the now widespread use of mitochondrial DNA analysis, and the development of suitable primers for mitochondrial gene cytochrome oxidase 1 (COI) in insects such as thrips (Kambhampati & Smith, 1995; Simon *et al*., 1994), has provided powerful methods to advance population and phylogenetic studies.

Brunner *et al*. (2004) posed three possibilities: *T. tabaci* might be (a) a single polyphagous species, (b) a complex of host races with partial genetic differentiation but ongoing gene flow, or (c) a complex of morphologically cryptic species no longer joined via gene flow. Their results present strong evidence for *T. tabaci* representing a complex of at least three taxa. Clustering analyses and haplotype networks based on sequence variation at a fragment of the mitochondrial cytochrome oxidase 1 gene produced three major evolutionary lineages; two associated with leek and the third with tobacco (Brunner *et al*., 2004). The findings suggested an ancient origin for the three major phylogenetic lineages, leading Brunner *et al*. (2004) to reject the idea that *T. tabaci* is a single cosmopolitan and polyphagous species. Unfortunately, this study was solely one of host-associated genetic differentiation, with no examination of vector competence of the different populations.

More recently, Jacobson and Kennedy (2010) demonstrated that competency to transmit TSWV is determined by genetic variation among *T. tabaci* populations and among TSWV isolates. Cabrera-La Rosa and Kennedy (2007) found that populations of *T. tabaci* differed significantly in their ability to transmit an isolate of TSWV collected from potato, and following reciprocal crosses between efficient and inefficient transmitting populations, determined that ability to transmit TSWV efficiently by *T. tabaci* is inherited as a recessive trait. Inoue and Sakurai (2006) found that *T. tabaci* had a longer latent period (the time between acquisition of the virus and its first transmission to plants) than other TSWV vector species, and that TSWV infection reduced adult thrips longevity, thereby shortening the potential transmission period, which may be responsible for the low transmissibility of TSWV as well as the particularly low transmission rate in *T. tabaci* populations.

The most extensive study of TSWV-transmission by *T. tabaci* in Australia prior to this study was conducted by Jericho (2005). Using the same methodology and environmental conditions, a population of *T. tabaci* collected from onion was given the opportunity to acquire TSWV from five hosts (potato, tomato, *Datura stramonium*, *Arctotheca calendula* and *Solanum nigrum*), and presented with ten transmission hosts (*Chenopdium album*, *A. calendula*, *S. nigrum* and seven potato cultivars). Despite virus titre in the accumulation hosts being high and feeding activity on each host confirmed,

no virus transmission occurred, leading Jericho (2005) to conclude that the population was not capable of TSWV transmission. Contrasting with these controlled experimental results, Jericho (2005) observed extensive TSWV-infections in potato crops in field experiments in southern Tasmania, where the only known TSWV-vector species present was *T. tabaci*.

The aim of this study was to investigate multiple *T. tabaci* populations from different hosts across Australia, determine whether TSWV-transmission by thelytokous populations of *T. tabaci* under controlled experimental conditions is possible and determine whether any genetic differences between populations are host-differentiated, and whether these can be linked to vector competence.

Materials and methods

Thrips populations

Four populations of thelytokous onion thrips (*Thrips tabaci*) were obtained in May 2005, from Dr Grant Herron (New South Wales Department of Primary Industries). These populations were originally collected from onion varieties of the 'Creamgold' group in Coleambally (NSW-C, Oct 2003) and Whitton (NSW-W, Nov 2004), New South Wales; Mypolonga, South Australia (SA-M, Dec 2004); and Boat Harbour, Tasmania (Tas-BH Feb, 2005) (Fig. 5.1). The thrips were transferred to common bean pods (*Phaseolus vulgaris*) in May 2005 and reared for approximately 11 months, according to a protocol modified from van de Wetering (1999) and Loomans and Murai (1997), before the first vector competence experiments began. The number of generations in this period was not specifically measured, but Murai (2000) found that the mean generation time of *T. tabaci* at 25°C and L16:D8, was 29.9 days, suggesting approximately 11 generations are likely to have occurred under these conditions.

Seven further *T. tabaci* populations were collected from mixed potato variety trials between 2006 and 2007 (three from Tasmania and four from South Australia) (Fig. 5.1). The populations from potato in South Australia (SA-P, SA-P1, SA-P2, SA-ATL) were all collected from Penola in Jan 2007 from cv. Atlantic. The populations from potato in Tasmania were all collected from Cambridge in Jan 2006 (Tas FT) and Jan 2007 (Tas P, Tas P1) with source cultivars not recorded. Another population (Tas-Capeweed) was collected from a capeweed (*Arctotheca calendula*) plant from within a mixed potato variety trial at Cambridge in Jan 2006. Of the two populations from potato that were tested for vector competence, one population (Sa-P) was reared for 11 months (approx. 11 generations) and the other (Tas-FT) reared for 5 months (approx 5 generations) on common bean before testing.

Three populations (Tas-Chr, Tas Impatiens, Tas-Nightshade) were collected in suburban Hobart in Dec 2006 from *Chrysanthemum* sp*. Impatiens* sp*.* and blackberry nightshade (*Solanum nigrum*). The final population (Tas-Lucerne) was collected in Feb 2007 from lucerne (*Medicago sativa*) adjacent to a lettuce crop at Richmond (Fig. 5.1). The population from *Chrysanthemum*, was reared for 11 months (approx. 11 generations) on common bean before being tested for vector competence. In all cases colonies were established by collecting a small number of thrips from a single plant of each host type, and immediately transferring to common bean. Collection times were made at different times during the day. All thrips were reared in 7cm x 9cm containers, at 25°C ± 1°C, 65 ± 5% RH, with a photoperiod of L16:D8 in a climate-control chamber, under 450μmol-m^{-2}.s^{-1} PAR (photosynthetically active radiation). Thrips were transferred twice-weekly on to fresh common bean pods. Rearing on common bean for multiple generations following collection aimed to standardise any temporary effects of host on transmission capacity or efficiency.

Figure 5.1 Map showing collection sites of Australian populations of *T. tabaci* from onion, potato and additional hosts. Populations were collected from onion at Mypolonga, South Australia (SA M), Whitton, New South Wales (NSW-C), Coleambally, New South Wales (NSW W) and Boat Harbour, Tasmania (TAS-BH). Four populations (SA-P, SA-P1, SA-P2, SA-ATL) were collected from potato at the same location in Penola, South Australia. Three populations (Tas-FT, Tas-P, Tas-P1) were collected from potato at Cambridge, Tasmania. One population (Tas-Capeweed) was collected from capeweed at Cambridge, Tasmania. One population (Tas-Lucerne) was collected from lucerne at Richmond, Tasmania. Three populations were collected from Hobart, Tasmania – one from *Chrysanthemum* sp. (Tas-Chr), one from *Impatiens* sp. (Tas-Impatiens) and one from *Solanum nigrum* (Tas-Nightshade).

Virus and plants

Host potato plants (cv. Atlantic) were grown from tissue culture samples obtained from the Vegetable and Associated Industries Branch of the Tasmanian Department of Primary Industries and Water (now incorporated into the Tasmanian Institute of Agriculture), Devonport, in April 2005. Tissue culture plants were grown in Potato Multiplication media (4.3 g Murashige-Skoog salts, 30 g sucrose, 0.5 g casein hydrolysate, 0.04 g ascorbic acid made up to 1 L with dH_20, and 8 g/L agar type A added before autoclaving) in 7cm x 9cm containers, at 22°C, near saturation RH, L16:D8, under cool white fluorescent light. Tissue culture plants were transplanted to soil in 10x10cm pots when about 5cm tall and grown for a further six weeks in a glasshouse. Other plants used were blackberry nightshade *(Solanum nigrum),* capeweed (A*rctotheca calendula)*, tomato cv. Grosse lisse (*Solanum lycopersicum*), *Datura* (*Datura stramonium*) and tobacco (*Nicotiana tabacum*). These were grown under the same conditions from locally obtained seed. All transmission experiments used TSWV isolate *An_{WA}-1*, which was kept in tomato before being used in mechanical inoculations of acquisition hosts. TSWV isolate *An_{WA}-1* was originally obtained from an infected ornamental host, *Anenome* sp., from Western Australia, which has been maintained for a number of years in a tomato host by the Tasmanian Institute of Agriculture, using routine mechanical inoculation with periodic vector transmission by natural thrips populations in exposure trials.

Enzyme-linked immunosorbent assay (ELISA)

TSWV specific antibodies (monoclonal mixture) (Agdia, Elkhart, Indiana USA) were used in double antibody sandwich ELISA as described by Clark and Adams (1977). Sap was extracted from the leaf disks (1g/10mL) in phosphate buffered saline with Tween (PBS-T) (1.5mM potassium phosphate, 137mM sodium chloride, 8 mM disodium hydrogen phosphate, 2.7 mM potassium chloride, 10 mM sodium sulphite, 0.2% (w/v) bovine serum albumin, 15mL/L of Tween 20 and 20g/L of polyvinyl pyrrolidone, pH 7.4). All samples and known TSWV-positive and negative controls were tested in duplicate. The substrate was 0.5mg/mL *p*-nitrophenyl phosphate in 97mL/L diethanolamine, pH 9.8. Results were assessed by spectrophotometric measurement of absorbance at 405 nm using a Labsystems Multiskan RC plate reader with Genesis software (Labsystems, Helsinki, Finland). Samples with absorbance values greater than twice the mean of negative controls were considered positive, as recommended by Clark and Adams (1977).

Mechanical inoculation of acquisition host plants

Host plants were placed in the dark (covered with damp newspaper) for at least 12 h prior to and post-inoculation, but exposed to light immediately before and during inoculation to enhance susceptibility to TSWV infection (Hull, 2002; Liu *et al*., 2009). TSWV-infected tomato leaves were ground in chilled inoculation buffer (0.18 M potassium phosphate, pH 7.5, plus 0.15% (w/v) cysteine hydrochloride) using a chilled mortar and pestle. The virus-containing sap was mixed with a small amount of celite (Celite corporation, Lompoc, CA, USA) and applied to three young leaves from each plant. Using a gloved finger the sap was gently rubbed down the surface of the lamina away from the plant stem. Plants were then gently washed with a fine water spray to remove sap and celite residue.

Determining vector competence of thrips populations

The ability of eight of the 15 thrips populations collected to vector TSWV was tested in a series of glasshouse and laboratory experiments. All four populations from onion (SA-M, NSW-C, NSW-W, Tas-BH) were included, as well as one population from potato from South Australia (SA-P), and two populations from potato in Tasmania (Tas-P, Tas-FT) collected in different years but from the same location. The final population tested was from *Chrysanthemum* (Tas-Chr) and chosen because it had been found on a TSWV-infected plant. First-instar larvae less than 12 h old were placed on freshly picked leaves from a TSWV-infected host plant, with an acquisition access period (AAP) of 24 h. After the AAP, larval thrips were individually placed on common bean pods and reared to adults. For each acquisition and transmission host combination, up to 20 adult thrips per population were placed singly on leaf disks cut from young, fully expanded leaves from a healthy susceptible host in sterile 1.5mL microcentrifuge tubes with a strip of paper towel to absorb free moisture, with an inoculation access period (IAP) of 72 h. Some experiments tested relatively few thrips and leaf disks due to insufficient availability of either first-instar thrips larvae or systemically infected hosts (Table 1). Adults were then removed and leaf disks were incubated for seven days at room temperature.

An equal number of leaf disks from the same host plant were kept thrips-free in microcentrifuge tubes as negative controls. These were tested by ELISA to confirm that all transmission hosts were free of TSWV. The number of leaf disks infected with TSWV was also determined by ELISA. Six acquisition and transmission host combinations were conducted over ten experiments (Table 5.1). The first five experiments were conducted in 2006, when only five populations (Tas-FT, SA-M, NSW-C, NSW-W, Tas-BH) were available for testing. Tomato was used as the acquisition host for these experiments due to the availability of significant amounts of TSWV-infected leaf material from this plant host. The remaining five experiments were conducted in 2008, when three additional

populations (Tas-P, SA-P, Tas-Chr) were available. *Datura* was used as the acquisition host for these experiments. Different susceptible transmission hosts were chosen depending on the availability of healthy leaf material at the time of each experiment, but when potato was introduced as a transmission host, the cultivar Atlantic was chosen because of its known susceptibility to TSWV.

Table 5.1 Transmission experiments were conducted on eight populations of T. tabaci using six acquisition and transmission host combinations across ten experiments. 1st instar larvae less than 12 h old, from each population, were taken from common bean pods and placed on detached leaves of acquisition hosts for 24 h, then reared to adults on common bean pods, and transferred to leaf disks of a transmission host for 72 h, with one thrips per leaf disk.

Experiment	Acquisition host	Transmission host	Number of thrips from each population	Populations tested
1	Tomato	Tobacco	12	Tas-FT
2	Tomato	Tobacco	20	Tas-FT, SA-M, Tas-BH, NSW-C, NSW-W
3	Tomato	Tobacco	3	Tas-FT, SA-M, Tas-BH, NSW-C
4	Tomato	Nightshade	4	Tas-FT
5	Tomato	Tomato	2	Tas-FT
6	*Datura*	*Datura*	10	Tas-FT, SA-P, SA-M, Tas-BH, Tas-Chr
7	*Datura*	*Datura*	10	Tas-FT, SA-P, SA-M, Tas-BH, Tas-Chr
8	*Datura*	Tobacco	10-20	Tas-FT, SA-M, Tas-BH
9	*Datura*	Potato cv. Atlantic	10	SA-P, SA-M, Tas-BH, Tas-Chr
10	*Datura*	Potato cv. Atlantic	20	Tas-FT, SA-P, SA-M, Tas-BH, Tas-Chr

A glasshouse experiment was also conducted in which a large number of adults (>100) from each thrips population was transferred from common bean pods to an infected host plant. One hundred 2nd-instar larvae were then removed from each host plant and reared to adulthood on common bean. All surviving adults were transferred to a healthy susceptible host plant. Successful transmission of TSWV to the susceptible host was determined by taking young leaf samples after four weeks and again after six weeks, and testing by ELISA. Seven acquisition and transmission host combinations of this experiment were conducted (Table 5.2).

All seven of these experiments were conducted in 2006, with the five available populations (Tas-FT, SA-M, NSW-C, NSW-W, Tas-BH). Tomato was used as the acquisition host for the first four experiments, with capeweed and *Datura* in the remaining three experiments. Susceptible transmission hosts were also chosen depending on the availability of healthy plants.

Table 5.2 TSWV-transmission experiments were conducted on five populations of T. tabaci using seven acquisition and transmission host combinations. Adults from each population were placed on acquisition hosts, and 100 2nd instar larvae were later removed, reared to adults on common bean pods, and then transferred to a transmission host. The transmission host in each experiment consisted of a single plant upon which more than 50 adult thrips were placed.

Experiment	Acquisition host	Transmission host	Populations tested
1	Tomato	Tomato	Tas-FT, SA-M, Tas-BH, NSW-C, NSW-W
2	Tomato	Nightshade	Tas-FT, SA-M, Tas-BH, NSW-C, NSW-W
3	Tomato	Tobacco	Tas-FT, SA-M, Tas-BH, NSW-C, NSW-W
4	Tomato	Capeweed	Tas-FT
5	Capeweed	Capeweed	Tas-FT
6	*Datura*	Tobacco	Tas-FT
7	*Datura*	Capeweed	Tas-FT

Mitochondrial DNA extraction

DNA was extracted from five individual *T. tabaci* collected from each colony shortly after the vector competence tests were conducted and stored in 75% ethanol, using a modified protocol of Morris and Mound (2004). Thrips were incubated in a solution of 100µL TNES buffer and 5µL Proteinase K ($10mg.mL^{-1}$) at either 45°C for 5h, or 37°C overnight. The lysis solution was precipitated using 85µL 5M NaCl. The supernatant was removed and DNA precipitated using 400µL of chilled 100% ethanol. The resulting DNA pellet was washed with 70% ethanol and dried, and re-suspended in 20µL sterile, dH_2O before use in PCR.

PCR amplification and DNA sequencing

A fragment of the mitochondrial gene cytochrome oxidase 1 (COI) was amplified using the primers C1-J-1751 and C1-N-2191 (Simon *et al*., 1994). PCR was performed in 25µL reaction volumes, with 12.5 µL HotStarTaq Master Mix (containing HotStarTaq DNA Polymerase, PCR Buffer, and dNTPs, providing a final concentration of 1.5mM $MgCl_2$ and 0.2mM of each dNTP. (Qiagen, Valencia, CA, USA), 0.3µM of each primer and sterile dH_2O, using the following PCR program: denaturation at 95°C for 15 min, 35 cycles of (94°C 30s, 50°C 30s, 72°C 45s), followed by extension at 72°C for 10 min. PCR product was then cleaned using a QIAquick PCR purification kit (Qiagen). Both forward and reverse strands were sequenced with the above primers using BigDye™ Terminator v.3.1 (Applied Biosystems, Foster City, CA, USA) by Griffith University DNA Sequencing Facility (GUDSF). Sequences have been made available at Genbank (Table 5.3).

Table 5.3 Accession numbers for Australian populations of *T. tabaci* and *F. occidentalis* used in this study.

Population name	Species	Source host	Genbank accession number
NSWC	*T. tabaci*	onion	JQ074095
SAATL	*T. tabaci*	potato	JQ074096
SAM	*T. tabaci*	onion	JQ074097
SAP1	*T. tabaci*	potato	JQ074098
SAP2	*T. tabaci*	potato	JQ074099
SAP	*T. tabaci*	potato	JQ074100
TASBH	*T. tabaci*	onion	JQ074101
TASCAPE	*T. tabaci*	capeweed	JQ074102
TASCHR	*T. tabaci*	*Chrysanthemum*	JQ074103
TASFT	*T. tabaci*	potato	JQ074104
TASIMP	*T. tabaci*	*Impatiens*	JQ074105
TASLUC	*T. tabaci*	lucerne	JQ074106
TASN	*T. tabaci*	Blackberry nightshade	JQ074107
TASP1	*T. tabaci*	potato	JQ074108
TASP	*T. tabaci*	potato	JQ074109
TASWFT	*F. occidentalis*	lettuce	JQ082479

DNA analyses

DNA sequences were edited; consensus sequences generated for each specimen, and the dataset aligned using the AlignX component of Invitrogen Vector NTI Advance 10.3 (Invitrogen Corp, Carlsbad, CA, USA). Phylogenetic trees were constructed using both the neighbour-joining and maximum-likelihood methods implemented in MEGA version 5, with the pair-wise deletion option and 1,000 bootstrap replicates (Tamura *et al.,* 2011). Where these two methods showed no difference in branching structure of the tree, the trees derived from the maximum-likelihood method are presented. Branches

corresponding to partitions reproduced in less than 50 percent bootstrap replicates were collapsed, and the trees drawn to scale.

Selected European sequences of *T. tabaci* from Brunner *et al*. (2004) (Genbank: AY196831, AY196838, AY196840, AY196841, AY196843, AY196844, AY196845, AY196847, AY196848), were combined with the Australian populations of *T. tabaci* (Genbank: JQ074095-JQ074109) in the phylogenetic tree to place the Australian populations in global context. *T. palmi* (GenBank: AB277231) served as an intra-generic comparison, because it is considered closely related to *T. tabaci* (Brunner *et al.*, 2002). *F. occidentalis* (GenBank: EF555889) and *F. occidentalis* (GenBank: JQ082479) taken from a protected cropping system in Tasmania served as out-groups.

Results

Of the ten virus transmission experiments, eight experiments resulted in successful virus transmission (Table 5.4). The three populations collected from potato, from South Australia and Tasmania (SA-P, Tas-FT, Tas-P), were able to transmit TSWV, with variable success ranging from 0 to 100 percent, averaging 20, 25 and 35 percent transmission respectively (Table 3). The four populations collected from onion from Tasmania, South Australia, and NSW (Tas-BH, SA-M, NSW-C, NSW-W), and the Tasmanian population from *Chrysanthemum* (Tas-CHR) failed to transmit TSWV. NSW-C and NSW-W were tested twice, Tas-BH, SA-M were tested seven times and Tas-CHR tested four times.

Table 5.4 TSWV vector competence of Australian *T. tabaci* populations - percentage transmission in different acquisition and transmission host combinations using individual thrips. Three populations collected from potato, from two Australian states (Tasmania and South Australia), four populations collected from onion across three Australian states (Tasmania, South Australia, and NSW) and one from *Chrysanthemum* collected from Tasmania were tested. SA = South Australia; TAS = Tasmania; NSW = New South Wales; Tom = tomato; Tob = tobacco; Night = blackberry nightshade; Dat = *Datura*; Pot = potato cv. Atlantic.

	Percentage transmission (total leaf disks per population)								
Experiment	SA-P (ex potato)	Tas-FT (ex potato)	Tas-P (ex potato)	SA-M (ex onion)	Tas-BH (ex onion)	NSW-C (ex onion)	NSW-W (ex onion)	Tas-CHR (ex *Chrysanthemum*)	Mean transmission (%)
1 (Tom>Tob)	-	100 (12)	-	-	-	-	-	-	100
2 (Tom>Tob)	-	0 (20)	-	0 (20)	0 (20)	0 (20)	0 (20)	-	0
3 (Tom>Tob)	-	33 (3)	-	0 (3)	0 (3)	0 (3)	-	-	8.3
4 (Tom>Night)	-	50 (4)	-	-	-	-	-	-	50
5 (Tom>Tom)	-	100 (2)	-	-	-	-	-	-	100
6 (Dat>Dat)	30 (10)	0 (10)	-	0 (10)	0 (10)	-	-	0 (10)	6
7 (Dat>Dat)	30 (10)	20 (10)	20 (10)	0 (10)	0 (10)	-	-	0 (10)	11.7
8 (Dat>Tob)	-	10 (20)	-	0 (10)	0 (10)	-	-	-	3.3
9 (Dat>Pot)	40 (10)	-	-	0 (10)	0 (10)	-	-	0 (10)	10
10 (Dat>Pot)	0 (20)	0 (20)	-	0 (20)	0 (20)	-	-	0 (20)	0
Mean transmission (%)	25	35	20	0	0	0	0	0	

In three experiments where many *T. tabaci* individuals were taken from an acquisition host and placed on a single transmission host, virus transmission occurred in all three host acquisition-transmission host combinations with the *T. tabaci* population originally sourced from potato (Tas-FT), but no transmission occurred in any host combination with any of four populations originally sourced from onion (Table 5.5). Successful transmission of TSWV by Tas-FT was further confirmed in four additional acquisition-transmission host combinations (Experiments 4-7 of Table 5.5).

Table 5.5 TSWV transmission by *T. tabaci* in different acquisition and transmission host combinations using multiple thrips (more than 50 individuals on each transmission host) from 5 different thrips populations. (+ = transmission, - = no transmission, n/a = not tested, SA = South Australia, TAS = Tasmania, NSW = New South Wales)

Experiment	Tas-FT (ex potato)	SA-M (ex onion)	Tas-BH (ex onion)	NSW-C (ex onion)	NSW-W (ex onion)
1 (Tomato > Tomato)	+	-	-	-	-
2 (Tomato > Nightshade)	+	-	-	-	-
3 (Tomato > Tobacco)	+	-	-	-	-
4 (Tomato > Capeweed)	+	n/a	n/a	n/a	n/a
5 (Capeweed > Capeweed)	+	n/a	n/a	n/a	n/a
6 (*Datura* > Tobacco)	+	n/a	n/a	n/a	n/a
7 (*Datura* > Capeweed)	+	n/a	n/a	n/a	n/a

Phylogenetic analysis showed that, the Australian and European populations formed three distinct clades supported by high bootstrap values. The three European clades are in accordance with those described by Brunner *et al*. (2004) (Fig. 5.2). All Australian populations of *T. tabaci* from different hosts and from different geographical areas clustered within the 'L2' European clade of Brunner *et al*. (2004). This European clade corresponded to populations from leek from Switzerland, Greece and Bulgaria, and to the '*communis*' biotype or subspecies. Individuals of seven *T. tabaci* populations taken from potato, but from different geographical locations, and one population taken from capeweed (Tas-Capeweed) in the middle of a potato crop (from which Tas-FT was collected), grouped together supported by a bootstrap score of 70 percent (Fig. 5.2). The three populations from onion clustered in a separate sub-group supported by a bootstrap

score of 72 percent. Populations from *Chrysanthemum*, *Impatiens* and blackberry nightshade clustered in a third sub-group supported by a bootstrap score of 59 percent.

Vector competence was associated with homology within the COI sequences. Of those populations tested for their TSWV-vector competence, the sequences clustered into three distinct sub-groups within the larger 'L2' clade supported by high bootstrap values. One sub-group contained all populations capable of transmitting TSWV, another sub-group forming all those sourced from onion hosts that did not transmit, with the population collected from *Chrysanthemum* being separate. The NSW-W population (ex-onion, ex-NSW) was lost prior to DNA extraction.

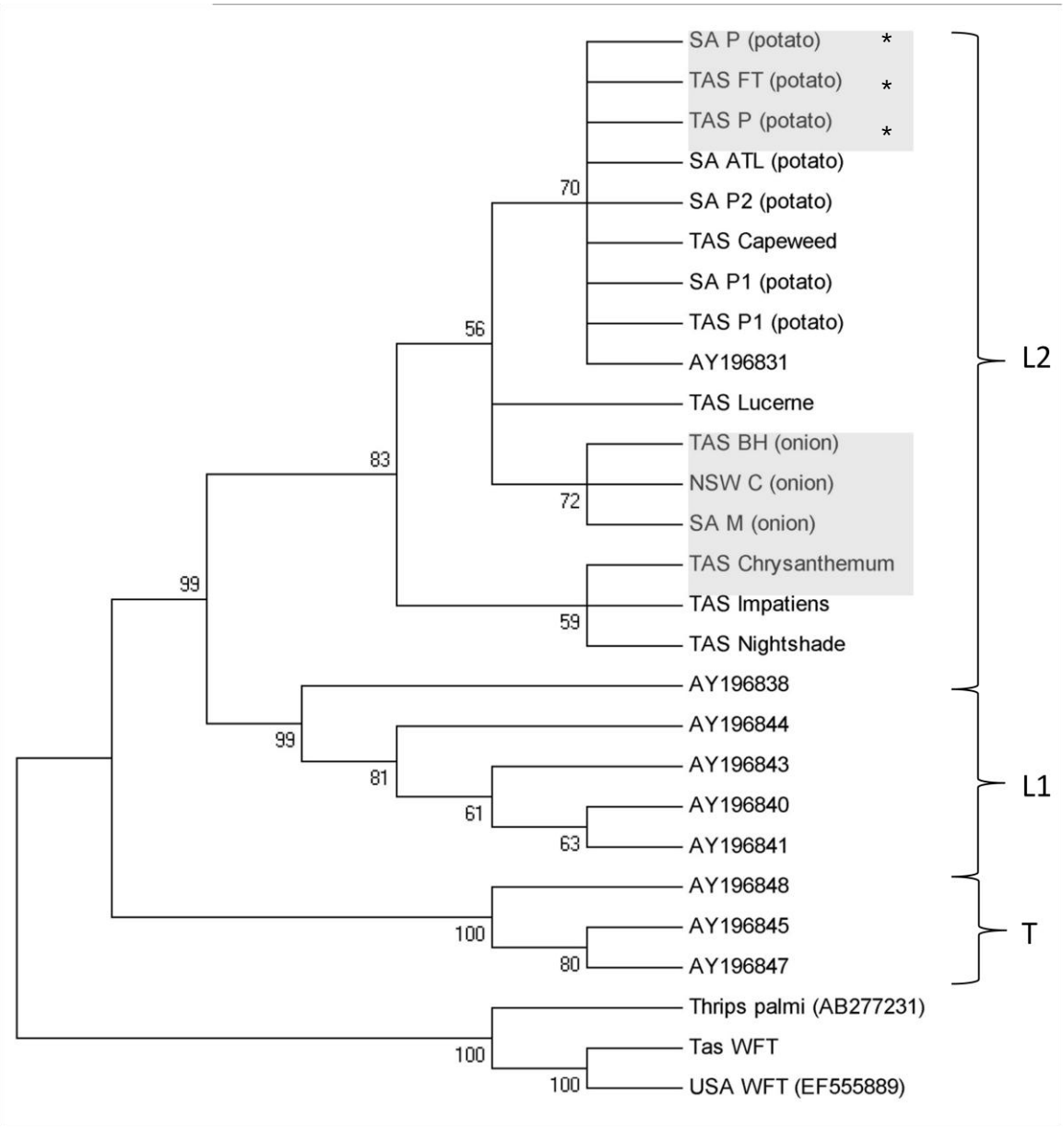

Figure 5.2 Phylogenetic analysis[1] of all *T. tabaci* populations collected from Australia (Genbank: JQ074095-JQ074109), selected sequences of *T. tabaci* from Europe (Genbank: AY196831, AY196838, AY196840, AY196841, AY196843, AY196844, AY196845, AY196847, AY196848), *T. palmi* (GenBank AB277231), *F. occidentalis* from the United States (GenBank EF555889) and *F. occidentalis* from Tasmania (Genbank: JQ082479). Clades are marked as per Brunner *et al*. (2004). Greyed out populations were tested for vector competence. * = known TSWV-vector competent populations

[1]The evolutionary history was inferred using the Maximum Likelihood method based on the Tamura-Nei model (Tamura & Nei, 1993). The bootstrap consensus tree inferred from 1000 replicates (Felsenstein, 1985) is taken to represent the evolutionary history of the taxa analysed (Felsenstein, 1985). The percentage of replicate trees in which the associated taxa clustered together in the bootstrap test (1000 replicates) are shown next to the branches (Felsenstein, 1985). Initial tree(s) for the heuristic search were obtained automatically as follows: when the number of common sites was < 100 or less than one fourth of the total number of sites, the maximum parsimony method was used; otherwise BIONJ method with MCL distance matrix was used. The analysis involved 27 nucleotide sequences. Codon positions included were

1st+2nd+3rd+Noncoding. All positions containing gaps and missing data were eliminated. There were a total of 433 positions in the final dataset. Evolutionary analyses were conducted in MEGA5 (Tamura *et al*., 2011).

DNA sequence variations between the specimens are shown in Table 5.6. Within the sequenced 433 bp fragment of the 15 Australian populations there were six variable sites, averaging one base substitution every 72 base pairs. There were only 2-3 site differences separating populations from onion and potato at positions 87 and 246. All populations from potato had an identical sequence to each other and to AY196831 (from leek, in Switzerland) from Brunner *et al*. (2004). All variation was in the form of silent, single base-pair substitutions.

Table 5.6 Variable positions in the 433 bp segment of the COI gene of 15 populations of *T. tabaci* from Australia. The reference sequence is Tas P (*T. tabaci* collected from potato in Tasmania). All other populations collected from potato (Tas P1, Tas FT, SA P, SA P1, SA P2, SA ATL) had identical sequences to Tas P and are not shown. Dots indicate nucleotides that are identical throughout the compared sequences.

	Nucleotide positions					
	78	**87**	**246**	**258**	**309**	**384**
Tas-P (potato)	A	G	G	A	G	A
Tas-Capeweed	.	.	.	.	.	.
Tas-CHR	.	A	A	.	.	.
Tas-*Impatiens*	.	A	A	.	.	.
Tas-Nightshade	.	A	A	.	.	.
Tas-Lucerne	G	.	A	.	A	.
NSW-C (onion)	.	.	A	C	.	G
SA-M (onion)	.	.	A	.	.	G
TAS-BH (onion)	.	.	A	.	.	G

Discussion

The vector competence experiments demonstrated Australian populations collected from onion hosts failed to transmit TSWV despite repeated attempts, while populations collected from potato were TSWV vector competent. Comparative transmission experiments using leaf disk tests and individual thrips showed considerable variability in the vector competence of populations from potato. While some of these experiments only used small numbers of thrips (see Table 5.1), preventing conclusions being drawn on specific acquisition-transmission host combinations, other experiments used sufficient numbers to give confidence in differences between populations. Additional experiments using 50-100 thrips on the one transmission host showed that a population collected from potato was capable of transmitting TSWV in nine different acquisition-transmission host combinations. Other studies have reported very low levels of transmission or no transmission for this species (Chatzivassiliou *et al*., 1998a, 1999, 2001; Jones, 1959, McPherson *et al.,* 1999; L. Mound, personal communication, 2005; Nagata *et al.,* 2002; Paliwal, 1974, 1976; Wijkamp *et al.,* 1995). When no virus transmission occurred in controlled transmission tests by Jericho (2005), it was suggested that non-transmission might have been due to rearing and experimental temperatures, such as described by Chatzivassiliou *et al.* (2002), and fitness trade-offs due to serial feeding on certain hosts, as found by Chatzivassiliou *et al.* (1999) in leek and Wijkamp *et al.* (1995) in bean. However, this study suggests that it could have been due to distinct differences in *T. tabaci* populations, as the Jericho (2005) experiments were conducted with thrips collected from onion.

Contrasting findings on the ability of *T. tabaci* to transmit TSWV in different parts of the world have existed for decades and continue today (Brunner *et al*., 2004; Chatzivassiliou *et al*., 1999, 2001; Jacobson & Kennedy, 2010; Jenser *et al*., 2002, 2003; Jericho, 2005; Jones 1959; Pittman, 1927; Sakimura, 1939; Samuel *et al.*, 1930; Tavella *et al*., 2002; Wijkamp*et al*., 1995). The factors affecting vector competency of *T. tabaci* is still an issue of debate. Diversity and biological variation among populations has been demonstrated (Jenser *et al*., 2002; Mound 1997, 2004; Murai & Toda, 2002; Zawirska, 1976), as has the inconsistency in TSWV transmission (Chatzivassiliou *et al*., 1999, 2001; Jenser *et al*., 2002, 2003; Jones 1959; Paliwal 1974, 1976; Sakimura, 1963b; Tavella *et al*., 2002; Wijkamp *et al*., 1995. An ongoing difference between Australian populations and those in other countries is that bisexual populations of *T. tabaci* have not been observed in Australia, although they may exist (L. Mound, personal communication, 2005). This study confirms that female-only populations are capable of transmitting TSWV.

Since the work of Storey (1932, 1933), intra-specific variation in vector competence has been demonstrated in many studies for plant viruses (Bencharki *et al*., 2000; Gray, 1999) and animal viruses (reviewed by Gooding, 1996). Some studies have simply reported an association (Bourdin *et al*., 1998; Gray *et al*., 2002; Tardieux, *et al*., 1990; Tesh *et al*., 1976), while others have shown there is genetic control over the ability to transmit a virus, usually through crossings of competent and incompetent populations (Anderson *et al*., 2005; Beerntsen *et al*., 2000; Bennett *et al*., 2005; Bosio *et al*., 2000; Fallioux *et al*., 1999; Gray *et al*., 2007; Miller & Mitchell, 1991; Tabachnick, 1991; Tabachnick, 1994; Tardieux *et al*., 1991). Vector competence has been associated with genetic differences between populations in other species of thrips (Cabrera-La Rosa & Kennedy, 2007; Halaweh & Poehling, 2009), mosquito (Black *et al*., 2002; Gray *et al*., 2007; Kilpatrick *et al.*, 2010; Mercado-Curiel *et al*., 2008; Miller & Mitchell, 1991; Tabachnick *et al*., 1985; Tabachnick, 1991; Tabachnick, 1994; Tardieux *et al*., 1991), planthopper (Zeigler & Morales, 1990), leafhopper (Storey, 1932), whitefly (Brown, 2007a, 2007b), tick (Reichard & Kocan, 2006), tsetse fly (Geiger *et al*., 2005, 2007). and aphid (Burrows *et al*., 2006, 2007; Dedryver *et al*., 2005; Gray *et al.*, 1999; Yang *et al*., 2008).

The groupings of these Australian populations based on COI sequence corresponded to differences in vector competence, as well as the host from which they were collected. Because sympatric populations from potato and onion were not tested for vector competence, the influence of geographical separation rather than host cannot be ruled out. However, the populations of *T. tabaci* collected from potato in Tasmania were taken from the same location as the population collected from onion by Jericho (2005), which was not able to vector TSWV in laboratory experiments. Recent work on vector competence of *T. tabaci* has suggested that the variation in TSWV transmission by this species is linked, at least in part, to genetic differentiation between populations, and/or the host from which the populations were collected (Brunner *et al*., 2004; Jacobson & Kennedy, 2010). The results of these vector competence experiments and phylogenetic analyses of multiple *T. tabaci* populations support this developing hypothesis.

In this study both vector competent and incompetent populations from potato and onion grouped within the 'L2' clade of Brunner *et al*. (2004), who stated that both 'L1' and 'L2' were non-vector lineages of the 'communis type', with 'L2' being thelytokous. Chatzivassiliou *et al*. (2002) also determined that arrhenotokous populations collected from tobacco transmitted TSWV efficiently (up to 49 percent transmission) while those from leek were poor transmitters (up to 3 percent), whereas no transmission occurred with thelytokous populations from leeks. This study contradicts those findings by confirming that parthenogenetically-reproducing, thelytokous *T. tabaci* populations found

on potato, are capable of vectoring TSWV. This study also shows that differences in vector competence between populations occur within at least one of the three major evolutionary lineages, and not just between lineages. Toda & Murai (2007) found 17 haplotypes of *T. tabaci* in Japan from across all three lineages proposed by Brunner *et al*. (2004). Of these, five were thelytokous populations, and only six nucleotide substitutions separated these populations, with 1-4 polymorphic sites amongst the haplotypes. By comparison the five haplotypes found in this study are also separated by only six nucleotide substitutions, albeit at different nucleotide positions, with 2-3 polymorphic sites amongst the haplotypes; however Toda and Murai (2007) used the 856 bp region of the mitochondrial COI gene, whereas this study only used a 433 bp fragment of this gene as was done by Brunner *et al*. (2004).

The phylogenetic analyses in this study show a lack of genetic segregation with geographical variation, and rather distinct clusters are associated with the host plant from which the populations were first collected. Also, it appears that TSWV vector capacity is associated with genetically distinct populations. It would be valuable in future studies to examine multiple TSWV isolates as Wijkamp *et al*. (1995), Mau *et al*. (1990), and others (Jenser *et al*., 2002; Naidu *et al*., 2004; van de Wetering *et al*., 1996), have shown distinct levels of specificity in transmission of different virus strains. Some suggestion of this was also raised by the results of the vector competence tests on *T. tabaci* from *Chrysanthemum*. The *T. tabaci* population (Tas-Chr) originally collected from TSWV-infected *Chrysanthemum* plants was assumed to be vector competent, however in the transmission tests using TSWV isolate An_{WA}*-1*, originally sourced from *Anenome* sp. but maintained in tomato and inoculated into a *Datura* acquisition host, no transmission occurred. Now that complete genome sequences of many TSWV isolates are being reported (Hu *et al*., 2011; Lee *et al*., 2011), the opportunity exists to study in detail the specific effects of virus genotype on TSWV transmission efficiency. The characterisation of isolate diversity in Tasmania and Australia, and the similarity of these isolates to those in other parts of the world, would provide the basis for further work looking at the interaction between thrips, virus, plant host and how this affects vector competence. It would be valuable to determine if Australian thrips populations collected from onion are unable to vector all known TSWV strains, or whether the failure to transmit TSWV in these experiments is because of the particular isolate used.

The results presented here provide a credible explanation for the highly variable results in many studies that have sought to determine the vector competence of *T. tabaci*, including those studies that concluded that this species is unable to vector TSWV. Further studies should, in addition to evaluating greater numbers of populations from

diverse hosts and locations, look at how genetic differentiation is related to vector competence. Possible factors that could be associated with vector capacity include differences in mid-gut receptors, mid-gut properties, salivary gland properties, connections between salivary glands and muscle tissue of the mid-gut during the first instar stage, feeding behaviour on different hosts, and length required for the acquisition and inoculation access periods.

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Chapter 6 - Summary and concluding remarks

This study was initiated following major outbreaks of *Tomato spotted wilt virus* (TSWV) in potato in Australia, and following a PhD study (Jericho, 2005) examining TSWV epidemiology in potato in light of these outbreaks. Experiments were formulated to examine the efficiency of TSWV transmission by onion thrips (*Thrips tabaci* Lindeman), and the presence of resistance to thrips in potato and its significance to field infection with TSWV. Three field trials were conducted examining cultivar differences in field resistance to TSWV and *T. tabaci* (Chapter 2). A population of *T. tabaci* collected from potato in Tasmania was subjected to choice experiments to test for colour preference (Chapter 3), and host preference and oviposition choice (Chapter 4), using a number of commercial potato cultivars, other plant hosts and coloured cards. Populations of *F. occidentalis* and *F. shultzei* were also tested for colour and host preference alongside *T. tabaci* in separate experiments.

On the basis that emerging work in other countries had found differentiation in vector competence between *T. tabaci* populations, possibly linked to host and vector thrips genetics, several populations of *T. tabaci* were collected from Tasmania, New South Wales and South Australia from potato and onion. These populations were tested for their ability to transmit TSWV to potato and other hosts, and subjected to a phylogenetic analysis following DNA extraction and PCR amplification of mitochondrial gene cytochrome c oxidase subunit 1 (COI) (Chapter 5).

The key findings from this study are summarised in Tables 6.1-6.4.

Table 6.1 Potato cultivar comparisons for TSWV foliar and tuber infection, thrips numbers on foliage, green intensity of foliage, cultivar preferences (choice) and oviposition preferences in choice and no-choice tests (1 = highest value for each category; 3 = lowest value; same number signifies no difference; ns = no significant difference between all cultivars).

	Cultivars												
	Atlantic	Bismark	Russet Burbank	Shepody	93-6-3	Coliban	Fergifry	Tasman	Spunta	Royal Blue	Russet Ranger	King Edward	Desiree
TSWV foliar infection (trial 1)	ns	ns	ns	ns	-	-	-	-	-	-	ns	ns	-
TSWV foliar infection (trial 3)	ns	ns	ns	ns	-	ns	ns	-	-	-	-	ns	ns
TSWV tuber infection (trial 3)	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
T. tabaci numbers on foliage	2,3	1	1,2,3	3	-	-	-	-	-	-	1	1,2	-
Green intensity of foliage	4	5	1	1	3	-	2	8	6	7	-	-	-
Cultivar preference of *T. tabaci* compared to cv. Atlantic	-	2	1	1	2	2	2	2	2	2	2	-	2
Oviposition preference of *T. tabaci* (no choice)	1	1	2,3	3	2,3	-	2,3	1,2,3	1,2	1	-	-	-
Oviposition preference of *T. tabaci* (choice) compared to cv. BIsmark	1	-	1	2	-	-	-	1	-	1	-	-	-

Table 6.2 Colour preferences of *T. tabaci, T. shultzei* and *F. occidentalis* in choice tests paired with mid-green (1 = most preferred colour for each species; 3 = least preferred colour; same number signifies no difference).

	Colours						
	Light green	Mid-green	Dark green	Yellow	Blue	Red	white
T. tabaci	1	1,2	3	2	3	3	3
T. shultzei	-	2	-	1	3	2	3
F. occidentalis	-	2	-	1	3	3	3

Table 6.3 Plant host preferences of *T. tabaci, T. shultzei* and *F. occidentalis* in choice tests paired with potato cv. Atlantic (1 = most preferred plant host for each species; 2 = least preferred plant host; same number signifies no difference; ns = no significant difference between all cultivars).

	Plant hosts							
	Potato	Tomato	Nightshade	*Datura*	Tobacco	Onion	Canola	*Calendula*
T. tabaci	ns	ns	ns	ns	ns	ns	-	-
F. occidentalis	ns	ns	-	ns	ns	-	ns	ns
T. shultzei	2	2	-	1	1	-	1	1

Table 6.4 Mean transmission rate of TSWV by different populations of *T. tabaci,* the source host and location of collected populations, and the phylogenetic subgroup in which each population clustered.

***T. tabaci* populations**	**Mean TSWV transmission (%)**	**Source host**	**Source location**	**Phylogenetic subgroup**
TASFT	35	potato	Tasmania	1
SAP	25	potato	South Australia	1
TASP	20	potato	Tasmania	1
NSWC	0	onion	New South Wales	2
TASBH	0	onion	Tasmania	2
SAM	0	onion	South Australia	2
TASCHR	0	*Chrysanthemum*	Tasmania	3
NSWW	-	onion	New South Wales	2
TASP1	-	potato	Tasmania	1
SAATL	-	potato	South Australia	1
SAP1	-	potato	South Australia	1
SAP2	-	potato	South Australia	1

The original motivation for this study was the hypothesis promoted by Jericho (2005) that some potato cultivars, namely cv. Bismark and cv. Royal Blue, may possess a high level of resistance to feeding or oviposition by the TSWV vector *T. tabaci*. Royal Blue was not able to be fully tested due to a shortage of TSWV-free planting stock at certain times, however Bismark was included in all field trials and in laboratory choice tests (Table 6.1). There were significant differences in thrips preference between cultivars in both field trial and choice tests. In the field, Bismark had signicantly higher numbers of thrips than many other cultivars whereas in the laboratory no evidence of it being significantly less preferred than other potato culitvars was found (Table 6.1). Similarly in oviposition tests, Royal Blue was a more preferred cultivar for oviposition. Both findings contradict Jericho's (2005) hypothesis of resistance for these cultivars, made on the basis of cage

trial results where cv. Bismark attracted the fewest adult *T. tabaci* and exhibited low feeding damage, while cv. Royal Blue exhibited an absence of juvenile thrips.

There were no differences in foliar and tuber infections between cultivars, as was also experienced, with one exception, by Jericho (2005). There were also no significant correlations between thrips numbers on foliage and the level of TSWV infection, although a positive relationship between the thrips four weeks after planting and final TSWV infection levels was close to being significant at $p = 0.08$, which is some support to the hypotheses of Jericho (2005) and Wilson (2001) that mature plant resistance to TSWV plays a role in the epidemiology of infections in potato relating to the timing of the first influx of viruliferous thrips into the crop.

Nevertheless, while significant differences were not evident in field trials, interesting differences were found in laboratory choice tests (Tables 6.1-6.3). *T. tabaci* showed a preference to move to cultivars Shepody and Russet Burbank over Atlantic, while these cultivars, particularly Shepody, were among the least preferred for oviposition. On the other hand, *T. tabaci* preferred Royal Blue and Bismark equally to Atlantic, and yet these were more highly preferred for oviposition than many other cultivars (Table 6.1). A spectral analysis showed that these cultivars differed in the green intensity (brightness) of their foliage, with Shepody and Russet Burbank higher in green intensity (lighter green leaves) and Atlantic, Bismark and Royal Blue with lower green intensity (Table 6.1). The strength of this preference for lighter green foliage was supported by tests in which *T. tabaci* showed a very strong preference for light green card over both dark green card and potato leaves. Future experiments to confirm this should test potato leaves in clear enclosures to exclude potential attractant or deterrent effect of volatiles, followed by tests using opaque barriers to test for chemical attraction in the absence of colour cues. Future experiments could also look at a greater variation of green hues and intensity approaching those of a range of potato varieties, in order to determine when the influence of colour on host preference breaks down.

Divergence of feeding and oviposition choice is not common in insect species where adults and larvae feed on the same type of host. Many examples, like Jones & Coleman (1988), show insects preferring to feed on stressed foliage but oviposit on healthy leaves. This could explain the attraction of *T. tabaci* to lighter green potato cultivars, and greater oviposition on darker green cultivars, with lighter green foliage usually associated with chlorosis, TSWV-infection, and senescence; while darker green leaves are usually associated with vigorously growing, healthy foliage. Another benefit of this strategy would be to reduce competition for food resources between adults and juveniles. An

examination of reproductive performance would have been improved by measuring the rate of juvenile development, rather than just total larval survival, as well as measuring the nutritive qualities of the leaves from each potato cultivar. An additional experiment to compare oviposition choice and larval development on TSWV-infected leaves with healthy leaves would have further enhanced this work. Further parameters that could be tested in future are total development times and reproductive capacities of *T. tabaci* on different potato cultivars. A further factor to consider would be differences in experimental designs with preference tests conducted on whole leaves while oviposition choice tests were conducted on leaf disks. Differences in volatile profiles may emerge between cultivars with leaf damage, which may result in differences in preference between the two types of test.

Crop protection against *T. tabaci* might be achieved utilising some of the findings of choice tests. It appears that *T. tabaci* may prefer different cultivars (mediated by leaf colour) in terms of initial attraction for feeding, compared to oviposition. If the prevailing determinant of TSWV infection levels in potato is the initial influx of vector thrips, as has been demonstrated in other crops (Coutts *et al*., 2004), rather than from the subsequent generations breeding on potato to larger numbers, then a darker leaved potato cultivar (see Chapter 3 for cultivar ranking) may be a way of reducing the size of the initial influx. This of course will depend on the pattern of the surrounding vegetation. In drier cropping areas, dependent on irrigation, with little vegetation surrounding the potato crop, then vector thrips may have little choice but to migrate to potato. Trap cropping is an option that might be considered for drier cropping regions, in order to introduce a push-pull effect, where a darker green potato crop surrounded by lighter green vegetation may lead to some reduction in thrips moving into potato. This is likely to be more effective in wetter cropping areas, such as Tasmania and coastal and hinterland cropping regions of the Australian mainland, where cropping fields are continuous in time and space, because thrips are more likely to travel shorter distances and encounter a trap crop before entering a commercial crop. The success of trap cropping based on colour might also be amplified by integrating a kairomone attractant, such as LUREM-TR®, and an insecticide to reduce populations once attracted into the trap crop (van Tol *et al*., 2007). These prescriptions also depend on *T. tabaci* being the dominant TSWV vector in potato, which can be said with certainty in Tasmania, but is less certain in mainland Australian States, where *F. schultzei* is widely distributed. However, the lack of correlation between thrips numbers on foliage and TSWV incidence in potato in field trials leads to caution that this approach might not achieve reductions in TSWV infection levels.

The lack of significant differences between cultivars in foliar and tuber TSWV infection in field trials here, following a similar paucity of cultivar difference in mechanical inoculations and field trials from Jericho (2005), suggests that the cultivar differences in TSWV translocation to tubers shown by Wilson (2001) in mechanical inoculation trials may not be as consistent and reliable as first reported. Certainly the strong resistance to TSWV translocation to tubers in Russet Burbank reported by Wilson (2001) was not seen here. In more recent years, potato crops in South Australia have also shown a high incidence of foliar and tuber infection in this cultivar (C. Wilson, personal communication, 2011), further questioning initial reports of resistance. Wilson (2001) has discussed several reasons for variability in cultivar comparison trials, including erratic virus distribution in plants affecting detection reliability, and TSWV strain virulence. Wilson (2001) also raised the possibility that the discordance between results from mechanical inoculation and field trials may be due in part to the behaviour of vector thrips. Evidence for this is provided here with *T. tabaci* showing differences in preference and oviposition choice across cultivars.

This study clearly found that yellow was the most attractive colour for *F. occidentalis* and *F. schultzei*, but also that green was more highly preferred than red, blue and white, questioning those studies which have promoted the use of blue traps to survey for *F. occidentalis. T. tabaci* preferred green and yellow equally and over the other three colours (Table 6.2). This contradicts several prior studies that suggested green is one of the least attractive colours for *T. tabaci* (Demirel & Yeldirim, 2008; Teulon & Penman, 1992) and *F. occidentalis* (Matteson & Terry, 1992; Vernon & Gillespie, 1990). In further testing, *T. tabaci* showed a strong preference for light-green over darker shades of green card tested and exhibited preference for this same light green over detached leaves of four potato cultivars (Shepody, Russet Burbank, Bismark, Atlantic), which were of varying hue, but all of a darker green. The strong preference of *T. tabaci* for light green colours could play an important role in host selection, including at the cultivar level, as well as suggesting the importance of preventing water stress in crops.

Intensity of green hue is often associated with other plant attributes, and so may be acting as an indirect cue for one or more factors that affect thrips survival and fecundity, such as amino acid profiles, phenolics, and leaf surface wax levels. The strong attraction to lighter green by *T. tabaci* may also be a strategy employed by thrips to target stressed plants, in particular to TSWV-infected plants, which often develop light-green to yellow mottling and areas of chlorosis (Naidu *et al*., 2008; Persley *et al*., 2007), and compromised induced plant defences against insect herbivory (Belliure *et al*., 2005; Felton *et al*., 1999; Felton & Korth, 2000). Another explanation for preference or non-

preference of *T. tabaci* for certain potato cultivars over others, may be the potential effect of one or more of the numerous allelochemicals that attract or deter different thrips species, which have been identified across many studies (Koschier, 2006; Teulon *et al*., 2007). Headspace sampling and GCMS analysis of potato volatiles by Wilson *et al*. (unpublished data) have suggested that there are distinct cultivar differences in the amount and ratio of compounds emitted by potato. Further delineation between colour and chemical cues would be beneficial to understanding these differences in cultivar preference.

The very low preference for blue colour card by all species of thrips in this study does not favour the view of Vernon and Gillespie (1990), who proposed that *F. occidentalis* has trichromatic vision, rather it supports the view of Harris *et al*. (2001) and Terry (1997) that only two types of photoreceptors, sensitive to UV and green-yellow wavelengths, exist in *F. occidentalis*, and perhaps also for all three species tested here. A more targeted approach could be employed in future by first selecting specific colours with peak reflectance at targeted wavelengths, and use these to help delineate the peak sensitivity of thrips photoreceptors. Electroretinography could also be used to clarify the types of photoreceptors possessed by thrips and whether this can explain the differences in colour preference between thrips species.

Overarching the interpretation of all results emerging from this thesis is the important finding of intra-specific genetic differences between *T. tabaci* populations in Australia, where populations appear to be associated with both their source host and their ability to vector TSWV (Chapter 5; Table 6.4). This is of particular importance because vector-competent populations were associated with one major crop host (potato), while non-vector populations were associated with another major crop host (onion). It is believed that this is the first study to link host-associated genetic differentiation with vector competence in *T. tabaci*. This study also dispels the claim that parthenogenetic, thelytokous populations are not capable of transmitting TSWV, and shows that differences in vector competence between populations occur within at least one of the three major evolutionary lineages - European ‘L2’ clade of Brunner *et al*. (2004) - and not just between lineages.

The scope of this study was not sufficient to identify any causative link within this apparent association. It does however provide a plausible explanation for the marked differences in observed vector competence of this species, and the sporadic nature of TSWV outbreaks in potato crops in Australia, despite the ever-presence of *T. tabaci*. This could explain why Jericho (2005) observed TSWV infections in field potatoes but

did not observe any transmission in laboratory experiments, as the population used in his tests was collected from onion. It may also help to explain the contradictory nature of many findings worldwide regarding the vector competence of this species. Many studies have been unable to facilitate *T. tabaci* to vector TSWV despite repeated attempts with many different acquisition-transmission host combinations, and yet here, the vector competent population that was most fully tested (TAS-FT) was able to transmit TSWV in nine different acquisition-transmission host combinations.

If populations are genetically distinct and some can vector TSWV while others cannot, then the question remains open as to whether they may also exhibit differences in preference for colour and cultivars of potato. The findings in this study may have been different if a population from a different phylogenetic sub-group had been used in preference tests. Future studies should evaluate similar preferences but across a range of populations, and in particular on vector and non-vector competent populations, to determine whether these preferences vary. Comparative studies of colour and host preference are usually conducted between species, so population differences within species have not been widely reported, providing an avenue to explore a little researched area.

It would also be valuable in future studies to examine multiple TSWV isolates as Wijkamp *et al*. (1995), Mau *et al*. (1990), and others (Jenser *et al*., 2002; Naidu *et al*., 2004; van de Wetering *et al*., 1996), have shown distinct levels of specificity in transmission of different virus strains. Testing the non-vectoring populations from onion against a range of TSWV isolates would help to elucidate whether these populations are unable to vector all known TSWV strains, or whether the failure to transmit TSWV in these experiments is because of the particular isolate used.

Overall, this study provides a credible explanation for the highly variable results in many studies that have sought to determine the vector competence of *T. tabaci*, and why some studies have even concluded that this thrips species is not capable of vectoring TSWV. It also provides further insight into the reasons for the sporadic nature of TSWV outbreaks in potato crops in Australia, despite the ever-presence of onion thrips. Further studies should, in addition to evaluating greater numbers of populations from diverse hosts and locations, look at how genetic differentiation is related to vector competence. Possible factors that could be associated with vector capacity include differences in mid-gut receptors, mid-gut properties, salivary gland properties, connections between salivary glands and muscle tissue of the mid-gut during the first instar stage, feeding behaviour on different hosts, and length required for the acquisition and inoculation access periods.

The finding that vector competence may be associated with distinct populations associated with host on the other hand offers a potentially valuable avenue for future research. If vector competent populations are found on certain hosts but not others, then the location of commercial seed potato crops within the landscape and their proximity to these hosts could affect the likelihood of large numbers of viruliferous thrips entering the crop. The timing of crop maturation in potato cropping areas could potentially be manipulated to reduce the numbers of vector competent populations of *T. tabaci* moving from such crops into potato during the most susceptible periods of growth. The existence of genetically distinct populations of *T. tabaci* associated with host and ability to vector TSWV also suggests that there may be differences in host preference and host-finding cues between populations. If so, then all future research on plant host resistance to thrips, push-pull systems, and other methods of reducing TSWV-incidence must take this into account to ensure that the methodologies developed are relevant to those vector-competent populations.

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