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Incursion preparedness: anticipating the arrival of an economically important plant pathogen *Xylella fastidiosa* Wells (Proteobacteria: Xanthomonadaceae) and the insect vector *Homalodisca vitripennis* (Germar) (Hemiptera: Cicadellidae) in Australia

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Abstract The glassy-winged sharpshooter, *Homalodisca vitripennis* (Germar) (Hemiptera: Cicadellidae), is an important insect vector of the xylem-limited plant pathogen *Xylella fastidiosa* Wells *et al*. that causes diseases in numerous plant species including food and feedstock crops, ornamentals and weeds. Both the pathogen and the vector are native to the Americas, and *H. vitripennis* has demonstrated high invasive ability but to date neither has been detected in Australia. The Australian wine grape, table grape, peach, plum, nectarine and citrus industries are particularly concerned about the arrival of *X. fastidiosa* and *H. vitripennis* because of the potential economic impact on these important commodities. Other commodity producers in Australia should also be concerned about this vector-pathogen, in particular the ornamental plant, avocado and olive industries. Past interceptions of *H. vitripennis* and the potential for *X. fastidiosa* to be moved in live plant material or within live vectors indicate the need for rapid detection of an incursion in areas considered at high risk. This requires identification of regions that have climatic and environmental conditions conducive to *X. fastidiosa* and *H. vitripennis* establishment as well as a detailed knowledge of their respective potential host plant ranges in new areas. These climatic regions and host plant species can then be targeted for monitoring in order to detect an incursion at an early stage. CLIMEX modelling has shown that much of coastal Australia has temperatures suitable for survival of both the vector and pathogen. A range of other requirements in addition to suitable climate must, however, be satisfied for an incursion to lead to establishment, proliferation and spread. This review article provides information that shows that the Australian environment is suitable for the establishment of *H. vitripennis* and that Australian native plant species are likely to serve as *X. fastidiosa* hosts and subsequent pathogen sources, and highlights future research directions.

Key words alternative host, biosecurity, insect pest, pathogen transmission, Pierce's disease.

INTRODUCTION

Xylella fastidiosa Wells *et al*. (Proteobacteria: Xanthomonadaceae) is a xylem-limited bacterium (Wells *et al*. 1987; Peroni *et al*. 2008) that causes disease in a wide range of economically significant agricultural plants. There are three key genotypes of the bacterium, each with a different host range, virulence and transmissibility (Schaad *et al*. 2004; Almeida *et al*. 2008; Nunney *et al*. 2010). The three genotypes that have been identified are *X. fastidiosa* subsp *piercei*, subsp.

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nov. (taxon 'A'), *X. fastidiosa* subsp. *multiplex* subsp.nov. (taxon 'B') and *X. fastidiosa* subsp. *pauca* subsp.nov (taxon 'C') (Schaad *et al*. 2004). Taxon 'A' contains strains isolated from grape (*Vitis vinifera* L.), almond (*Prunus dulcis* (Mill.)), alfalfa (*Medicago sativa* L.) and maple (*Acer* spp.) while taxon 'B' contains strains from peach (*Prunus persica* L. Batsch), plum (*Prunus domestica* L.), almond, sycamore (*Platanus* spp.), elm (*Ulmus Americana* L.) and pigeon grape (*Vitis aestivalis* L.). Taxon 'C' contain strains from citrus (*Citrus* spp.) only (Schaad *et al*. 2004). Although the mechanism by which *X. fastidiosa* causes disease is not well understood, bacterial multiplication leading to biofilm formation and xylem blockage is believed to play an important role in the accumulation of the water stress-like symptoms that occur in most hosts (Hopkins 1989). The pathogen is responsible for Pierce's disease in grapevines, citrus variegated chlorosis, leaf scorch in almonds and oleander, phony peach disease, alfalfa dwarf and numerous other diseases including the recent emergence of strains pathogenic to avocados (Montero-Astua *et al*. 2008) in Costa Rica.

Pierce's disease was first described in 1892 when it destroyed 40 000 acres of vineyards in Southern California (Gleeson 2001). Pierce's disease did not re-emerge as a major disease in Southern California until 1999 when an invasive vector, the glassy-winged sharpshooter (*Homalodisca vitripennis* (Germar) (Hemiptera: Cicadellidae) previously known as *Homalodisca coagulata* (Say)) became widely established. This insect, originally detected in Southern California in the late 1980s, is now found in 13 of California's 58 counties (California Department of Food and Agriculture 2010) (Table 1) and plant material exported to Australia from these infested regions could pose a significant quarantine risk.

Xylella fastidiosa is transmitted by insects that feed exclusively on xylem fluid. The *X. fastidiosa* strain, as well as the plant host and insect vector species, has been found to influence transmissibility of the pathogen (Lopes *et al*. 2009). In California, *H. vitripennis* can feed on old wood in addition to young prunable shoots and flies further and changes host plants more frequently than other native vectors (e.g. *Graphocephala atropunctata* (Signoret)) of *X. fastidiosa* making it a significant disease vector (Almeida & Purcell 2003a,b; Blua & Morgan 2003) that has permanently changed the ecology of *X. fastidiosa* transmission in California. The insect can also achieve relatively high abundance, in favourable habitats, especially citrus. Twice yearly oviposition has been reported in California (Blua *et al*. 1999), with a partial third egg-laying period possible in some regions (Hummel *et al*. 2006). Six to eight overlapping generations have been estimated to occur per year in Tahiti (Grandgirard *et al*. 2006), and a single mating is sufficient to fertilise an entire complement of eggs that can then be oviposited throughout an individual's lifetime (Sisterson 2008).

Table 1 Californian counties infested with or which erradicated *H. vitripennis* as of December 2010 (California Department of Food and Agriculture 2010)

Permanent infestation	Partial infestation	Eradicated
San Diego	Kern	Butte
San Bernadino	Santa Barbara	Sacramento
Riverside	Tulare	Solano
Orange	San Luis Obispo	Contra Costa
Los Angeles	Fresno	Santa Clara (partially)
Ventura	Madera	Fresno (partially)
	Santa Clara	Imperial

Both the bacteria and vector species originated in the Americas (Purcell 1997; Triapitsyn & Phillips 2000) and have expanded their range to other countries. *Xylella fastidiosa* has been reported from South America in Peru, Argentina, Brazil, Paraguay and Central America (Hopkins & Purcell 2002). Two geographically distant populations occur in Kosovo (Berisha *et al*. 1998) and Taiwan (Leu & Su 1993). *Homalodisca vitripennis* is native to the south eastern region of the United States, and is abundant in eastern Texas, southern Georgia and northern Florida (Young 1958; Triapitsyn & Phillips 2000). The species is also present in central Texas, central Florida, Arizona and northeastern Mexico, however, it is rarer in these regions (Turner & Pollard 1959; Triapitsyn & Phillips 2000). *Homalodisca vitripennis* has dispersed through the Pacific and populations now exist in French Polynesia (detected 1999), Hawaii (2004), Easter Island (2005) and the Cook Islands (2007) (Secretariat of the Pacific Community 2002; Bautista *et al*. 2005; The Ministry of Agriculture and Forestry 2007; Petit *et al*. 2008). Both pest species are considered high risk invaders to various horticultural industries and there is a need for Australia to anticipate an incursion from the United States, Central America, South America or, perhaps more likely, infested island regions in the South Pacific. Both species can be difficult to detect during quarantine procedures as egg masses of *H. vitripennis* are laid beneath the epidermis on the underside of leaves and host plants that are infected with the pathogen are often symptomless. This makes detection difficult and an obvious biosecurity risk to Australia (Plant Health Australia 2009a,b). The challenge is to anticipate which regions provide a set of environmental conditions suitable for the establishment of both species and are most at risk from potential incursion events.

The most likely entry pathway for *X. fastidiosa* is via nursery plants imported legally or smuggled illegally into Australia (Luck *et al*. 2002, 2004; Hoddle 2004; Pilkington *et al*. 2005). Symptomless host plant material from the United States, Central America, South America (which has the strain of *X. fastidiosa* causing citrus variegated chlorosis) (Hopkins & Purcell 2002; Chung & Brlansky 2005), Taiwan and Kosovo may also contain the pathogen. Inadvertent introduction of *X. fastidiosa* into Australia may have already occurred and there is a possibility that the pathogen is harboured in symptomless hosts that are currently present in Australia (Hoddle 2004). However, surveys for *X. fastidiosa* in over 100 host species growing in Australia (Doughty & Luck 2005; Constable *et al*. 2007) have not identified the presence of bacterium. *Homalodisca vitripennis* can be introduced as either eggs or motiles. Egg masses on imported plants are the most likely means of transport (Sorensen & Gill 1996; Grandgirard

Table 2 Approximate number of direct and indirect flights to Sydney, Australia per day from areas infested with *H. vitripennis* (Webjet 2011)

Flight origin	Approximate number of direct flights	Approximate number of flights with stopovers
Los Angeles, USA	5	21
Miami, USA	0	30
Honolulu, USA	2	15
Rarotonga, Cook Islands	0	10
Papeete, French Polynesia	0	16
Total	7	92

et al. 2006) to Australia. In addition, live adult insects pose a threat and have been accidentally transported in aircraft between islands in French Polynesia. Air travel from French Polynesia almost certainly introduced *H. vitripennis* to Easter Island and could have also contributed to the invasion of the Cook Islands. Anecdotal evidence suggests that live *H. vitripennis* adults have been found in planes in Japan, indicating the insect can survive the flight from Tahiti to Japan (Grandgirard *et al*. 2006). Dead *H. vitripennis* adults have been intercepted in planes in Cairns, Australia that had flown from Tahiti via New Caledonia (Grandgirard *et al*. 2006), illustrating that unintentional transport to Australia may be possible. Almost 100 flights a day arrive in Sydney from areas infested with *H. vitripennis* indicating a high number of opportunities for this pest and *X. fastidiosa* to arrive each day, in just one Australian city that has a suitable environment (Table 2).

Four possible scenarios exist in terms of *X. fastidiosa* and *H. vitripennis* invasion in Australia. First, there is the possibility that *X. fastidiosa* could arrive without *H. vitripennis*. This will become a concern if Australian insects (native or exotic) can acquire and efficiently transmit the bacterium. A second scenario is that *H. vitripennis* may arrive without the bacterium, similar to the introduction on ornamental hosts into Tahiti (Luck *et al*. 2002). This could result in development of a new or enhanced vector-pathogen system and increased transmission of xylem-limited plant pathogens already established in Australia. Thirdly, both the pathogen and the insect vector could be simultaneously introduced, in which case the pathosystem that is seen in California and the Southeast USA would be likely to operate eventually. This pathosystem might use native Australian plant species that are presently not known as hosts of the insect or bacterium in addition to known host plant species introduced into Australia (e.g. grapes). Fourthly, incursions of *H. vitripennis* and *X. fastidiosa* do not result in the establishment of either pest because host plants, variable climates and resident natural enemy complexes prevent the successful confluence of events needed for the establishment of both the vector and pathogen.

For either species to establish in a new geographical area and cause disease, a number of conditions must be satisfied. Both the pathogen and the vector require the presence of suitable host species to ensure survival, and the bacterium needs a vector or human-mediated plant propagation and transport in order to spread and proliferate. Both species must occur together and interact with an environment that provides abiotic conditions conducive to survival and long-term establishment. For the *X. fastidiosa–H. vitripennis* pathosystem to establish and operate in Australia as it does in California and other regions, the receiving area in Australia must have suitable host plants and climatic conditions that allow survival of the pathogen and its vector.

The aim of this review is to synthesise the available information on biotic and abiotic conditions in Australia that are conducive to the establishment of *X. fastidiosa* and *H. vitripennis*. The potential geographical range of both species will be elucidated and the likely impacts of an incursion of either or both species will be discussed in an Australian context.

Potential impact of *Homalodisca vitripennis* and *Xylella fastidiosa* in Australia

Preliminary estimates indicate that Pierce's disease could be as serious in Australia as it has been in California (Luck *et al*. 2001). Pierce's disease currently threatens California's entire grape industry (California Department of Food and Agriculture 2009). Infected plants in vineyards are removed and a 5- to 6-year establishment period is needed before new plantings reach full production (Hewitt *et al*. 1949; Jackson *et al*. 2008). In areas where *X. fastidiosa* is prevalent, such as the grape-growing regions of Southern California where *H. vitripennis* is also present, the economic ramifications of the pathogen are immense (Siebert 2001). The Napa and Sonoma counties in northern California are free from *H. vitripennis* and only contain native vectors, yet between 1994 and 2000 the estimated cost of loses to grape growers due to *X. fastidiosa,* mediated by native sharpshooters was over US$30 million (Siebert 2001). In 2002, 120 million citrus trees had citrus variegated chlorosis symptoms in Brazil (Hopkins & Purcell 2002), indicating that the pathogen also has severe impacts on citrus crops including reduced vigour and abnormal fruit set (Chung & Brlansky 2005). Ornamental species such as oleander (*Nerium oleander* L.) are also at risk from *X. fastidiosa* and are a widely used ornamental shrub in southern California. In 1999, they occurred in 20% of all home gardens and were planted along 3380 km of freeway in California alone (Blua *et al*. 1999). Damage to these freeway plantings caused by *X. fastidiosa* has been estimated to have cost over US$52 million (Costa *et al*. 2004).

In addition to impacts caused by the pathogen, large populations of *H. vitripennis* can cause problems. It has been suggested that in extreme cases water stress may occur due to the large quantities of xylem fluid that are removed from the plant (Grandgirard *et al*. 2006), though there have not been adequate measurements to date to determine the level of impact. Adult insects have been reported to consume 0.21–0.27 mL/h on host species such as plum and peach (Andersen *et al*. 1989). Crops and plant stock with large infestations of *H. vitripennis* require additional irrigation to make up for the xylem fluid extracted by the insects (Blua *et al*. 1999). Adequate irrigation water is

currently a critical issue through much of rural Australia and there is the potential that the establishment of *H. vitripennis* would exacerbate the existing situation. High density *H. vitripennis* populations can be a social problem when huge numbers of insects congregate near lights and from high quantities of excreta produced as they feed on trees (Andersen *et al*. 1989; Blua *et al*. 1999; Grandgirard *et al*. 2006). A 'rain' of excreta can be experienced under trees laden with feeding *H. vitripennis* and unattractive white residues build up on the vegetation below and can disfigure fruit (Blua *et al*. 1999; Grandgirard *et al*. 2006).

In an Australian context, it is expected that the main agricultural impact of the pathosystem will be felt in areas of Australia where grape and citrus production are the dominant land uses. Areas with both grape and citrus production are located in all states and the Murray-Darling River system is the key grape/citrus area (Luck *et al*. 2001). In 2009–2010, 157 000 hectares of land were used for wine grape production nationally and wine exports were valued at A$2.2 billion (Australian Bureau of Statistics 2010). In addition, the value of dried vine fruit exports was A$13 million in 2007–2008 (ABARE 2008). In terms of citrus, every state with the exception of Tasmania grows citrus commercially (Australian Citrus Growers Inc 2008). The value of citrus, including Navel and Valencia oranges, mandarins, lemons, limes and grapefruit was over A$166 million in 2007–2008 (ABARE 2008) and this does not take into account the large number of citrus trees throughout residential areas of Australia. In California, it is estimated that the numbers of backyard citrus plants exceeds those planted commercially (M Hoddle pers. comm. 2011).

It is difficult to predict the economic costs to these plant species without precise knowledge of the extent of vector and disease spread (Luck *et al*. 2001). An economic analysis of a hypothetical Pierce's disease outbreak in South Australia concluded that even if the incursion were controlled within 5 years and limited damage occurred at the regional level, the welfare loss would still equate to A$135 million in that state alone (Wittwer *et al*. 2006). Export of Australian produced wine has continued to increase, reaching 788.5 million L during 2009–2010. Domestic sales of Australian wine have also increased slightly and 2009–2010 domestic wine sales were valued at A$2122.6 million (Australian Bureau of Statistics 2010). On top of these direct costs, indirect losses in Australia following establishment of *H. viripennis* and *X. fastidiosa* would consist of job losses, a reduction in tourism and domestic and international shipping restrictions on potentially infested goods (Luck *et al*. 2001).

Xylella fastidiosa and *Homalodisca vitripennis* establishment in Australia

Current climate

Laboratory studies show that *Xylella fastidiosa* multiplication in media is hindered at low temperatures meaning that cool nights (<15°C) possibly interrupt daily multiplication (Feil & Purcell 2001). The northern two-thirds of Australia have an average annual daily minimum temperature >15°C (Australian Bureau of Meteorology 2009), a regime that is more similar to that of Florida, where warm nights promote *X. fastidiosa* multiplication than to California where cool nights slow population growth (Feil & Purcell 2001). *Xylella fastidiosa* is rare in areas where the temperatures during winter fall below 1.1°C as this is the lower temperature limit for survival of the bacterium (Feil & Purcell 2001; College of Natural Resources 2005), although the length of time spent at low temperatures is likely to be as important as the absolute minimum temperature experienced. *Xylella fastidiosa* has been reported during late summer in areas that experience seasonal temperatures lower than 1.1°C such as Ontario, Canada (Goodwin & Zhang 1997). Climate data showing the minimum temperatures in winter indicate that the majority of Australian grape-growing regions experience minimums of 3–6°C (Australian Bureau of Meteorology 2009) so are suitable for *X. fastidiosa*. These regions include much of Queensland, coastal Northern Territory, New South Wales, South Australia and southern Western Australia. It is predicted that cold stress will exclude Pierce's disease from some areas of Victoria and from Tasmania (Hoddle 2004). Frost prone regions in New South Wales, such as around Orange, will similarly be at a lower risk of establishment.

The distribution of *H. vitripennis* is also limited by cold stress and drought stress. Insect populations decline considerably during the winter in central Texas, part of the vector's native range (Lauziere *et al*. 2008). Although sharpshooter abundance decreased in the coldest months, more insects were found in uncultivated habitats than in cultivated areas, indicating that adult insects have the ability to overwinter in natural and unmanaged areas if suitable host species are available (Lauziere *et al*. 2008). CLIMEX models have shown that climatic conditions suitable for *H. vitripennis* currently exist in south eastern Queensland, eastern New South Wales, the majority of Victoria and Tasmania, south-eastern South Australia and south-western Western Australia (Luck *et al*. 2001). This approximate distribution has also been supported by subsequent CLIMEX modelling (Hoddle 2004), with the addition of north eastern Queensland and the extreme north of the Northern Territory. Rapid population growth in invaded regions such as California has been aided by irrigation systems in an otherwise arid environment, reducing drought stress that would have prevented *H. vitripennis* establishment (Hoddle 2004). Dry stress may exclude the insect from the interior of Australia, aside from irrigated cropping areas such as Mildura, because of the arid nature of such regions.

In terms of incursion severity, it is predicted that the tropical and sub-tropical northern regions of Australia will have conditions favourable for *H. vitripennis* and *X. fastidiosa* establishment, should sufficient propagule pressure occur to overcome stochastic events that reduce establishment probabilities (M Hoddle pers. comm. 2009). The warm climate of northern Australia would facilitate plant species that host *X. fastidiosa* and *H. vitripennis* and such hosts could be imported or smuggled from the Americas and Pacific Islands and grown in urban landscapes by horticultural enthusiasts.

The risk these urban areas pose is enhanced because gardens are characterised by high exotic plant diversity as well as plant care in terms of pruning, watering and fertilization, which greatly increases the survivorship likelihood of the plant and the pests infesting it. There is also the potential that these imported plants are asymptomatic disease reservoirs. Imported plant material may legally or illegally enter the country through high thoroughfare ports and airports in urban centres such as Brisbane and Sydney as well as Darwin and Cairns in northern Australia. Given that the insect is a strong flyer and is readily transported inadvertently by people through the movement of host plants or accidentally inside aircraft, *H. vitripennis* could potentially extend over the majority of the Australian mainland in which climatic conditions are favourable.

Land use and abundance of host plants

Xylella fastidiosa is able to infect a wide variety of host plants, though disease severity differs greatly among different host species and pathogen strains (Hopkins & Purcell 2002). Of the approximately 130 known *X. fastidiosa* host species, over 90 are present in Australia (Luck *et al*. 2001, 2004) providing an abundance of host plants in the event of an incursion. The species range includes common weeds, e.g. ivy (*Hedera helix* L.) and blackberry (*Rubus fruticosus* L.), ornamentals and several Australian native species. Sharpshooter transmission efficiency depends on several factors, including vector species, host plant species and pathogen strain (Lopes *et al*. 2009). Acquisition efficiency, assuming a plant species can host *X. fastidiosa*, depends on the bacterial population; below 10^4 cfu/g it is unlikely that sharpshooters will be able to acquire the pathogen (Hill & Purcell 1997). Currently, *Acacia longifolia* (Andrews) Willd. (golden wattle) is the only Australian native plant species known to host the pathogen and serve as a substrate for *H. vitripennis* feeding and oviposition (Luck *et al*. 2001). This number of plants is likely an underestimate and this uncertainty can be addressed very quickly and easily. Field surveys in the United States, especially in Florida and California, where native Australian plants are abundant in urban areas or as invasive weeds, should be screened for *X. fastidiosa*. These results would indicate the taxonomic breadth of hosts at risk from infection. This research opportunity has not been seized and is seen as a major shortcoming in understanding the risk this vector–pathogen combination poses to Australia.

Although the native range of *H. vitripennis* in south-eastern USA and north eastern Mexico includes natural areas, this pest can also sustain populations in commercial crops and urban ornamentals (Pilkington *et al*. 2005), and high plant diversity in well-managed gardens favour the insect. *Homalodisca vitripennis* has approximately 175 described hosts for feeding and breeding and almost all of these species are present in Australia (Luck *et al*. 2001). Numerous locations in Western Australia, New South Wales, Victoria and South Australia contain vineyards, citrus orchards and riparian vegetation, the type of agricultural land use that has proven to be ideal *H. vitripennis* and *X. fastidiosa* habitat in California (Hill & Purcell 1995; Perring *et al*. 2001). *Eucalyptus* is both a feeding and breeding host (Luck *et al*. 2001; Hoddle *et al*. 2003) implying that tracts of *Eucalyptus*-rich Australian bush may be suitable habitat for the pest.

Homalodisca vitripennis has a number of adaptations in order to gain enough sustenance from nutrient-poor xylem fluid (Raven 1983), which can be composed of up to 99% water in some plant species (Andersen *et al*. 1992). These adaptations include high conversion efficiency of organic nitrogen and carbon, high consumption and the selection of an amide rich diet by utilising a range of hosts (Andersen *et al*. 1989, 1992; Brodbeck *et al*. 1990, 1993). *Homalodisca vitripennis* adjust their feeding rates and host plant selection in relation to diurnal xylem fluid chemistry fluctuations (Brodbeck *et al*. 1993). Amides, glutamine and asparagine are positively correlated with *H. vitripennis* abundance and feeding and nitrogen-rich amides are thought to be important for egg production and adult growth (Andersen *et al*. 2005; Mizell *et al*. 2008; Brodbeck *et al*. 2011).

The ability of *H. vitripennis* to use hundreds of species as hosts for reproduction, development and feeding allows the insect to cope with diurnal and seasonal changes in xylem fluid (Mizell *et al*. 2008). In greenhouse studies, it has been shown that *H. vitripennis* rarely persist on just one host plant. Suboptimal hosts may be fed upon for short periods of time, but the energy expended in taking up the food is not exceeded by the energy in the xylem fluid (Andersen *et al*. 1992; Brodbeck *et al*. 2007; Mizell *et al*. 2008). In order to avoid this situation in monoculture crops, variation in hosts can be found in the weedy understorey species (Mizell *et al*. 2008). The advantage of feeding on xylem fluid is the lack of defensive secondary plant compounds, digestive inhibitors and toxins. Insects can then expend more energy on extracting the food than detoxifying it (Raven 1983; Andersen *et al*. 1989). The xylem also provides water to the insects, a factor that is important in arid environments (Raven 1983), and the high water content of excreta means nitrogenous wastes can be removed as ammonia (Andersen *et al*. 1989; Brodbeck *et al*. 1993) instead of converted to the more energetically costly form, uric acid.

In addition to the documented hosts of both the pathogen and the vector, it is possible that many additional Australian native plants could host the pest species (Table 3).

Preliminary surveys in California have not shown Australian native plants to host the pathogen when subject to natural levels of inoculation pressure (A Rathe, unpubl. data 2009). Twelve widespread native Australian plant species that are commonly grown in California were tested for pathogen presence using both culturing on Periwinkle Wilt Gelrite (PWG) media (Davis *et al*. 1983) and polymerase chain reaction (PCR) with the primers RST31 and RST33 (Minsavage *et al*. 1994). These plants were subject to a high level of *H. vitripennis* pressure, yet this survey did not reveal any *X. fastidiosa* infections but this may be due to the patchy distribution of *X. fastidiosa* within the plant and subsequent difficulty in detecting low levels of the pathogen. This work is ongoing. However, if the scope of these surveys was expanded to include more plant species that have experienced longer

Table 3 Plant genera known to host *Xylella fastidiosa*, *Homalodisca vitripennis* or both, which also contain a native Australian plant species. The host status of the genera with blank cells is not yet known

Genus	*Xylella fastidiosa* host	*Homalodisca vitripennis* feeding host (*oviposition host)
Acacia	Freitag (1951)	De Leon *et al*. (2004)*
Agonis	–	CDFA (2008)*
Ajuga	–	CDFA (2008)
Albizia	–	Hoddle *et al*. (2003)*
Archontophoenix	–	CDFA (2008)
Brachychiton	–	De Leon *et al*. (2004)*
Brassaia	–	Hoddle *et al*. (2003)
Callistemon	–	Hoddle *et al*. (2003)
Cassia	–	Turner and Pollard (1959)*
Castanospermum	–	CDFA (2008)
Casuarina	–	Hoddle *et al*. (2003)
Clematis	–	CDFA (2008)
Cordyline	–	Grandgirard *et al*. (2009)*
Dodonaea	–	Fiksdal (2000)
Elaeocarpus	–	CDFA (2008)*
Eucalyptus	–	Hoddle *et al*. (2003)*
Geijera	–	CDFA (2008)*
Geranium	Sutton *et al*. (2008)	CDFA (2008)
Glycine	–	Hoddle *et al*. (2003)
Gossypium	–	Turner and Pollard (1959)
Grevillea	–	CDFA (2008)
Hardenbergia	–	Fiksdal (2000)*
Hibiscus	McGaha *et al*. (2007)	Hoddle *et al*. (2003)*
Hymenosporum	–	CDFA (2008)*
Macadamia	–	CDFA (2008)*
Melaleuca	–	Hoddle *et al*. (2003)*
Melia	–	Turner and Pollard (1959)
Myoporum	–	CDFA (2008)*
Nephrolepis	–	CDFA (2008)*
Pandorea	–	CDFA (2008)*
Passiflora	–	Triapitsyn *et al.* (1998)*
Pelargonium	Freitag (1951)	CDFA (2008)
Pinus	McGaha *et al*. (2007)	Sorensen and Gill (1996)
Pittosporum	Freitag (1951)	Turner and Pollard (1959)*
Platycerium	–	CDFA (2008)
Plectranthus	–	CDFA (2008)
Podocarpus	–	Fiksdal (2000)*
Rhododendron	–	CDFA (2008)*
Schefflera	–	CDFA (2008)*
Solanum	Sutton *et al*. (2008)	Lauziere and Setamou (2009)*
Syzygium	PaDIL (2010)	CDFA (2008)*
Tristania	–	Fiksdal (2000)*
Veronica	Freitag (1951)	CDFA (2008)*
Viola	–	CDFA (2008)*

exposure times (i.e. >5 years) from *H. vitripennis* populations over more diverse geographical areas in southern California, a different picture about the susceptibility of native Australian plants to *X. fastidiosa* may emerge. There is a strong need to take advantage of this large naturally occurring field experiment in southern California.

Lack of biotic constraints

When an invasive species enters a new geographic area, it may be released from the biotic constraints of its native range that control population size such as competition or predation and parasitism (Levine *et al*. 2004; Gilbert & Parker 2006). It is unknown whether *X. fastidiosa* would be released from the biotic constraints it faces in the Americas if introduced to Australia. It is plausible, however, that hosts present in Australia may be particularly sensitive to the bacterium due to a lack of evolutionary history. For example, introduced European grapes in America tend to have more severe disease symptoms than native American grapes that have a higher tolerance (Loomis 1958; Hoddle 2004). Spread of the pathogen may be inhibited if Australian host plants are particularly sensitive to *X. fastidiosa* due to high disease-induced mortality of these susceptible species. Rapid mortality eliminates the possibility of the individual plant acting as a reservoir (Toscano *et al*. 2004) from which the bacterium can spread further, although *X. fastidiosa* tends to exist as a benign presence in most host species (Wistrom & Purcell 2005). In most of the susceptible hosts, disease progresses slowly, yet the pace and severity of symptoms varies depending on host species, cultivar or pathogen strain (Daugherty *et al*. 2010; Lopes *et al*. 2010).

It has been hypothesised that insect species that have the ability to transmit the pathogen may not actively transmit the bacterium in the field due to competition for space caused by other microbes within the foregut (Almeida & Purcell 2003b) and this may influence transmission of the pathogen by any native Australian insect vectors. Surfaces within the insect foregut that are important attachment sites for *X. fastidiosa* such as the diaphragm and longitudinal grooves may already be occupied by native bacterial populations, preventing multiplication of the pathogen and hindering transmission (Alves *et al*. 2008). This possibility warrants investigation in Australia.

It is difficult to predict how biotic constraints would influence an *H. vitripennis* invasion into Australia. In terms of competition, only 14 xylem fluid-feeding leafhoppers from the tribe Cicadellini are known to exist in Australia (Fletcher 2009 + updates) but none from the tribe Proconiini, to which *H. vitripennis* belongs, are present (Fletcher 2009 + updates). In contrast, over 50 species of leafhopper from both tribes exist in North America (Wilson *et al*. 2009). This indicates that *H. vitripennis* is less likely to experience competition from closely related species in Australia than it would in its home range, though the intensity of competition is not necessarily correlated with phylogenetic proximity. A similar situation exists in French Polynesia (and other South Pacific islands) and the lack of strong competition from native and introduced cicadellids was likely one of several factors that facilitated the successful invasion of *H. vitripennis*.

Australia contains congenerics of the egg parasitoid *Gonatocerus ashmeadi* Girault (Naumann 1991), which is one of the main natural enemies of *H. vitripennis* in the United States (Triapitsyn & Phillips 2000; Grandgirard *et al*. 2007).

There are 270 species of Mymaridae in Australia (Naumann 1991), although the native species are poorly described, and so exact numbers from the genus *Gonatocerus* are unknown. These species quite possibly have the ability to attack *H. vitripennis* eggs and *G. ashmeadi* could be present but not yet recognised in the fauna, which means that *H. vitripennis* may not escape parasitism in Australia. In French Polynesia, resident egg parasitoids failed to provide significant parasitism of *H. vitripennis*, hence the introduction of the specialist egg parasitoid *G. ashmeadi* was necessary (Grandgirard *et al*. 2007).

Vectors

Alternative vectors of *X. fastidiosa* may exist in Australia but this has yet to be determined. None of the known insect vectors from the Americas has been detected in Australia but there are a range of insect species that are closely related to vectors found in other countries. A key characteristic that insect vectors of *X. fastidiosa* must possess is a xylem-based feeding habit (Purcell 1980; Almeida *et al*. 2005). Within the xylem fluid-feeding specialists, it appears that most species can transmit the pathogen with varying degrees of efficiency (Redak *et al*. 2004). Three groups of xylem fluid-feeding arthropods exist in Australia that may have the ability to transmit *X. fastidiosa* should it arrive. These all belong to the Auchenorrhyncha, a suborder of Hemiptera, in the leafhopper subfamily Cicadellinae, the spittlebugs and froghoppers (Cercopoidea) and the cicadas (Cicadoidea) (Fletcher 2009). A variety of sharpshooters are known *X. fastidiosa* vectors and these sharpshooters account for over 80% of the reported vectors of the pathogen (Redak *et al*. 2004) indicating that this group is likely to be important in an Australian invasion scenario. In comparison, only four species of spittlebug are known vectors and there is just one laboratory-based record of a cicada species transmitting the pathogen (Severin 1950; Krell *et al*. 2007), suggesting that these groups of insects may play a smaller role. Within Australia, there are a total of 14 native leafhopper species in the subfamily Cicadellinae, over 30 species of spittlebugs and planthoppers and over 200 different species of cicada that may have the ability to transmit *X. fastidisoa* (Moulds 1990; Fletcher 2009).

Cicadellinae are present in all states excluding South Australia but they are most prolific in Queensland and New South Wales. The most common xylem fluid-feeding species are *Cofana spectra* (Distant), *Conoguinula coeruleopennis* (Fabricius) and *Ishidaella angustata* (Evans) (M Fletcher pers. comm.. 2009). *Cofana spectra* (Distant), the white leafhopper, is a crop pest that transmits rice yellow mottle virus in rice, which can move through the xylem of plants (Opalka *et al*. 1998) and occurs in Africa and Asia (Nwilene *et al*. 2009) and it is possible that it may have the ability to transmit *X. fastidiosa*. A number of these species feed upon known *X. fastidiosa* host plants including sorghum, barley and a range of grass species (Fletcher 2009) from which the bacterium could be acquired and transmitted if it became established in Australia.

Spittlebugs and froghoppers are distributed throughout Australia. New South Wales and Queensland most likely contain the highest number of species. Australian native species tend to be below 12 mm in length. Insects from the genus *Hindola* Kirkaldy (Clastopteridae: Machaerotinae) have been identified as vectors of a xylem-limited bacterium (*Pseudomonas syzygii*) in cloves in Indonesia (Eden Green *et al*. 1992). There are nine Australian species of Machaerotinae although none is placed in the genus *Hindola*. *Pseudomonas syzygii* is morphologically similar to *X. fastidiosa* in that it is rod-shaped, but is slightly smaller being 0.5–0.6 μm by 1.0–2.5 μm (Roberts *et al*. 1990). This indicates that xylem fluid-feeding insects from this family may be able to transmit *X. fastidiosa* in Australia provided all other conditions for successful transmission are satisfied. Two of the Australian spittlebug species, one of which is the common *Philagra parva* (Donovan) are known to feed upon *Acacia*, which has been identified as a host of *X. fastidiosa*.

Cicadas feed on both xylem (Cheung & Marshall 1973; White & Strehl 1978) and phloem fluid and although there is currently little evidence of them acting as vectors of *X. fastidisoa*, they may have the ability to do so as they occasionally probe the xylem (Krell *et al*. 2007). Cicadas are large insects (up to 70 mm long) (Hadlington & Johnston 1982), are strong fliers and can reach high abundance in summer (Froggatt 1958). Given that cicadas can be found across Australia in a range of habitats from coastal areas to the desert interior (Moulds 1990), they may be important vectors of *X. fastidiosa* if they are able to transmit the bacterium (Moulds 1990).

The geographical distribution of these potential vector species is important, as they must occupy areas with a climate suitable for the establishment of *X. fastidiosa*. There must be an overlap in distribution between the pathogen and vector for the pathosystem to function (Hoddle 2004) and the more xylem fluid-feeding insect species in an area, the more likely that there will be one species present that is a suitable vector in that area (Redak *et al*. 2004). Within Australia, Queensland and New South Wales are most likely to contain one or a number of native insect vectors of *X. fastidiosa*. This is due to the number of xylem fluid-feeding insect species distributed in these two states (Fig. 1).

Management options

Chemical control methods such as the application of insecticides (e.g. neonicotinoids and repellents) are currently used for *H. vitripennis* in California (Almeida *et al*. 2005) and would be the first line of defence for an Australian incursion event. Control of adult motiles can be achieved with the foliar insecticides fenpropathrin, carbaryl and fenpropathrin mixed with acephate. However, carbaryl causes significant mortality for only 1 day as opposed to 3 weeks for the other two foliar sprays (Bethke *et al*. 2001). Soil applied imidacloprid causes consistent high adult mortality for up to 4 weeks but would likely have the same effect on non-target native Australian herbivorous insects. The egg mass stage is difficult to control with insecticides as the developing embryo is encased within

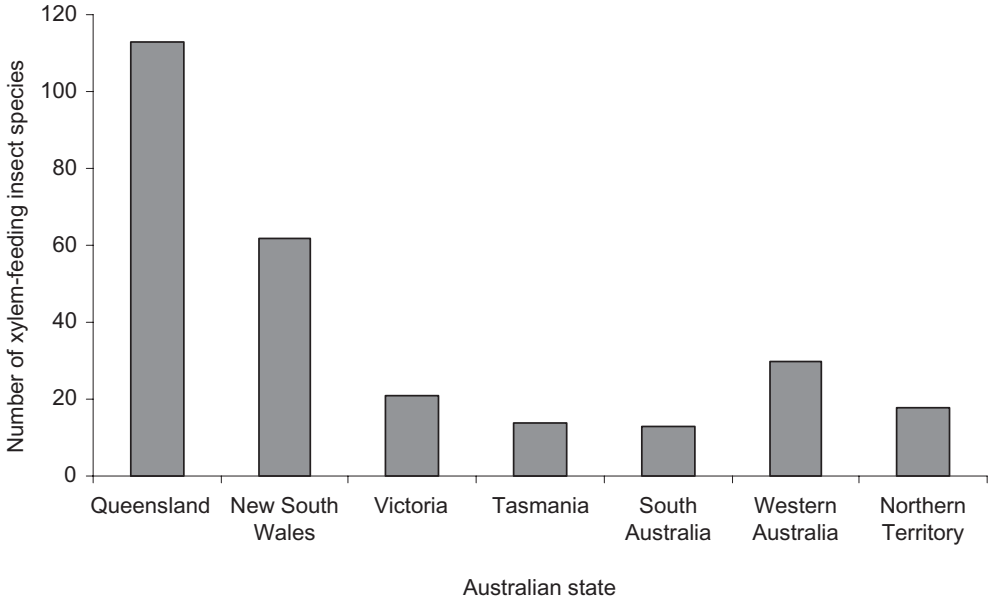

Fig. 1. Number of known Australian native xylem feeding insect species, in each state, which have potential ability to transmit *X. fastidiosa.*

the leaf. High concentrations of the systemic insecticide imidacloprid do not induce mortality in egg masses, but residues in the surrounding leaf tissues resulted in nymph mortality following emergence and subsequent feeding (Byrne & Toscano 2007). High levels of parasitoid mortality were, however, also observed (Byrne & Toscano 2007).

There is no chemical control method currently available for *X. fastidiosa*; however, neonicotinoids have been shown to slow the spread of the pathogen and block vector feeding in some instances (Redak & Blua 2001). Also, kaolin clay disrupts the insect's feeding behaviour, and grapevines treated with kaolin were found to have half the incidence of Pierce's disease seen in control grapevines (Tubajika *et al*. 2003). However, kaolin can be a contaminant of harvested grapes. Soil-applied insecticides and growth regulators are being investigated, and minimise effects on non-target species due to their activity or method of application (Almeida *et al*. 2005). These chemical-based tactics are costly, not entirely effective nor sustainable.

When the Allee effect (i.e. the depressed growth rate of a species at low densities) applies to the founding populations of an invasive species, as it would likely do with *H. vitripennis*, a minimum population threshold must be reached before the species can overcome this effect and achieve permanent establishment and sustained waves of spread (McCarthy 1997; Keitt *et al*. 2001; Petit *et al*. 2008). For this reason, the introduction of biological control agents early (Taylor & Hastings 2005) in an *H. vitripennis* invasion could be particularly effective. In this way, small-scale control can be implemented without enormous resources (Simberloff 2003), reducing propagule pressure on uninfested areas. This was observed in contained island settings such as Tahiti (Grandgirard *et al*. 2008). Biological control is a preferred management method as it has the ability to significantly reduce the target population for long periods, often permanently, requires little human maintenance and acts over a large area (Grandgirard *et al*. 2008). Biological control of *H. vitripennis* should be considered for Australia should an invasion occur.

Natural enemies from the south eastern United States and Mexico include mymarid and trichogrammatid parasitoids (Triapitsyn & Phillips 2000) and fungal pathogens such as *Hirsutella homalodiscae* nom. Prov. and *Pseudogibellula formicarum* (Mains) Samson & H.C. Evans 1973 (Kanga *et al*. 2004; Boucias *et al*. 2007). Little is known about the inoculum source and disease dynamics of the fungal pathogens (Kanga *et al*. 2004; Boucias *et al*. 2007). Mymarids have been introduced into California and French Polynesia (Pilkington *et al*. 2005) for the classical biological control of *H. vitripennis* (Grandgirard *et al*. 2008). In the United States, *G. ashmeadi* was found to be the most common natural enemy of *H. vitripennis* in three states (California, Louisiana and Florida) (Triapitsyn *et al*. 1998). This egg parasitoid is an effective biological control agent as the time it takes for *G. ashmeadi* to mature into an adult is approximately four times faster than *H. vitripennis* (Pilkington & Hoddle 2006) and on average, there are three females for every male that emerges from a parasitised egg mass (Irvin & Hoddle 2005).

Egg parasitoids introduced to California include *G. ashmeadi*, *G. triguttatus* Girault, *G. morilli* (Howard) and *G. fasciatus* Girault (all are Hymenoptera: Mymaridae), which parasitise *H. vitripennis* eggs (Pilkington *et al*. 2005). Parasitoids were introduced between 2000 and 2005, although the self-introduced *G. ashmeadi* was already present. A native congeneric sharpshooter species, *H. liturata* Ball, also a vector of Pierce's disease, is vulnerable to attack by *G. ashmeadi* in agricultural areas. Parasitism has not been observed in desert

areas where *H. liturata* naturally resides (Boyd & Hoddle 2007). Egg parasitoids in California survive the winter in low numbers and do not build to appreciable numbers until summer. However, approximately 10 years ago the spring generation of *H. vitripennis* used to be significant in California, but currently it is almost undetectable, and the summer generation has been reduced by ~93% (Hoddle 2010). It is possible that a constant rate of ~25% parasitism of eggs by *G. ashmeadi* has contributed to this significant reduction in *H. vitripennis* densities in southern California. In an Australian setting, implementing effective biological control of *H. vitripennis* may be difficult in the southern regions due to cool winters that could reduce *H. vitripennis* populations and consequently the number of egg masses available for parasitism (D Morgan pers. comm. 2010).

Biological control of *H. vitripennis* was extremely successful in French Polynesia. Since the parasitoid *G. ashmeadi* was introduced to Tahiti in 2005, parasitism of *H. vitripennis* eggs has been high, with an average of 80–100% (Grandgirard *et al*. 2008). *Gonatocerus ashmeadi* became established throughout Tahiti within 2–3 months of release. After the parasitoid colonised a site, *H. vitripennis* nymphs decreased within 2 months, adults decreased after 4–6 months and eggs decreased after 6–7 months. Populations of *H. vitripennis* nymphs and adults have declined by over 90% since the end of 2005 and this was achieved within 7 months of the release of *G. ashmeadi* (Grandgirard *et al*. 2008). This success was likely due to overlapping *H. vitripennis* generations, which provide a continuous supply of egg masses for parasitoids, a situation that may occur in tropical northern Australia.

In advance of a possible *H. vitripennis* invasion, it is recommended that proactive screening of *G. ashmeadi* should be undertaken in quarantine. Should non-target impact studies indicate acceptable levels of risk, this parasitoid would be available for immediate establishment against *H. vitripennis*. This forward-thinking stance would take advantage of the 'crisis free' window and pre-approved release of *G. ashmeadi* could greatly reduce the invasion speed of *H. vitripennis*, which would allow development of quarantine measures and area-specific control tactics based around classical biological control. We are unaware of this approach ever being undertaken before and it would be truly novel if achieved, perhaps setting a new precedent in invasive species management.

CONCLUSIONS

The literature suggests that should *X. fastidiosa* and *H. vitripennis* become established in Australia, a pathosystem involving native and exotic Australian plants will function in a similar manner to that seen in California. As in California, and in other geographical locations, economic losses would be anticipated to be serious should the vector and pathogen coexist. The risk of establishment of both species in at least some parts of Australia is considered high due to favourable climatic conditions for both species, an abundance of host plants that both can utilise, probable lack of effective natural enemies (especially host specific egg parasitoids), and the presence of xylem fluid-feeding native insects that may act as vectors (Luck *et al*. 2001). If both *H. vitripennis* and *X. fastidiosa* were to establish, there is potential for mitigating disease spread via the management of the insect vector as has been achieved in other countries. This could potentially include the utilisation of native Australian parasitoids if they are shown to be effective biological control agents. More likely however, would be the importation, screening in quarantine and release and establishment of *G. ashmeadi* for use in a classical biological control program against *H. vitripennis*. There is an urgent need to determine which Australian native plants can host the pathogen and the vector in order to predict how the pathosystem may operate in Australia. This large-scale natural experiment is already underway in the United States where native Australian plants are grown in sympatry with *H. vitripennis* and *X. fastidiosa*. This overseas system in California and Florida should be studied to provide insight into how this pathosystem could operate in Australia. Once the host status of native plant species is known, those species that are identified as hosts can be monitored in areas identified as high risk in Australia in order to detect an incursion early, and can be targeted for control, minimising the spread and impact of an incursion should it occur. Proactive screening of *G. ashmeadi* should be undertaken so it could be approved for release in advance of the establishment of *H. vitripennis*.

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REFERENCES

Almeida RPP, Blua MJ, Lopes JRS & Purcell AH. 2005. Vector transmission of *Xylella fastidiosa*: applying fundamental knowledge to generate disease management strategies. *Annals of the Entomological Society of America* **98**, 775–786.

Almeida RPP, Nascimento FE, Chau J *et al*. 2008. Genetic structure and biology of *Xylella fastidiosa* strains causing disease in citrus and coffee in Brazil. *Applied and Environmental Microbiology* **74** (12), 3690–3701.

Almeida RPP & Purcell AH. 2003a. *Homalodisca coagulata* (Hemiptera, Cicadellidae) Transmission of *Xylella fastidiosa* to Almond. *Plant Disease* **87**, 1255–1259.

Almeida RPP & Purcell AH. 2003b. Transmission of *Xylella fastidiosa* to grapevines by *Homalodisca coagulata* (Hemiptera: Cicadellidae). *Journal of Economic Entomology* **96** (2), 264–271.

Alves E, Leite B, Marucci RC, Pascholati SF, Lopes JRS & Andersen PC. 2008. Retention sites for *Xylella fastidiosa* in four sharpshooter vectors (Hemiptera : Cicadellidae) analyzed by scanning electron microscopy. *Current Microbiology* **56**, 531–538.

Andersen PC, Brodbeck BV & Mizell RF. 1989. Metabolism of amino acids, organic acids and sugars extracted from the xylem fluid of four host plants by adult *Homalodisca coagulata*. *Entomologia Experimentalis et Applicata* **50**, 149–159.

Andersen PC, Brodbeck BV & Mizell RF. 1992. Feeding by the leafhopper, *Homalodisca coagulata*, in relation to xylem fluid chemistry and tension. *Journal of Insect Physiology* **38** (8), 611–622.

Andersen PC, Brodbeck BV, Mizell RF & Oden S. 2005. Abundance and feeding of *Homalodisca coagulata* (Hemiptera: Auchenorrhyncha: Cicadellidae) on *Vitis* genotypes in north Florida. *Environmental Entomology* **34** (2), 466–478.

Australian Bureau of Agricultural and Resource Economics. 2008. Australian commodity statistics, Canberra.

Australian Bureau of Meteorology. Trend maps – Australian Climate Variability and Change. 2009. [Accessed 12 Apr 2009.] Available from URL: http://www.bom.gov.au/

Australian Bureau of Statistics. 2010. *Australian Wine and Grape Industry, 2010*. Commonwealth of Australia, Canberra, Australia.

Australian Citrus Growers Inc. 2008. *Citrus*. Horticulture Australia Limited, Mildura, Australia.

Bautista RC, Yalemar JA, Suh TH, Heu RA & Teramoto KK. 2005. The glassy-winged sharpshooter gets no 'lei' or a welcome 'aloha' from the island. *11th Pacific entomology conference*, Hawaii.

Bethke JA, Blua MJ & Redak RA. 2001. Effect of selected insecticides on *Homalodisca coagulata* (Homoptera: Cicadellidae) and transmission of Oleander Leaf Scorch in a greenhouse study. *Journal of Economic Entomology* **94** (5), 1031–1036.

Berisha B, Chen YD, Zhang GY, Xu BY & Chen TA. 1998. Isolation of Pierce's disease bacteria from grapevines in Europe. *European Journal of Plant Pathology* **104** (5), 427–433.

Blua MJ & Morgan DJW. 2003. Dispersion of *Homalodisca coagulata* (Hemiptera: Cicadellidae), a vector of *Xylella fastidiosa*, into vineyards in southern California. *Journal of Economic Entomology* **96**, 1369–1374.

Blua MJ, Phillips PA & Redak RA. 1999. A new sharpshooter threatens both crops and ornamentals. *California Agriculture* **53**, 22–24.

Boucias DG, Scharf DW, Breaux SE, Purcell DH & Mizell RE. 2007. Studies on the fungi associated with the glassy-winged sharpshooter *Homalodisca coagulata* with emphasis on a new species *Hirsutella homalodiscae* nom. Prov. *BioControl* **52**, 231–258.

Boyd EA & Hoddle MS. 2007. Host specificity testing of *Gonatocerus* spp. egg-parasitoids used in a classical biological control program against *Homalodisca vitripennis*: a retrospective analysis for non-target impacts in southern California. *Biological Control* **43**, 56–70.

Brodbeck BV, Andersen PC & Mizell RF. 2011. Nutrient mediation of behavioural plasticity and resource allocation in a xylem-feeding leafhopper. *Oecologia* **165**, 111–122.

Brodbeck BV, Andersen PC, Oden S & Mizell RF. 2007. Preference-performance linkage of the xylem feeding leafhopper, *Homalodisca vitripennis* (Hemiptera Cicadellidae). *Environmental Entomology* **36** (6), 1512–1522.

Brodbeck BV, Mizell RF & Andersen PC. 1993. Physiological and behavioural adaptations of 3 species of leafhoppers in response to the dilute nutrient content of xylem fluid. *Journal of Insect Physiology* **39** (1), 73–81.

Brodbeck BV, Mizell RF, French RJ, Andersen PJ & Aldrich JH. 1990. Amino acids as determinants for the xylem feeding leafhopper, *Homalodisca coagulata* (Homoptera: Cicadellidae). *Oecologia* **83**, 338–345.

Byrne FJ & Toscano NC. 2007. Lethal toxicity of systemic residues of imidacloprid against *Homalodisca vitripennis* (Homoptera: Cicadellidae) eggs and its parasitoid *Gonatocerus ashmeadi* (Hymenoptera: Mymaridae). *Biological Control* **43** (1), 130–135.

California Department of Food and Agriculture. 2008. Glassy-winged sharpshooter nursery stock approved treatment manual. In: *Glassy-Winged Sharpshooter Nursery Stock Approved Treatment Manual*, 1st edn (eds J Kabashima & G Morris), pp. 1–41. UC Cooperative Extension: Sacramento, USA.

California Department of Food and Agriculture. 2009. Pierce's disease control program. Sacramento, USA.

California Department of Food and Agriculture. 2010. Pierce's disease control program. Sacramento, USA.

Cheung WWK & Marshall AT. 1973. Water and ion regulation in cicadas in relation to xylem feeding. *Journal of Insect Physiology* **19**, 1801–1806.

Chung KR & Brlansky RH. 2005. *Citrus Diseases Exotic to Florida: Citrus Variegated Chlorosis (CVC)*. University of Florida, Gainesville, FL, USA.

College of Natural Resources. 2005. *An Introduction to Pierce's Disease*. University of California, Berkeley, California, USA.

Constable FE, Joyce PA & Rodoni BC. 2007. A survey of key Australian pome fruit growing districts for exotic and endemic pathogens. *Australasian Plant Pathology* **36** (2), 165–172.

Costa HS, Raetz E, Pinkard TR *et al*. 2004. Plant hosts of *Xylella fastidiosa* in and near Southern California Vineyards. *Plant Disease* **88**, 1255–1261.

Daugherty MP, Lopes JRS & Almeida RPP. 2010. Strain-specific alfalfa water stress induced by *Xylella fastidiosa*. *European Journal of Plant Pathology* **127**, 333–340.

Davis MJ, Raju BC, Brlansky RH *et al*. 1983. Periwinkle Wilt Bacterium: axenic culture, pathogenicity, and relationships to other gram-negative, xylem inhabiting bacteria. *Phytopathology* **73**, 1510–1515.

De Leon JH, Jones WA & Morgan DJW. 2004. Population genetic structure of *Homalodisca coagulata* (Homoptera: Cicadellidae), the vector of the bacterium *Xylella fastidiosa* causing Pierce's disease in grapevines. *Annals of the Entomological Society of America* **94**, 809–818.

Doughty S & Luck JE. 2005. Report on the incidence of *Xylella fastidiosa* on host plants in Australia.

Eden Green SJ, Balfas R, Sutarjo T & Jamalius. 1992. Characteristics of the transmission of Sumatra disease of cloves by tube-building cercopoids, *Hindola* spp. *Plant Pathology* **41**, 702–712.

Feil H & Purcell AH. 2001. Temperature-dependent growth and survival of *Xylella fastidiosa in vitro* and in potted grapevines. *Plant Disease* **85**, 1230–1234.

Fiksdal CR. 2000. Crop and Livestock Report Los Angeles, County Agricultural Commissioner/Weights and Measures Department. Los Angeles, USA.

Fletcher M. Identification keys and checklists for the leafhoppers, planthoppers and their relatives occurring in Australia and neighbouring areas (Hemiptera: Auchenorrhyncha). 2009 + updates. [Accessed 24 May 2010.] Available from URL: http://www1.dpi.nsw.gov.au/keys/auch/index.html

Freitag JH. 1951. Host range of Pierce's disease virus of grapes as determined by insect transmission. *Phytopathology* **41**, 920–934.

Froggatt WW. 1958. *Australian Insects*. William Brooks and Company Ltd, Sydney, New South Wales, Australia.

Gilbert GS & Parker IM. 2006. Invasions and the regulation of plant populations by pathogens. In: *Conceptual Ecology and Invasion Biology: Reciprocal Approaches to Nature* (eds MW Cadotte, SM M^{c}Mahon & T Fukami), pp. 289–305. Springer, Dordrecht, The Netherlands.

Gleeson P. 2001. *Glassy-Winged Sharpshooter and Pierce's Disease Research Summaries – Financial Year 2000–2002*. California Department of Food and Agriculture, Sacramento, California, USA.

Goodwin PH & Zhang S. 1997. Distribution of *Xylella fastidiosa* in southern Ontario as determined by the polymerase chain reaction. *Canadian Journal of Plant Pathology* **19**, 13–18.

Grandgirard J, Hoddle MS, Petit JN, Roderick GK & Davies N. 2008. Engineering an invasion: classical biological control of the glassy-winged sharpshooter, *Homalodisca vitripennis*, by the egg parasitoid *Gonatocerus ashmeadi* in Tahiti and Moorea, French Polynesia. *Biological Invasions* **10** (2), 135–148.

Grandgirard J, Hoddle MS, Petit JN, Roderick GK & Davies N. 2009. Classicalbiological control of the glassy-winged sharpshooter, *Homalodisca vitripennis*, by the egg parasitoid *Gonatocerus ashmeadi* in the Society, Marquesas and Austral archipelagos of French Polynesia. *Biological Control* **48**, 155–163.

Grandgirard J, Hoddle MS, Roderick GK *et al*. 2006. Invasion of French Polynesia by the glassy-winged sharpshooter, *Homalodisca coagulata* (Hemiptera: Cicadellidae): a new threat to the South Pacific. *Pacific Science* **60**, 429–438.

Grandgirard J, Hoddle MS, Triapitsyn SV, Petit JN, Roderick GK & Davies N. 2007. First records of *Gonatocerus dolichocerus* Ashmead (Hymenoptera: Mymaridae), *Centrodora* sp. (Hymenoptera: Aphelinidae), *Chaetomymar* sp. and *Anagrus* sp.(Hymenoptera: Mymaridae) in French Polynesia with notes on egg parasitism of the glassy-winged sharpshooter. *Pan-Pacific Entomologist* **83**, 177–184.

Hadlington PW & Johnston JA. 1982. *An Introduction to Australian Insects*. New South Wales University Press, Kensington, UK.

Hewitt WB, Frazier NW, Freitag JH & Winkler AJ. 1949. Pierce's disease investigations. *Hilgardia* **19**, 207–264.

Hill BL & Purcell AH. 1995. Multiplication and movement of *Xylella fastidiosa* within grapevine and 4 other plants. *Phytopathology* **85**, 1368–1372.

Hill BL & Purcell AH. 1997. Populations of *Xylella fastidiosa* in plants required for transmission by an efficient vector. *Phytopathology* **87**, 1197–1201.

Hoddle MS. 2004. The potential adventive geographic range of glassy-winged sharpshooter, *Homalodisca coagulata* and the grape pathogen *Xylella fastidiosa*: implications for California and other grape growing regions of the world. *Crop Protection* **23**, 691–699.

Hoddle MS. 2010. Are natural enemies controlling glassy-winged sharpshooter populations in southern California? CDFA Pierce's Disease Control Program Symposium Proceedings. pp. 16–19.

Hoddle MS, Triapitsyn SV & Morgan DJW. 2003. Distribution and plant association records for *Homalodisca coagulata* (Hemiptera: Cicadellidae) in Florida. *Florida Entomologist* **86**, 89–91.

Hopkins DL. 1989. *Xylella fastidiosa*: xylem-limited bacterial pathogen of plants. *Annual Review of Phytopathology* **27**, 271–290.

Hopkins DL & Purcell AH. 2002. *Xylella fastidiosa*: cause of Pierce's disease of grapevine and other emergent diseases. *Plant Disease* **86**, 1056–1066.

Hummel NA, Zalom FG, Toscano NC, Burman P & Peng CYS. 2006. Seasonal patterns of female *Homalodisca coagulata* (Say) (Hemiptera: Cicadellidae) reproductive physiology in Riverside, California. *Environmental Entomology* **35** (4), 901–906.

Irvin NA & Hoddle MS. 2005. Determination of *Homalodisca coagulata* (Hemiptera: Cicadellidae) egg ages suitable for oviposition by *Gonatocerus ashmeadi, Gonatocerus triguttatus*, and *Gonatocerus fasciatus* (Hymenoptera: Mymaridae). *Biological Control* **32** (3), 391–400.

Jackson BC, Blua MJ & Bextine B. 2008. Impact of duration versus frequency of probing by *Homalodisca vitripennis* (Hemiptera: Cicadellidae) on inoculation of *Xylella fastidiosa*. *Journal of Economic Entomology* **101**, 1122–1126.

Kanga LHB, Jones WA, Humber RA & Boyd DW Jr. 2004. Fungal pathogens of the glassy-winged sharpshooter *Homalodisca coagulata* (Homoptera: Cicadellidae). *Florida Entomologist* **87** (2), 225–228.

Keitt TH, Lewis MA & Holt RD. 2001. Allee effects, invasion pinning, and species borders. *The American Naturalist* **157** (2), 203–216.

Krell RK, Boyd EA, Nay JE, Park YL & Perring TM. 2007. Mechanical and insect transmission of *Xylella fastidiosa* to *Vitis vinifera*. *American Journal of Enology and Viticulture* **58**, 211–216.

Lauziere I & Setamou M. 2009. Suitability of different host plants for oviposition and development of *Homalodisca vitripennis* (Hemiptera: Cicadellidae) and its implication on mass rearing. *Annals of the Entomological Society of America* **102**, 642–649.

Lauziere I, Sheather S & Mitchell F. 2008. Seasonal abundance and spatio-temporal distribution of dominant xylem fluid-feeding Hemiptera in vineyards of central Texas and surrounding habitats. *Environmental Entomology* **37**, 925–937.

Leu LS & Su CC. 1993. Isolation, cultivation, and pathogenicity of *Xylella fastidiosa*, the causal bacterium of Pear Leaf Scorch disease in Taiwan. *Plant Disease* **77** (6), 642–646.

Levine JM, Adler PB & Yelenik SG. 2004. A meta-analysis of biotic resistance to exotic plant invasions. *Ecology Letters* **7**, 975–989.

Loomis NH. 1958. Performance of *Vitis* species in the south as an indication of their relative resistance to Pierce's disease. *Plant Disease Reporter* **42**, 833–836.

Lopes JRS, Daugherty MP & Almeida RPP. 2009. Context- dependent transmission of a generalist plant pathogen: host species and pathogen strain mediate insect vector competence. *Entomologia Experimentalis et Applicata* **131**, 216–224.

Lopes JRS, Daugherty MP & Almeida RPP. 2010. Strain origin drives virulence and persistence of *Xylella fastidiosa* in alfalfa. *Plant Pathology* **59**, 963–971.

Luck J, Letham D, McKirdy S & Brown B. 2002. Pierce's disease and the glassy-winged sharpshooter: understanding the threat and minimising the risks. *The Australian & New Zealand Grapegrower & Winemaker* **462**, 22–26.

Luck J, Traicevski V, Mann R & Moran J. 2001. The potential for the establishment of Pierce's Disease in Australian grapevines. Final Report to Grape and Wine Research and Development Corporation, DNR00/1, Melbourne.

Luck J, Van Rijswijk B & Williamson V. 2004. Post entry quarantine protocols for host plants of *Xylella fastidiosa*. Final Report to Grape and Wine Research and Development Corporation, Melbourne.

McCarthy MA. 1997. The Allee effect, finding mates and theoretical models. *Ecological Modelling* **103**, 99–102.

McGaha LA, Jackson B, Bextine B, McCullough D & Morano L. 2007. Potential plant reservoirs for *Xylella fastidiosa* in South Texas. *American Journal of Enology and Viticulture* **58**, 398–401.

Minsavage GV, Thompson CM, Hopkins DL, Leite RMVBC & Stall RE. 1994. Development of a polymerase chain reaction protocol for detection of *Xylella fastidiosa* in plant tissue. *Phytopathology* **84**, 456–461.

Mizell RF, Tipping C, Andersen PC, Brodbeck BV, Hunter WB & Northfield T. 2008. Behavioral model for *Homalodisca vitripennis* (Hemiptera: Cicadellidae): optimization of host plant utilization and management implications. *Environmental Entomology* **37** (5), 1049–1062.

Montero-Astua M, Saborio RG, Chacon-Diaz C *et al*. 2008. First reports of *Xylella fastidiosa* in avocado in Costa Rica. *Plant Disease* **92** (1), 175.

Moulds MS. 1990. *Australian Cicadas*. New South Wales University Press, Sydney, New South Wales, Australia.

Naumann ID. 1991. Hymenoptera. In: *The Insects of Australia* (eds ID Naumann, PB Carne, JF Lawrence *et al*.), pp. 916–1000. Melbourne University Press, Melbourne, Victoria, Australia.

Nunney L, Yuan X, Bromley R *et al*. 2010. Population genomic analysis of a bacterial plant pathogen: novel insight into the origin of Pierce's disease of grapevines in the US. *PLoS ONE* **5** (11), e15488.

Nwilene FE, Traore AK, Asidid AN, Sere Y, Onasanya A & Abo ME. 2009. New Records of Insect Vectors of Rice Yellow Mottle Virus (RYMV) in Cote d'Ivoire, West Africa. *Journal of Entomology* **6**, 189–197.

Opalka N, Brugidou C, Nicloe M, Beachy RN, Yeager M & Fauquet C. 1998. Movement of rice yellow mottle virus between xylem cells through pit membranes. *Proceedings of the National Academy of Sciences of the United States of America* **95**, 3323–3328.

Peroni LA, Dos Reis JRR, Della Coletta H, De Souza AA, Machado MA & Stach-Machado DR. 2008. Assessment of the diagnostic potential of immmunocapture-PCR and immuno-PCR for citrus variegated chlorosis. *Journal of Microbiological Methods* **75**, 302–307.

Perring TM, Farrar CA & Blua MJ. 2001. Proximity to citrus influences Pierce's disease in Temecula Valley vineyards. *California Agriculture* **55**, 13–18.

Pests and Diseases Image Library. Pierce's disease. 2010. [Accessed 15 Aug 2010.] Available from URL: http://www.padil.gov.au/

Petit JN, Hoddle MS, Grandgirard J, Roderick GK & Davies N. 2008. Invasion dynamics of the glassy-winged sharpshooter *Homalodisca vitripennis* (Germar) (Hemiptera: Cicadellidae) in French Polynesia. *Biological Invasions* **10** (7), 955–967.

Pilkington LJ & Hoddle MS. 2006. Reproductive and developmental biology of *Gonatocerus ashmeadi* (Hymenoptera: Mymaridae), an egg parasitoid of *Homalodisca coagulata* (Hemiptera: Cicadellidae). *Biological Control* **37**, 266–275.

Pilkington LJ, Irvin NA, Boyd EA *et al*. 2005. Introduced parasitic wasps could control glassy-winged sharpshooter. *California Agriculture* **59**, 223–228.

Plant Health Australia. 2009a. *Industry Biosecurity Plan for the Citrus Industry*. Plant Health Australia, Canberra, Australian Capital Territory, Australia.

Plant Health Australia. 2009b. *Industry Biosecurity Plan for the Viticulture Industry*. Plant Health Australia, Canberra, Australian Capital Territory, Australia.

Purcell AH. 1980. Almond Leaf Scorch: leafhopper and spittlebug vectors. *Journal of Economic Entomology* **73**, 834–838.

Purcell AH. 1997. *Xylella fastidiosa*, a regional problem or global threat? *Journal of Plant Pathology* **79**, 99–105.

Raven JA. 1983. Phytophages of xylem and phloem: a comparison of animal and plant sap-feeders. In: *Advances in Ecological Research* (eds A MacFayden & ED Ford), pp. 136–233. Academic Press, London, UK.

Redak R & Blua M. 2001. *Impact of Layering Control Tactics on the Spread of Pierce's Disease by the Glassy-Winged Sharpshooter*. University of California, Riverside, California, USA.

Redak RA, Purcell AH, Lopes JRS, Blua MJ, Mizell RF III & Andersen PC. 2004. The biology of xylem fluid-feeding insect vectors of *Xylella fastidiosa* and their relation to disease epidemiology. *Annual Reviews in Entomology* **49**, 243–270.

Roberts SJ, Eden-Green SJ, Jones P & Ambler DJ. 1990. *Pseudomonas syzygii*, sp. nov., the cause of Sumatra disease of cloves. *Systematic and Applied Microbiology* **13**, 34–43.

Schaad NW, Postnikova E, Lacy G, Fatmi MB & Chang C-J. 2004. *Xylella fastidiosa* subspecies: *X. fastidiosa* subsp *piercei*, subsp. nov., *X. fastidiosa* subsp. *multiplex* subsp. nov., and *X. fastidiosa* subsp. *Pauca* subsp. nov. *Systematic and Applied Microbiology* **27**, 290–300.

Secretariat of the Pacific Community. 2002. *Incursion of Glassy-Winged Sharpshooter Homalodisca Coagulata in French Polynesia*. Plant Protection Service, Papette, French Polynesia.

Severin HP. 1950. Spittle insect vectors of Pierce's disease virus ll. Life history and virus transmission. *Hilgardia* **19**, 357–375.

Siebert J. 2001. *Economic Impact of Pierce's Disease on the California Grape Industry*. University of California, Berkeley, California, USA.

Simberloff D. 2003. Eradications preventing invasions at the outset. *Weed Science* **51** (2), 247–253.

Sisterson MS. 2008. Egg load dynamics of *Homalodisca vitripennis*. *Environmental Entomology* **37**, 1200–1207.

Sorensen JT & Gill RJ. 1996. A range extension of *Homalodisca coagulata* (Say) (Hemiptera: Clypeorrhyncha: Cicadellidae) to southern California. *The Pan-Pacific Entomologist (USA)* **72** (3), 160–161.

Sutton TB, Villanueva R, Cline B & Kennedy GG. 2008. A survey for vectors of the Pierce's disease bacterium in Muscadine and Vinifera Vineyards and their reservoir hosts. *Progress Report*, 1–7.

Taylor CM & Hastings A. 2005. Allee effects in biological invasions. *Ecology Letters* **8** (8), 895–908.

The Ministry of Agriculture and Forestry. Cook Island imports under extra scrutiny after insect pest detected. 2007. [Accessed 14 May 2009.] Available from URL: http://www.maf.govt.nz/mafnet/press/070404gwss.htm

Toscano NC, Cooksey DB, Dumenyo JK & Hernandez-Martinez R. 2004. Impact of host plant xylem fluid on *Xylella fastidiosa* multiplication, aggregation and attachment. *Proceedings of Pierce's disease research symposium.* Coronado Island, USA.

Triapitsyn SV, Mizell RF, Bossart JL & Carlton EC. 1998. Egg parasitoids of *Homalodisca vitripennis* (Homoptera:Cicadellidae). *Florida Entomologist* **81** (2), 241–243.

Triapitsyn SV & Phillips PA. 2000. First record of *Gonatocerus triguttatus* (Hymenoptera : Mymaridae) from eggs of *Homalodisca coagulata* (Homoptera: Cicadellidae) with notes on the distribution of the host. *Florida Entomologist* **83**, 200–203.

Tubajika KM, Civerolo EL, Purteka G *et al*. 2003. Messenger and particle film surround reduces Pierce's disease development in grape. *Phytopathology* **93S** (6S), 84.

Turner WF & Pollard HN. 1959. Life histories and behavior of five insect vectors of phony peach disease. *Technical Bulletin of the United States Department of Agriculture* **1188**, 1–28.

Webjet. Webjet homepage. 2011. [Accessed 22 Feb 2011.] Available from URL: http://www.webjet.com.au/

Wells JM, Raju BC, Hung HY, Weisburg WG, Mandelco-Paul L & Brenner DJ. 1987. *Xylella fastidiosa* gen. nov., sp. nov: gram-negative, xylem-limited, fastidious plant bacteria related to *Xanthomonas* spp. *International Journal of Systematic Bacteriology* **37**, 136–143.

White J & Strehl CE. 1978. Xylem feeding by periodical cicada nymphs on tree roots. *Ecological Entomology* **3**, 323–327.

Wilson MR, Turner JA & M^{c}Kamey SH. 2009. *Sharpshooter Leafhoppers of the World*. National Museum Wales, Cardiff, UK.

Wistrom C & Purcell AH. 2005. The fate of *Xylella fastidiosa* in vineyard weeds and other alternate hosts in California. *Plant Disease* **89** (9), 994–999.

Wittwer G, McKirdy S & Wilson R. 2006. *Analysing a Hypothetical Pierce's Disease Outbreak in South Australia Using a Dynamic CGE Approach*. Clayton: Monash University, Melbourne, Victoria, Australia.

Young DA. 1958. A synopsis of the species of *Homalodisca* in the United States. *Bulletin of the Brooklyn Entomological Society* **53** (1), 7–13.

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