HARPER ADAMS UNIVERSITY

IMPROVING BIOLOGICAL CONTROL IN PROTECTED CROPS

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A THESIS SUBMITTED FOR THE DEGREE OF DOCTOR OF PHILOSOPHY
NOVEMBER 2020
Harper Adams University

Abstract

Management of the leafhopper *Hauptidia maroccana* is inadequate. Despite not being a regular pest in glasshouses, *H. maroccana* is capable of significant damage. Current conrol methods rely on one chemical agent (Indoxacarb) and a putative predator. In the face of widespread chemical resistance and unreliability of generalist predators, the risk to growers under these conditions is increased. Part of the problem facing growers is that only very basic information about this pest is known, with few studies on the ecological interactions that will be vital for suffifcient control. It is these knowledge gaps that this thesis addresses. A summary literature review introduces the main topics of study and examines the failure of a previously attempted biological control agent. Chapter 2 builds on evidence from similar species and looks at improving trapping of the pest in glasshouses. Non-yellow traps are tested for efficacy and selectivity under laboratory conditions, and indicate that there is scope for improvement in this area. The visual ecology of this pest is examined again in Chapter 4 where the use of LED technology to increase the visual signal of traps is examined. The results of which again indicate that there is more complexity to the visual cues evaluated by *H. maroccana* than the consensus implies. The importance of plant volatiles to herbivores is well studied. For *H. maroccana* however, much is not known. Of particular importance is the ability of this pest to detect and respond to the volatile blends released by plants under attack by conspecifics. Growers have reported that *H. maroccana* forms hotspots within crops. Whether this is due to aggregation or a lack of migration is unknown. Information from experiments here suggests that it is largely due to lack of emigration rather than aggregative behaviours. The use of the generalist predator *Macrolophus* caliginosus for control of leafhopper is critically examined and tested under laboratory conditions. The overall picture is mixed with predation of leafhopper nymphs approaching levels of consumption seen for other pests, but predation on adults being almost zero. Furthermore, the response of *Macrolophus* to plant volatiles from infested plants was mixed, which may indicate that under a more complex environment, the ability of this predator to locate *H. maroccana* is reduced. In the final chapter the project is reviewed as a whole against the objectives and summarised.

Acknowledgements

The production of this thesis would not have been possible without the funding provided by BBSRC and AHDB. From AHDB, particular thanks are extended to Georgina Key and Joe Martin.

Guidance and industry consultation was provided generously by Vitacress Herbs and Cantelo Nurseries. Within those companies support was gratefully received from Simon Budge and Neal Ward respectively.

The project took place on Harper Adams University sites and thanks are extended to the staff and fellow students of that place for assistance, advice and companionship. There are people who have contributed greatly to the project and to my own personal wellbeing during this time. These people are too many to list in completion, so to avoid leaving anyone out, the list will remain unstated.

Above and beyond all others are my supervisory team, Dr Tom Pope, and Professor Simon Leather. For these gentlemen I was probably one student among others, but for me they were in a league of their own.

Finally, the confidence to undertake this work in the first place was hard to find, and harder still to maintain. At any point when my stores were running low, I knew I could turn to my family. To Michelle, Hefin and Bryce, an unpayable debt is owed. But that’s what family is for, right?

Per Ardua, mutatio.

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1 Literature review

1.1 Introduction

In the last 100 years, agriculture has changed more than in the previous thousand. The change from a low-input, low-tech approach to a high-input, high-tech, science-driven system has seen yields and quality increase dramatically. IN the current era, new stresses on the food production system (e.g. climate change, a growing population, increasing demand for luxury foodstuffs) mean that this high-input system of agriculture is not sustainable and that in order to guarantee future yields we must shift towards methods of agricultural production with reduced inputs (Reijntjes *et al.*, 1992; Kogan, 1998). Of particular import is the use of pesticides, where historic mismanagement of the use of these chemicals has caused problems both to food producers in the form of pesticide resistance (*see* Roush & Tabashnik, 1991), and to the wider community in the form of environmental contamination and bioaccumulation (*e.g.* Weber *et al.*, 2010). To avoid further harms resulting from this, legislation has shifted from regulation based on managed risk, to hazard reduction (Kogan, 1998). The precautionary principle thinking has been written into European law in the form of 2009/128/EC, which stipulates that "integrated pest management and alternative approaches or techniques in order to reduce dependency on the use of pesticides should be used". This has resulted in many previously approved chemicals being withdrawn from the market due to increased scrutiny of potential harms. Removal of old chemistry has coupled with increased regulation for new products leading to many of these banned products not being replaced. In some ways, narrowing the suite of available chemistries may be detrimental to long-term sustainability as increased dependency on a few modes of action is more likely to increased prevalence of resistance.

Integrated pest management (IPM) is a strategy that promotes the use of all available strategies in a programme that seeks to manage populations of pests. Design of an IPM strategy may involve non-chemical methods such as biocontrol or traps, alongside conventional control. These methods may be deployed prophylactically, or at the point where evidence-based pest thresholds are reached (E. Birch *et al.*, 2011). IPM therefore relies heavily on scouting for pest invasion, monitoring populations, and knowledge of interactions with other species. This contrasts with prophylactic or calendar spraying for pest population management that does not take into account local conditions or possible beneficial organisms (Kogan, 1998). In order that the correct strategy is utilised, IPM strategies must be built on a foundation of accurate pest identification that allows understanding of its biology and ecology. Integrated pest management, by definition, is a process of integrating pest management strategies, no single control method is relied on in isolation. IPM forms a responsive suite of control methods that are specific to the crop and environment. An IPM system that provides control of pests in arable cropping situations may not be suitable for use in small-scale hydroponic cropped environments. IPM allows growers versatility and, where possible, favours low-impact management strategies. Contrasting to management strategies following the chemical revolution, IPM does not seek the total extirpation of a pest from within a crop. Instead, the pest population is lowered to below the Economic Injury Level (EIL). Resultingly, IPM is seen to have a reduced impact on the agro-ecosystem as well as the surrounding environment. A major component in determining the EIL is accurate knowledge of the current pest population as well as likely population trends, the damage the plants will sustain from the pest, and whether or not the plant will compensate for low levels of damage (Sadras, 1995). As such, any successful IPM strategy must be based on thorough monitoring and knowledge of the ecology of the pest.

In some respects, glasshouse cultivation makes the job of pest managers easier. The presence of a physical barrier to invasion of the crop may help to mitigate initial levels of pest species. This effect can be improved by adding insect screens to vents so that management of the internal conditions can be achieved with a reduced risk of invasion. The stable, warm conditions provided by glasshouses, however, often favour both the pest as well as the host plant. Furthermore, the reduction in biodiversity within a glasshouse has been suggested to increase the instability of the “ecosystem” created within . This can lead to explosive population growth by pests due to ecological release (Veyrat *et al.*, 2016). A key strategy for control of pests in glasshouses is the use of biological control, due to the importing of pesticide-susceptible pollinators into many fruiting crops . Biocontrol is the use of living organisms or viruses as effectors to lower pest populations (van Lenteren, 2012). In protected horticulture biocontrol agents are often deployed against herbivorous insects that threaten crops. This literature review serves as the introduction to a project improving biological control in glasshouse crops. The review will address key aspects of pest control specific to the project and describe knowledge gaps that may provide avenues for research. Broadly the review will cover the following main topics; (1) insect-plant interactions, (2) insect colour perception and its influence on trapping using colour, (3) the study organisms, and (4) a brief summary and detailing of aims.

1.2 Insect-Plant interactions

1.2.1 Herbivory

Photosynthetic organisms represent the most abundant and ubiquitous source of energy in the natural world and are the foundation of almost all heterotrophic feeding systems

(Schoonhoven *et al.*, 2005). The few trophic systems that do not utilise plants or phytoplankton are characterised by low diversity and extremely specialised biochemistry and physiology (Bernardino *et al.*, 2012). As the most diverse taxa, the Class Insecta have an incredible range of feeding strategies that allow them to take advantage of the productivity of plants (Grimaldi & Engel, 2005). Over a quarter of living eukaryotic organisms (discounting algae and fungi) are herbivorous insects (Strong *et al.*, 1984). The relationship between plants and herbivorous insects is complex, reflecting the place of insects as the most important Class of herbivores. It has been suggested that a key driver of the diversification of plants into the myriad forms extant and extinct is insect herbivory (Ehrlich & Raven, 1964). As plants have developed methods for repelling insect pests, so the insects have adapted to these defences. Many species of insect show close associations with genera or species of plants, selectively feeding on a group of closely related species within a genus (Schoonhoven *et al.*, 2005). Others demonstrate a broad host range, feeding on plants in different families but this is rare (Bernays & Graham, 1988). The level of polyphagy varies with order and feeding habit, for example, 54% of British Orthoptera are polyphagous whereas there are very few recorded cases of endophages feeding on more than one host species (Gaston *et al.*, 1992; Schoonhoven *et al.*, 2005).

The feeding strategies of insects on plants can be broadly placed into two descriptive groups; chewers and suckers (Lewinsohn *et al.*, 2005) with notable exceptions being nectar-feeding and gall forming (Leather, 1986). The chewers include species belonging to the orders Orthoptera, Coleoptera, Lepidoptera, Hymenoptera, and Dipteran herbivores. These insects consume solid plant matter using mandibles or other masticating oral structures to aid ingestion (Gullan & Cranston, 2004). The second group; dominated by Hemipteran and Thysanopteran herbivores, use specialised mouthparts to pierce plant tissue and extract fluids. In both groups, there is a large amount of variation around where on the plant architecture the insects feed. Not only does the plant present a three-dimensional choice to the insect when considered at a whole organism level but within the chosen feeding area there may be multiple suitable sites for feeding from which the insect must make a choice that maximises fitness (*e.g.* Awmack & Leather, 2002). The impact of feeding location within the confines of a specific plant organ has been shown to significantly alter reproductive success in some herbivores (Whitham, 1986).

The cues that allow insects to evaluate plant quality are complex with physical, chemical and ecological components.

1.2.2 Plant defences

As a living organism, plants can detect and respond to changes in the environment and their own condition. Contrasting to animals, plants can be thought of as modular, with the ability to sustain loss of substantial portions of their tissue (Salisbury, 1962; Pino *et al.*, 1995). Nonetheless, there is a strong selective pressure to reduce the amount of damage inflicted by herbivory. Almost all plants possess a two-tiered defence strategy combining both constitutive and induced defences (War *et al.*, 2012). *Constitutive defences* are always present, often physical, external components and serve to hamper the actions of the herbivore through inconvenience (Woodman & Fernandes, 1991; van Lenteren *et al.*, 1995) or injury (Quiring *et al.*, 1992). Other constitutive defences are internally expressed such as chemicals that reduce the digestibility of the plant or intercellular silica structures (Liang *et al.*, 2015). *Induced defences*, by comparison, are not present until the plant has suffered attack and often take the form of secondary metabolites (Karban, 2011). Induced defences are initiated in the area of attack, but using signalling chemicals, the reaction is spread to the rest of the plant. The most common primary signalling chemical involved in plant defences against insects is Jasmonic Acid (JA). Initially the signalling chemicals act at the point of release, causing Local Induced Resistance (LIR). Transported by the phloem, they can also effect change on undamaged leaves leading to Systemic Induced Resistance (SIR). As the transport is mediated by the vasculature of the plant, the level to which other leaves respond to herbivory is related to the directness of the vascular connection between them (Jones *et al.*, 1993).

The after-the-fact expression of induced defences can be assumed to be due to a trade-off in costs and benefits. The cost of constitutively expressing the induced response must outweigh any beneficial mitigation in herbivory (Baldwin & Preston, 1999). The toxic nature of the induced defences may be one of the costs associated. Experiments have shown that even in plants that endogenously express the toxic alkaloid nicotine as a defence strategy (*Nicotiana sylvestris* and *N. glauca*) exogenous application of nicotine causes a reduction in photosynthetic capacity and overall lower growth (Baldwin & Callahan, 1993). Other than autotoxicity, previous workers have suggested that the non-recyclable nature of secondary metabolites leads to them acting as a sink for nutrients reducing fitness potential (Baldwin *et al.*, 2001; Heil & Baldwin, 2002). As with many biological trade-offs the relative values of cost and benefit are influenced by biotic and abiotic factors as well as cyclical seasonal changes (Burney *et al.*, 2012). Experiments with soil fertilisation have shown that plants with greater nitrogen availability emit higher levels of Volatile Organic Compounds (VOCs) (Burney *et al.*, 2012; Fernández-Martínez *et al.*, 2018). VOCs are commonly associated with plant stress responses. However, Fernández-Martínez *et al.* (2018) also found that foliar phosphorus levels were negatively correlated with VOC emission. This result is of interest when considering plant-insect interactions as there is an as-yet unexplained link between arbuscular mycorrhyzal fungi, phosphorus, VOC production and aphid host choice (Babikova *et al.*, 2014). Furthermore, the complicating factor of tritrophic interactions is likely to be relevant to many species. An interaction between nutrient availability, plant condition and herbivory has been documented among species of Eucalyptus. In this case nutritional quality was again higher when greater nutrient levels were available (Low *et al.*, 2014). Thus, the level of VOCs produced by plants in response to damage could provide herbivores with relevant information about the quality of the host. That is, high nutrient hosts, able to sustain higher levels of VOC emission, inadvertently signal their status to the organisms the VOC emission is evolved to repel (Low *et al.*, 2014). This may be particularly relevant for plant species that have highly evolved chemical responses that favour toxin-resistant specialist herbivores over non-resistant generalists. For example, in the case of glucosinolate and terpene producing brassica crops host location by herbivores can be mediated by these defence chemicals (Guarino *et al.*, 2018).

This is likely to be of import to those species that have evolved methods of sequestering plant metabolites as a mechanism of self-defence. Given the acute effects that sequestered metabolites can have on predatory and parasitic species, the potential implications for herbivores are substantial (Campbell & Duffey, 1981; Barbosa *et al.*, 1991; J. Ode *et al.*, 2004; Leitner *et al.*, 2005). Thus, for sequestering insect species, there may well be an incentive to pursue the more toxin-rich individuals in a population.

Insect feeding causes mechanical damage to plant tissues, causing biochemical changes to cells within the tissue, in turn stimulating remaining cells to alter transcriptional budgets and produce increased quantities of intercellular signalling chemicals. The three most significant chemicals involved in plant defence are Jasmonic Acid (JA), Salicylic Acid (SA) and Ethylene (ET). Broadly, JA is primarily involved in herbivore defence, SA in pathogen resistance and ET providing a modulating role. In addition to mechanical damage, plants respond to specific chemicals that are associated with insect feeding (Pare *et al.*, 2005). Grouped under the umbrella term elicitors, these chemicals interact with specific receptors within plant cells causing metabolic chain reactions that alter the biochemistry of the whole plant at the scale of hours. While it is known that plants can detect elicitors, and that mechanical damage in the absence of them causes differing responses, a level of uncertainty around the exact biochemical pathways and results remains.

Considering the fitness cost to the insect of plant defences (Baldwin & Preston, 1999; Walling, 2000; Lou *et al.*, 2005a; Wu & Baldwin, 2010) there must be an equally significant benefit to retaining elicitors in the saliva. The first described elicitor was volicitin, a fatty acid Amino-acid Conjugate (FAC) purified from the oral secretions of the lepidopteran pest *M. sexta*. This was demonstrated in a series of papers to be a causal agent in the herbivore-specific transcription changes seen in its native host, *Nicotiana attenuata*. Application of volicitin to wound sites lead to alteration of transcriptional patterns consistent with attack by *M. sexta* (Halitschke *et al.*, 2000). Studies have now shown that the FACs are important to lepidopteran larvae for nitrogen assimilation. *Spodoptera exigua* larvae fed on an artificial diet containing labelled nitrogen showed significant increases in nitrogen assimilation (as glutamine) when the diet also contained additional labelled fatty acids (notably glutamic and linolenic acid, Yoshinaga *et al.*, 2008). Glutamine is a non-essential amino acid of great importance to most heterotrophs for its role in a variety of crucial biosynthetic pathways (e.g. the Krebs cycle). As such its synthesis and assimilation from the diet is tightly controlled. The catalysing role of FACs in efficient uptake of nitrogen, synthesis and mobilisation of Glutamine give clues as to the retention of apparently deleterious chemicals in oral secretions.

1.2.3 Insect responses to plant volatiles

The interactions between plants and their environment or conspecifics are almost entirely chemically mediated. Arguably, herbivore host location via visual cues (discussed in chapter 1.3 below) and the repulsion of these herbivores via external physical defences (covered briefly in 1.2.2 Plant defences) are not. Very few plants have the ability to "move" in the same way that other organisms can and are therefore reliant on their sophisticated biochemical machinery to respond to challenges posed by biotic and abiotic stress (Baldwin, 2010; Schuman & Baldwin, 2016). It has long been known that a large proportion of the carbon fixed by plants is re-released into the atmosphere in the form of volatile organic chemicals often referred to as Green Leaf Volatiles (GLV). These serve many functions, from plant-plant communication to ozone quenching (Holopainen, 2004).

All animals have chemoreceptors that allow them to perceive chemicals in their environment. Due to small size and the evolution exoskeletons, vision of a high resolving power is limited. An exoskeleton cannot support soft "camera style" eyes of the kind seen in vertebrates and cephalopods as these cannot be constructed from the hard inflexible chitin of the insect exoskeleton. As such compound eyes of individual facets with hard lenses of chitin have been selected for. In compound eyes, resolving power increases with the number of facets. Due to size constraints arising from an overall small body size, increasing the number of facets often results in smaller facets which in turn limits their ability to take in light through aperture reduction. In order to increase resolving power while retaining reasonable light sensitivity, a large number of large facets would be required. While evolution has selected for this strategy in some insects, (notably the Odonata) the resulting increase in the size of the eyes would not benefit the majority of insects. Consequently, insects are highly attuned to plant volatiles and utilise them to great effect. Conversely, many plants utilise the sensitivity of insects to volatiles for their own advantage. Volatiles can, therefore, be assigned to different semiochemical categorisations (kairomone, allomone, synomone, etc) dependent on the trophic level of the receiver. While plants always give off GLV, some volatiles, termed herbivore induced plant volatiles (HIPV), are only produced in response to herbivory or mechanical damage. As with SIR, the plant responds to elicitors in the saliva of the insect, leading to upregulation of metabolic pathways and a change in the proportions of chemicals within the volatile mix (Dicke *et al.*, 2009).

Volatile mediated plant-herbivore interactions can be direct or indirect. Direct interactions occur when volatiles are detected by the herbivore and often alter aspects of behaviour relating to feeding or host acceptance (Dicke *et al.*, 2009; St Onge *et al.*, 2018; Vuts *et al.*, 2018). Direct HIPV such as (*Z*)-jasmone have been demonstrated to be repellent to multiple species of aphid (Birkett *et al.*, 2000). The repellence caused by (*Z*)-jasmone may be direct, due to its toxicity or noxious qualities (Becker *et al.*, 2015). However, (*Z*)-jasmone also has a phytohormone role and can cause upregulation of chemical defence genes in plants (Bruce *et al.*, 2003; Moraes *et al.*, 2008). It may be that herbivorous insects simply avoid plants with greater emission of (*Z*)-jasmone or another HIPV due to the increased levels of defence chemicals in the plant tissue. Some HIPVs that act as repellent to generalist feeders may have an attractive quality to specialist herbivores. Hop plants (*Humulus lupulus*) treated with (*Z*)-jasmone were more attractive to *Phorodon humuli* (Hemiptera: Aphididae) spring migrants (Pope *et al.*, 2007). This illustrates the complexity of plant volatile systems with specialist herbivores eavesdropping on the volatiles plants use for defence. For some insects the presence of HIPV modulates the attractiveness of the sex pheromones showing just how close the interaction between herbivores and plant volatiles can be (Landolt & Phillips, 1997).

Plants use HIPV indirectly to alter herbivore pressure through attraction of predatory and parasitic species. This is a well-documented phenomenon that has been shown to have a substantial impact on ecological interactions both in crops and in the natural environment. The ability of plants to discriminate between different herbivores and respond with distinct volatile blends has been documented in numerous plant species. Discrimination is frequently via the elicitors in saliva previously described in Plant defences1.2.2, however other methods are known. This allows specific parasitoids or monophagous predators to fine tune their host searching to maximise fitness. The mutually beneficial interactions between plants and a third, carnivorous trophic level mediated by HIPV are complex, with the herbivore attempting to avoid detection by both the plant and the carnivore. For polyphagous carnivores the ability to learn from previous exposure to infested host plants and prey items will be advantageous if the host plant has complex macrostructure or the prey item has defensive behaviours (Ardanuy *et al.*, 2016). Reduction in prey handling time or increased attentiveness to previously encountered hosts could lead to greater fitness for foraging carnivores. Carnivorous insects can detect and respond to the volatiles that indicate the presence of a desirable prey item (Gebreziher & Nakamuta, 2016). The evolutionary pressure to accurately locate relevant herbivores is much greater for parasitoids than predators as it more directly impacts fitness outcomes for the individual. It has been documented that a fourth trophic level, hyperparasitoids, are able to distinguish between plants under attack from parasitised prey compared to unparasitised prey (Cusumano *et al.*, 2019). These interactions appear to be mediated by changes in the saliva content of parasitised hosts (Chapter 5, Zhu, 2015).

1.3 Insect colour vision

Most insects have some degree of vision. For many herbivorous insects, host location uses both chemosensory and visual cues (Bruce & Pickett, 2011; Tsuji & Coe, 2014). Both of these traits have been exploited by pest control strategies, with baited lures and coloured sticky traps among commonly used methods (Vick *et al.*, 1990). It is generally thought that insects use airborne olfactory cues to locate hosts at a distance, visual over medium range and a combination of the two for short range location. Host or prey evaluation may also include the use of contact cues. Contact cues may be thought of as non-volatile olfactory or taste cues. The cues used are often influenced by the feeding guild or host type of the insect in consideration. Floral resources often produce specific volatiles for the attraction of pollinators, which floral foragers utilise to locate patchy resources. A great many flowers enhance their attractiveness through high contrast areas of UV reflective pigment that are thought to act as guides for foraging insects (Kevan *et al.*, 1996). The benefit from this attraction and the production of floral volatiles is predominantly mutual, though nectar robbing is known.

Any form of wavelength discrimination (a key factor of colour vision) requires there to be more than one photoreceptor cell type of differing sensitivities. Insect visual pigments are largely similar across orders, most insects possess a trichromatic system of blue, green, UV (Briscoe & Chittka, 2001). There are some exceptions to this rule, with as many as 15 known in the tropical butterfly *Graphium sarpedon nipponum* (Chen *et al.*, 2016a). As with many vertebrates, it is thought that this system acts in the neural opposition model with stimulation of one class of photopigment (e.g. green) acting to inhibit the firing potential of another (e.g. blue) (Takemura *et al.*, 2005; Skorupski & Chittka, 2011). In this way, it is thought that insects have both colour vision as well as wavelength specific behaviours. Colour vision, as opposed to wavelength specific behaviour is the process of creating an internal representation of the external environment that is sensitive to changes in chromaticity, contrast, and intensity (Song & Lee, 2018). This internal model will be interpreted in such a way that more complex evaluation, decision making, and learning (Chen *et al.*, 2016a) are possible . By contrast wavelength specific behaviours are simple actions undertaken in response to the presence of a narrow band of adjacent wavelengths. The most notable of these is the settling response of herbivorous insects to green wavelengths (Song & Lee, 2018). Wavelength specific behaviours often show common characteristics in that a stronger response is seen to brighter light of the relevant wavelength (Booth *et al.*, 2004). It is also common for the response to be diminished or altered if a competing wavelength is present too. This is clearly illustrated in the response of many herbivorous insects to yellow traps. While previous there were suggestions that yellow attraction was adaptive due to it being associated with a higher leaf nitrogen content (Mooney & Gulmon, 1982; Moericke, 2009), it is now generally accepted that this is not the case. The attractiveness of yellow is thought to be a factor of its relatively high level of green light reflectance coupled with a lower relative blue fraction leading to a supernormal foliage stimulus (Döring & Chittka, 2007). This illustrates that it is possible to utilise limitations in the insect visual system to their detriment. Though commonly engendering a more complex response than green or blue light, the same manipulation is used in UV light traps where insects are lured onto high voltage wires (Sliney *et al.*, 2016). The rapid diversification of LED colours available following their invention in the 1960s has opened new possibilities for fine tuning the wavelengths available in cropped environments. Unlike previous lighting technologies, LEDs are monochromatic. This means that any LED that appears white is either a phosphorescent coated blue LED (Nakamura & Fasol, 1997), or a combination of red, blue, green diodes at the same intensity (Yam & Hassan, 2005). The inherent monochromaticity of the diodes allows tests to be done with specific regions of visible light far more easily than previously, where coloured filters or dispersing prisms were required. It should be noted however, that LEDS have discrete peak wavelengths, and although a great proportion of the visible spectrum is represented, there are gaps.

Plants rely on light to produce simple carbohydrates. From these sugars, many other synthetic reactions are possible and plant life is sustained. With the general assumption that more light is better, commercial glasshouse plant production has a driven towards larger panes of increasingly chemically sophisticated glass and reduced metal framework (Heuvelinka *et al.*, 1995). Further enhancements in the availability of light within the structure has relied on the use of electric lighting, historically with high pressure sodium lamps (Blom & Ingratta, 1984). A current area of interest in glasshouses is enrichment of plant growth environments with LED lighting rigs (Massa *et al.*, 2008; Samuoliene *et al.*, 2012; He *et al.*, 2019). Modern understanding of photosynthetic pathways indicates that LEDs with emission spectra in the red (630–740 nm) and blue (450–485 nm) regions of visible light will provide the most significant benefits in terms of photosynthetic enhancement. There is evidence, however, that specific colours of light act as cues that lead to changes in plant growth patterns (Cosgrove, 1981; Mølmann *et al.*, 2006) and transcription levels (Sellaro *et al.*, 2009; Tang *et al.*, 2019). Evidence suggests that for select crops or traits, growers may be able to use light to manipulate a crop such that specific desirable outcomes are emphasised (Ali *et al.*, 2019), or undesireable outcomes minimised (Kitayama *et al.*, 2019). In the age of CRISPR gene editing, the ability to manipulate the biochemistry of crops may seem already solved, however it is important to remember the consumer perception of these technologies and the potential for backlash.

By contrast, LED lighting is more cost-effective to run, can be spectrum specific, and is unlikely to cause concern among consumers.

The assumption that yellow traps are the most effective traps for all species has been questioned previously, with evidence indicating that some species are more attracted to other wavelengths. It is now common to see blue sticky traps used for western flower thrips (*Frankliniella occidentalis*) (Mateus & Mexia, 1995) and responses to other wavelengths of light have been documented in weevils (Wen *et al.*, 2018), blunt-nosed leafhopper (Rodriguez-Saona *et al.*, 2012), *Drosophila suzukii* (Kirkpatrick *et al.*, 2016; Rice *et al.*, 2016). These preferences reflect the ecology of the species, providing individuals a method for locating relevant resources. This is particularly true for *D. suzukii*, where the most effective traps are red and spherical, most closely mimicking the ripe fruits that the fly oviposits in (Kirkpatrick *et al.*, 2018). It should be noted that in that study, black spheres and red spheres showed similar responses. This illustrates a limitation in the insect visual system, in that, colours far beyond the green region of visible light (500-565nm) are largely indistinguishable from black. This can be utilised by researchers looking to investigate behaviour of insects under dark conditions where infra-red cameras can be used to record insect behaviour.

The use of sticky traps for control of pest species can pose a risk to beneficial insects, as the colours used have broad spectrum appeal to insects. In particular there are many recorded cases of improted pollinator species being caught on sticky traps introduced for pest control (James & Pitts-Singer, 2008). The same is true of biocontrol agents, which can also be detected on sticky traps. There is evidence to suggest that this by-catch of sticky traps is insufficient to alter the level of control afforded by biocontrols (Hoelmer & Simmons, 2008), however these studies used a density of traps more in keeping with pest monitoring than mass trapping for population control. Consequently, it may be that the higher density of traps or use of roller traps for mass capture of pests may lead to a reduction in the efficacy of biocontrol agents.

1.4 Leafhoppers

Leafhoppers are herbivorous hemipterans in the family Cicadellidae (Le Quesne & Payne, 1981). Their common name refers to their well -developed saltatorial hind legs. As with all hemiptera, feeding is via a stylet mouth that is used to pierce food items and ingest fluids (Gullan & Cranston, 2004). Leafhopper feed in a variety of locations on host plants; some leafhoppers are phloem feeders (Nielsen *et al.*, 1990; Lamp *et al.*, 2004), others xylem (Biedermann, 2003). Many leafhoppers feed on the stem of host plants, which can cause serious problems by disrupting the ability of the vascular system to transport metabolites through the plant. There is a connection between leafhoppers that feed in this manner, and the physiological condition known as hopperburn. Initially suspected to be pathogenic, it was later elucidated that hopperburn was entirely mediated by internal chemistry within the plant. This condition is non-contagious and is the result of the mechanics of leafhopper feeding as well as toxic chemicals in the saliva leading to a metabolic cascade throughout the plant. Hopperburn can be extremely serious and lead to total crop failure (Graham, 1978; Schoonhoven & Cardona, 1980). Hopperburn is a substantial risk to rice growers across most of Asia (Wilson & Claridge, 1991), bean crops in South America (Graham, 1978; Backus & Hunter, 1989; Wilson & Claridge, 1991), and Alfalfa crops in the USA where costs in a single year can be in the tens of millions of dollars (Manglitz & Ratcliffe, 1988) . The method by which hopperburn is caused seems to be restricted to certain species of leafhopper and relates to the feeding method of these species. A subset of the Cicadellidae feed on the cells of the leaves of host plants. These species are largely confined to the genus *Empoasca* and feed through a destructive mechanism known as pierce and flush. This feeding strategy causes damage over substantial areas of foliage known as stippling. Electropenetrogram data indicate that leafhopper feeding in this method rapidly insert and retract their mouthparts from leaf tissues. The lacerated cells are flushed with very watery saliva and the resulting suspension of cellular contents is taken up (Backus & Hunter, 1989; Hunter & Backus, 1989). This introduces a great quantity of the saliva to the plant cells and, through rupture, increases the surface area on which it will be detected by the plant.

Leafhoppers are also vectors for a number of plant diseases that are increasing in significance. Of greatest concern is *Xylella fastidiosa*, a bacterial infection of a number of economically important crops across much of the world (Sisterson, 2012; Del Cid *et al.*, 2018). Though very few of the 15,000 species of Cicadellidae species vector plant diseases, the risk posed by infection is substantial (Nault & Ammar, 1989). The Cicadellidae are capable of vectoring both circulative (virus that do not replicate in the insect body) as well as propagative (viruses that are capable of replication in vector cells) virus species. Within the two types of virus outlined (circulative & propagative) persistent, semi-persistent and nonpersistent species are known. Of these, the propagative persistent viruses are most significant as pathogens due to their long (potentially indefinite) persistence in the host. For highly mobile insects like leafhopper, the risk to growers posed by vectored plant diseases is substantial. It should be noted, however that there are reports that these persistent propagative viruses can cause negative outcomes to the host (Chen *et al.*, 2016b). This risk may be further exacerbated by climate change, which has the potential to alter the susceptibility of the host plant and insect, as well as the range of the insect vectors. The implications of climate change are not known, with some evidence suggesting that increased leaf temperatures will lead to a more effective immune response by infected plants (Szittya *et al.*, 2003). As the dominant hemipteran vector group, much research has focused on aphid vector species (Canto *et al.*, 2009). Within this group it has been commented that a far greater risk is posed by the alate forms due to their ability to move from plant to plant more easily (Canto *et al.*, 2009). As all leafhopper species are winged as adults, and increasing temperatures will allow greater mobility (Walters & Dixon, 1983) and potential range increases, this may lead to further spread of virus species into new areas. Further, once a virus enters a new area, there may be extant species capable of acting as a novel vector. While this is a rare event, there have been recorded instances of this occurring in significant insect vectored viruses (Meiswinkel *et al.*, 2007).

1.4.1 Hauptidia *maroccana*

Genus *Hauptidia* has several defunct synonyms from different naming authorities in two separate genera, (*Zygina* and *Erythroneura*) reflecting the cosmopolitan distribution of the species and sporadic pest status. *Hauptidia maroccana* (Melichar) is a poorly studied, sporadic pest in glasshouse cultivation. Occurring natively in the UK, it is unusual among the British Typhlocybinae in feeding on a wide range of wild and cultivated plants (Le Quesne & Payne, 1981). *Hauptidia maroccana* feeds on living plant tissues, predominantly on the underside of the leaf and is not recorded as attacking the petiole or stem (Fox-Wilson, 1938). The Typhlocybinae subfamily, have been recorded exhibiting multiple feeding behaviours targeting different plant tissues, though the predominant behaviour is lacerate-and-flush feeding on the mesophyll (Hunter & Backus, 1989). Many leafhoppers are vectors for a number of viruses, and *H. maroccana* has been demonstrated to be a vector of viruses in tomato crops including Tomato pseudocurly top virus (TPCTV) (Maisonneuve *et al.*, 1995; Hogenhout *et al.*, 2008). However, no such formal literature exists for diseases of Capsicum, indicative of the relative lack of study of this insect.

Adult *H. maroccana* are approximately 3mm long, pale and narrow bodied. Resembling many of the UK Typhlocybinae, the head is dominated by large dark eyes (MacGill, 1932). With a cosmopolitan feeding range and possessing strong flight capabilities, *H. maroccana* has been described as the most important of leafhopper pests (Copland & Soeprapto, 1985). Eggs are laid singly into secondary leaf veins and hatch after 17 days at 18°C (Copland & Soeprapto, 1985). Incubation duration decreases with increasing temperature up to an optimum temperature of approximately 25°C (Choudhury, 2002). Host plant also influences development time, with data indicating that at 21 °c eggs reared on tomato will hatch 3 days earlier than those laid in cucumber (Choudhury, 2002). However, this difference is seen to disappear at the thermal optimum (Choudhury, 2002). The same study also indicated that host plant had an effect on the lower developmental threshold (LDT: the minimum temperature at which the insect will continue to develop). Data indicates that eggs laid in *Primula vulgaris* leaves showed the lowest LDT and the longest development time (Choudhury, 2002). By contrast leafhoppers reared on *Capsicum anuum* plants had the highest LDT and shortest development time. In the previous study, *H. maroccana* was mass-cultured on a variety of plant species with separate cultures for each plant species. Thus, the difference in developmental time and LDT seen for each plant species was attributed to the nutritional value of each plant; higher nutritional content results in reduced cold tolerance and shorter development time. Choudhury (2002) cites two supporting studies on other species for this claim. The first reports the impact of diet and temperature on *Tribolium confusum* (Coleoptera: Tenebrionidae), with results indicating that a high nutrient diet reduces development time and has no significant impact on survival (Lamb & Loschiavo, 1981). The second, by Dixon *et al.* (1982) indicates a similar conclusion for *Aphis fabae* (Hemiptera: Aphididae) but indicates that when given high nutrient food at a high temperature, adult body weight is reduced leading to lowered fecundity. Neither study supports the assertion that higher quality food reduces the cold tolerance of insects. Contrastingly, there are many studies that provide evidence that higher diet quality, in particular the presence of key amino acids, increase the ability of insects to survive cold stress (Andersen *et al.*, 2010; Colinet & Renault, 2014; Li *et al.*, 2014; Bayliak *et al.*, 2016).

Following a single mating, female *H. maroccana* remain fertile for the duration of their adult life and do not mate again (Copland & Soeprapto, 1985).Other species of leafhopper are known to mate multiple times and to seek multiple matings in the event of poor copulatory performance of the male (Bailey & Nuhardiyati, 2005). Research has indicated that for species capable of multiple matings, there is a potential fitness tradeoff, with multiple mated females laying fewer eggs per day and having reduced lifespans (Nielson & Toles, 1968). In this way, there may be a selective advantage to *H. maroccana* pursuing only one mating event. There are no reports of mating rituals, or selective behaviours for *H. maroccana* (Copland & Soeprapto, 1985). This contrasts with many other members of the Cicadellidae where highly sophisticated mating behaviours have been documented. Notable among these are the use of substrate-borne vibration cues which have been documented across multiple genera (Ichikawa, 1976; Mazzoni *et al.*, 2009; Derlink *et al.*, 2018; Krugner & Gordon, 2018)

1.4.2 Pest status and controls

Hauptidia maroccana is a sporadic pest, with growers reporting years with no pest pressure and others with high incidence of pest damage (N. ward, pers comm). Closely related species are seen to be the primary vectors of a number of significant crop diseases in Europe (Riolo *et al.*, 2006) and *H. maroccana* itself has been shown to be capable of vectoring phytoplasmas (Maisonneuve *et al.*, 1995), though this is not widely reported in crops. Given the sporadic nature of the pest occurrence and lack of regular vector action, it is hard to support the claim that *H. maroccana* is the most economically important leafhopper pest.

Control of *H. maroccana* lacks specificity. As yet there is no specific parasitoid or predator of this species commercially available. Without this, attempts have been made to find if not a specific biological control agent, at least an oligovorous or leafhopper specific control. Previously, a mymarid wasp was researched (*Anagrus atomus*, L.) and despite promising initial results, scaling up production and distribution was unsuccessful. Introduction of *A. atomus* into experimental glasshouse conditions indicated that reductions of leafhopper populations by 54% were possible. Unfortunately, the *A. atomus* was never successfully commercialised (Jervis & Kidd, 1996). Further detail on the limitations for biological control is discussed below in section 1.5.2. Wild populations of related leafhoppers are subject to both predation and parasitism and substantial effort has been expended in determining the potential suitability for commercialisation. The organisms so far most studied for this purpose have been Mymarid wasps (see Family Mymaridae, below). Other commonly noted natural enemies include members of the Trichogrammatidae, Pipunculidae and Dynidae (Freytag, 1985).

1.5 Family Mymaridae

Mymarid wasps are small, solitary obligate endoparasitoids. Cosmopolitan in distribution, the family is typical of the insects with a far greater diversity at low latitudes than in temperate climates (Gauld *et al.*, 1992; Basset *et al.*, 2012). They are easily collected in natural settings by pan or Malaise trap, and can represent up to 10% of sampled Chalcidoidea (Chiappini & Huber, 2008). Their common name, fairy flies, refers to their (sometimes extreme) small size and delicate, fringed wings. The smallest known insect is a species of mymarid, *Dicopomorpha echmepterygis*, a parasite of Psocoptera eggs. Adult males are around 139μm, smaller than some protozoa (Mockford, 1997). Though this is an extreme example, many of the mymaridae are less than two millimeters; which makes them challenging to identify. Resultingly there have been many taxonomic revisions, though for European species the most recent was conducted in 1996 (Chiappini *et al.*, 1996). Within the family there are around 1400 species comprising 100 genera. Subfamilies and tribes are derived from the number of tarsal segments or metasomal attachment. This has led to confusion resulting in the proposal of a third, simpler method based on male genital morphology (Chiappini & Huber, 2008). Though gloablly distributed, species are unequally dispersed within the genera with over 50% of known species placed within four genera; *Anagrus*, *Anaphes*, *Gonatocerus* and *Polynema*.

Fossil specimens of Mymaridae are known from the Upper Albian age (around 97-110mya) in Burmese and Canadian amber (Yoshimoto, 1975; Poinar & Huber, 2011) making them the oldest known family in Chalcidoidea. Mymaridae show a high level of specialism in hosts across their range with the majority of species with known hosts attacking eggs of phytophagous Hemipteran, in particular the Auchenorrhyncha. This host range has been suggested to be an artefact of study bias rather than an actual biological trend (Chiappini & Huber, 2008). It is true that much of the literature on the mymarids relates to their agricultural or medical uses. As less than fifteen species have been successfully employed as biocontrol agents (BCAs) there are a great many species for which the basic biology is unknown. Those that are known exhibit a high level of diversity in life histories with hosts from multiple insect orders recorded, though there are a substantially higher number of hosts recorded from the Hemimetabola. A notable example of the diversity of the Mymaridae can be seen in the genus *Caraphractus* which parasitises eggs of diving beetles (Coleoptera; Dytiscidae). These highly specialised insects use their wings as "oars" to swim through the water column in search of suitable hosts (Jackson, 2009).

Mymaridae complete larval development within the host egg either gregariously or in solitude. In some *Anagrus* species, the larvae of Mymaridae can be separated into two types of instars that vary in motility. Between genera, there are differences in where the immobile stage occurs; for species of genus *Anagrus* it is the second instar that is characterised by high activity levels. By contrast, larvae from the genus *Anaphes* show almost complete immobility in the second stage.

In natural ecosystems mymarids are able to exert a substantial level of control on host species however, attempts to use them as biological controls have proved challenging, especially as classical control agents in unprotected cropping environments (Huber, 1986). An example of the challenges presented when using Mymaridae as a BCA is given by the use of the North American mymarid *Anagrus armatus nigriventis* Girault as a control agent of *Typhlocybia froggatti* Baker in cropped apples. In New Zealand, where *A. armatus* is presumed to have been accidentally introduced it provides no control of *T. froggatti* (Huber, 1986), however, in Tasmania it is able to provide satisfactory control of the same pest (Miller, 1947). Following success in Tasmania, *A. armatus* was introduced to mainland Australia where it again failed to provide any benefit to growers (Clausen, 1978). Speculatively, the reasons for the lack of success in mainland Australia and New Zealand may in part be due to the presence of competing species in what can be a very challenging environment (Chiappini & Huber, 2008). Tasmania is a far smaller island, as a result, the potential for closer relationships between trophic levels is higher. As a result, *A. armatus* may have been to parasitise the non-native *T. froggatti* due to competition limiting its ability to utilise native leafhoppers as hosts.

1.5.1 Genus *Anagrus*

Anagrus is a relatively diverse genus within the family with around 60 species recorded from three subgenera: *Anagrus*, *Paranagrus* and *Anagrella*. *Anagrus* species are all small, with most species under 1.5 mm (Chiappini, 2008). Globally distributed, a number of *Anagrus* species are of economic importance, parasitising agricultural pests. Of particular importance is the species *Anagrus nilaparvatae* which uses the rice brown planthopper, *Nilaparvata lugens*, as a host. *N. lugens* is a significant pest that shows resistance to insecticides and acts as a vector of a number of severe diseases of rice (Ou, 1985; Liu *et al.*, 2005).

The bauplan of *Anagrus* is generally conserved within the genus. Adults can be separated based on morphological traits such as tarsal number, setae, and copulatory structures. Identification can be challenging with multiple misidentifications thoughout the published literature (Chiappini *et al.*, 1996; Triapitsyn, 1998). A comparative study on the male copulatory organs of a number of *Anagrus* species indicated that although it is possible to separate males based on genitalia to species level, it is far more accurate when considering species groups (Chiappini & Mazzoni, 2000). In sexual species, mating is very brief and takes place immediately after emergence from the host, with little to no courting behaviour (Chiappini & Mazzoni, 2000). As such, species separation is via chemical cues and the “lock-and-key” hypothesis with sufficient difference in the copulatory appendages that interspecies intercourse is impossible.

Anagrus species show a narrow host range with most parasitising eggs of Odonata or Hemiptera (Huber, 1986). Almost all species parasitise eggs laid into plant tissues, with many ovipositing through the initial oviposition scar. Among the known hosts, there are many records of *Anagrus* species attacking leaf and planthoppers associated with riparian *Carex* species (Huber, 1986; Chiappini & Huber, 2008). Why this is remains to be seen, but may be as a result of niche separation.

Anagrus is well suited for use as an ecological model of host-parasitoid interactions. In particular, experiments on dispersal, aggregation, superparasitism and host location have been carried out. Experiments on dispersal of *Anagrus* species has been facilitated by species occupying intertidal mudflats with multiple discrete islets and oyster bars. These spatially separated stands undergo seasonal extinction and recolonisation of *Anagrus delicatus* (=*Anagrus sophiae*) and its hemipteran host *Proskelisia marginata*. Studies of these haloseral communities have shown that wasps lay greater numbers of eggs when they undertake dispersal of more than 10 metres (Cronin & Strong, 1999). It should be noted that the increase is not as a result of increased ovariole number but due to increased reproductive effort resulting in a greater percentage of eggs being laid (Cronin & Strong, 1999). This contrasts to other insects, where dispersal ability is “traded off” against reproductive ability (Walters & Dixon, 1983). Ovipositing females have been reported to under-utilise available hosts within a patch, rejecting suitable hosts and dispersing even though fewer than 10% of suitable hosts were parasitised (Cronin & Strong, 1993a). The lack of oviposition was not due to inability to locate hosts, as more probes than ovipositions were recorded and *Anagrus* are known to probe only when eggs are present (Cronin & Strong, 1993b). The low rate of parasitism per patch is thought to be a mechanism by which the wasps can avoid larval mortality due to host-induced leaf senescence (Cronin & Strong, 1993a).

Other species of hymenopteran parasitoid are able to detect and respond to variables such as host density, host size, eggs already within the host, and conspecific density in order to maximise fitness (Wylie, 1966). The cues that result in a host being selected or rejected are not known, however *Anagrus* species, unlike some other parasitoids, show no aversion to superparasitism (Cronin & Strong, 1993b; Ivens *et al.*, 2009). In observed cases of superparasitism, only one adult *Anagrus* emerges from the host. This implies that either *Anagrus* species cannot detect the presence of the initial larvae or that there is a fitness advantage to superparasitism. Given the rate of rejection of hosts by *Anagrus*, it can be assumed that the ovipositior posesses sensory cells that allow the parasitoid to discriminate between hosts. It can be extrapolated that the presence of a conspecific egg or larvae would be detected by the same mechanisms. As a proovigenic species, *Anagrus* females are limited by their ovariole number with no further vitellogenesis or egg maturation following eclosion (Cronin & Strong, 1990; Virla, 2001; Chiappini, 2008). Thus, eggs represent a particularly valuable "currency" that must be spent wisely to maximise reproductive success. These aspects of the ovipositing behaviour of *Anagrus* seem incompatible; the ability to make decisions on host quality and the limitation of egg number seem at odds with the lack of aversion to superparasitism. Studies into the behaviour and competitiveness of superparasitic larvae within host eggs could reveal the causes of what, at first, appears to be evolutionarily sub-optimal behaviour.

1.5.2 Anagrus atomus

1.5.2.1 Biology

Anagrus (Anagrus) atomus (L.) Haliday is a parasitoid wasp within the family Mymaridae (Hymenoptera: Chalcioidea). As a member of a large, poorly studied family, there is a surprising amount known about the biology. Many studies revolve around the use of this species as a biological control agent and do not describe niche or microhabitat of this widely distributed species (Huber, 1986; Triapitsyn, 2002). An idiobiont egg parasite *A. atomus* primarily parasitises Auchenorrhyncha. Thirty five hosts are known to species level (Appendix 1). Though the majority of the known hosts are Hemimetabolous, there are reports of *A. atomus* parasitising Hymenopteran and Lepidopteran species. There is, however, a degree of uncertainty surrounding the veracity of these reports (Chiappini, 2008).

1.5.2.2 As a biocontrol agent

The use of parasitoids as biocontrol agents has been largely successful, representing approximately 50% of all commercialised biocontrol agents (van Lenteren, 2012). Many of these parasitoids are from the same superfamily as *A. atomus* and have similar life history traits (van Lenteren, 2012). Despite this, the uptake of *Anagrus* species as BCAs has been low. This may partly be due to the fact that *Anagrus* species parasitise hosts within the plant tissue. This makes them harder to mass produce compared to a parasitoid that uses an exophagous pest host. Parasitoids of endophagous pests present a challenge in that they must either be delivered to the grower in severed plant tissue, which runs the risk of fungal growth and desiccation, or excised from the plant matter without harm in turn driving up costs. Other parasitoids utilising endophage hosts have been successfully commercialised however, with two examples (*Dacnusa sibirica* and *Diglyphis isaea*) falling in van Lenteren's list of most important biocontrol agents (2012).

Anagrus species have been utilised in conservation, innoculative and classical biocontrol strategies (Miller, 1947; Huber, 1986; Chiappini *et al.*, 2004) however *A. atomus* has predominantly been used in glasshouse settings where the predominant strategy is innoculative/augmentative releases (Choudhury, 2002). Though a.atomus has primarily been used to control the glasshouse leafhopper, *H. maroccana*, and green leafhopper, *Cicadella viridis*, there is evidence that it is able to provide control of other species, eg. *Eupteryx melissae*. This is, however, suggested to be as a result of host specialisation and may be related to the existence separate biotypes or cryptic species within a species group.

The suitability of *Angrus* as a biocontrol agent will in part depend on it's compatibility with other extant control strategies, chemical or otherwise. Studies have been conducted on the compatibility of *Anagrus* species with current controls; these are summarised in Table 1.1 below.

Table 1.1 Compatibility of Anagrus species with chemical controls .

SPECIES	CONTROL	COMPATIBILITY	RATE	FIELD/BIOASSAY	REFERENCE
Anagrus spp.	Captan (fungicide)	Sig. increase in adult mortality	Label rate	Bioassay	(Martinson *et al.*, 2001)
Anagrus spp.	Ferbam (fungicide)	Sig. increase in adult mortality	Label rate	Bioassay	(Martinson *et al.*, 2001)
Anagrus spp.	Cu $(OH)_2$+Lime fungicide	Sig. increase in adult mortality	9600 ppm + 4800 ppm	Bioassay	(Martinson *et al.*, 2001)
Anagrus spp.	Sulfur	Sig. increase in adult mortality	960 ppm	Bioassay	(Martinson *et al.*, 2001)
Anagrus spp.	Mancozeb	No sig. difference	Label	Bioassay	(Martinson *et al.*, 2001)
Anagrus spp.	Myclobutanil	No sig. difference	Label	Bioassay	(Martinson *et al.*, 2001)
Anagrus spp.	Carbaryl	100% adult mortality	1200 ppm	Bioassay	(Martinson *et al.*, 2001)
Anagrus spp.	Methyl parathion	100% adult mortality	4800 ppm	Bioassay	(Martinson *et al.*, 2001)

1.6 *Macrolophus* spp.

Macrolophus caliginosus (Heteroptera: Miridae) Wagner is a polyphagous omnivorous bug found in europe. *Macrolophus caliginosus* has been successfully commercialised as a biological control of aphids, spider-mite and whitefly (Hansen *et al.*, 1999). As a generalist predator, however, there are reports of *Macrolophus* species being deployed to control leafhopper and moth species (Neal Ward, Pers. Comm. 2016).

1.6.1 Taxonomic status

Reviewing the literature for *Macrolophus* species and their use in biocontrol strategies has revealed confusion surrounding three species; *M. caliginosus*, *M. pygmaeus* and *M. melanotoma*. In part this uncertainty may be due to the original species description for *M. caliginosus* which not only fails to adequately differentiate between it and a sympatric species *M. pygmaeus*, but claims that in the mediterranean region, the two are frequently confused (Wagner, 1831). The situation is compounded by the fact that the more commonly used *M. caliginosus* is the junior synonym of *M. melanotoma*. The resulting situation is one of uncertainty (Martinez-Cascales *et al.*, 2006). Previous failures of biological control strategies have been attributed to misidentification, highlighting the need for clarification in this area (De Bach, 1964). Attempts to elucidate the taxonomic relationships between the three based on morphology proved challenging due to the absence of distinctive morphological features and high degree of interspecific variation (Josifov, 1992; Goula *et al.*, 1994; Kerzhner & Josifov, 1999). Studies using both morphological characters and DNA have concluded that there was no accurate way to morphologically discriminate between *M. melanotoma* and *M. pygmaeus* (Perdikis *et al.*, 2004; Martinez-Cascales *et al.*, 2006). The most commonly cited distinguishing feature (black marking behind compound eye) provided 92.3% (*melanotoma*) and 55.2% (*pygmaeus*) accuracy in correctly assigning individuals to species (Castañé *et al.*, 2012). Both species have been described as being suitable for use in biocontrol strategies, however, niche separation may cause unexpected variation in efficacy if the wrong species is applied. This is highlighted in the conclusions of work by Martinez-Cascales *et al.* (Martinez-Cascales *et al.*, 2006) where differences in the host plants of the two species were observed suggesting that the two species are sympatric with host preferences allowing for speciation.

1.6.2 As a biocontrol agent

Due to its polyphagy, including *Macrolophus* species in biocontrol programmes must be carefully planned. Utilisation of multiple generalist predators increases the likelyhood of intraguild predation, where predators become prey for other predatory species within a feeding guild (Polis *et al.*, 1989). This is thought to be more likely when the interacting predators are also in competition for food resources (Fantinou *et al.*, 2009). Intraguild predation (IGP) has been documented to be a reason for loss of control of pest species in biological control systems . As well as inteacting with other predators, the addition of generalist predators like *Macrolophus* to systems with specialist parasitoids has been shown to disrupt the level of control of pest species (Snyder & Ives, 2003). There is evidence that *Macrolophus* is able to act as an intraguild predator but that in tested species, this has not resulted in reduction of the overall level of control provided (Malo *et al.*, 2012). Though much research has focused on the potential of *Macrolophus* to act as an intraguild predator, there is evidence that *Macrolophus* may in-turn become intraguild prey for *Dicyphus tamaninii*. It should be noted, however, that there is only one study reporting this (Lucas & Alomar, 2001). In this study by Lucas and Alomar (2001), frozen *Macrolophus* nymphs were presented to *D. tamaninii* nymphs. While *D. tamaninii* was able to reach adulthood when feeding on these nymphs, no experimental work to examine the ability of *D. tamaninii* to predate living nymphs has been undertaken. Given that dead nymphs do not readily defend themselves, nor flee, the relevance of this data for biological control programmes is dubious. By contrast, the potential of *Macrolophus* to act as IGP prey for Adalia bipunctata under artificial conditions and when extraguild prey numbers are low has been demonstrated (Trotta *et al.*, 2015).

Macrolophus facultatively feeds on plant material in the absence of sufficient prey items and can damage crop plants when numbers are high in the absence of prey (Castañé *et al.*, 2011). Although *Macrolophus* species can be separated by molecular techniques, there is a possibility that the initial identification of study species may have been incorrect, leading to potentially misattributed information regarding the potential for crop damage (Goula *et al.*, 1994; Martinez-Cascales *et al.*, 2006). This possibility is of particular importance given that Martinez-Cascales *et al.* (2006) reported that when sampling for the two species, *M. melanotoma* was only found on *Dittricha viscosa* L. (Asteraceae) while *M. pygmaeus* was located on tomato plants. One of the advantages of *Macrolophus* as a biocontrol agent is that it is able to survive on plant matter in the absence of prey. This ensures that in the event of pest invasion into the crop, there is already a population able to provide some level of control. Unfortunately, this ability also poses a risk as populations can increase to the point that the facultative herbivory becomes sufficient to cause damage to the crop (Castañé *et al.*, 2011). Further, the ability of the pest to survive on plant matter and reproduce may represent a problem in areas where it is introduced as a non-native control. One of the major risks posed by biological control is the establishment of a non-native species that has the potential to disrupt native ecosystems (Simberloff & Stiling, 1996; Johnson *et al.*, 2005). While many of the mistakes made by pest managers are from an earlier era, care must still be taken to ensure delicate interspecies relationships are not harmed by the introduction of a novel species. When considering the potential for a species to establish iteself in a new place, key areas to consider are the host range (polyphagy vs, oligo- or monophagy) and the ability to survive year-round in the new location (Hart *et al.*, 2002a; Bürgi & Mills, 2010). In the case of *Macrolophus*, a strong capability for omnivory, well developed flight ability, and documented overwintering potential all contribute to the risks posed to both growers and the wider ecosystems it is introduced into. Existing studies on *Macrolophus caliginosus* in the UK have shown that with access to prey items it is possible for escaped individuals to survive almost an entire winter (Hart *et al.*, 2002b).

1.7 Summary

IPM relies on accurate knowledge of the pest being managed. In the case of *Hauptidia maroccana*, there are many areas in which the knowledge of this pest is lacking. In particular, behavioural ecology within a crop, the susceptibility to generalist predators and efficacy of monitoring traps. Previous attempts to introduce parasitoids into cropped environments have been unsuccessful, and while this may be possible in the future with non *Mymarid* species, the scale of the work needed to identify and evaluate novel candidates is beyond the scope of this project. In order to improve the control of this sporadic species a better understanding of how the pest behaves in a crop and its relationship to other extant biocontrols is neeed. In particular, the ability of generalists such as *Macrolophus* to locate and predate individuals has not been examined. Determining the impact of these control strategies will require sensitive monitoring of populations. Increasing the catch rate and/or selectivity of sticky traps will enable growers to achieve this.

1.8 Aims of the thesis

This thesis aims to answer key questions about the ecology of the pest leafhopper *Hauptidia maroccana* in order that management of this pest be improved. The thesis will examine the currently available strategies for management and monitoring with the intention of determining the efficacy of these as well as any directions for improvement.

1.8.1 Objectives

1. Examine the response of *H. maroccana* to visual cues to optimise the selectivity and/or efficacy of sticky traps.
2. Test the efficacy of generalist predators for control of *H. maroccana*. This will encompass foraging behaviours, feeding rate and prey preference.
3. Test for aggregative behaviours of the pest species to provide evidence for or against the formation of hotspots.

2 Non-yellow traps for glasshouse leafhopper monitoring; evidence for effective alternative colours

2.1 Abstract

Coloured sticky traps are frequently used for monitoring pest levels within cropped environments. While the dominant colour used for this purpose is yellow, there is evidence that for some members of the order Hemiptera, other colours may prove equally or more effective. Multiple pairwise choice tests were completed to compare responses of adult *Hauptidia maroccana (*Cicadellidae, Typhlocybinae) to a range of coloured traps. Nine colours were compared with yellow and to each other, of which one (gold) was seen to perform as well as yellow traps under laboratory conditions. Other colours were ineffective at capturing leafhoppers. Results presented here indicate that there is potential for new, more selective trap colours to be deployed for pest monitoring.

2.2 Introduction

Hauptidia maroccana (Melichar) is a leafhopper in the family Cicadellidae. Many of the Typhlocybinae are specialist feeders on a few related species but *H. maroccana* feeds on a wide range of plants from multiple taxonomic groups (Le Quesne & Payne, 1981). In glasshouse cultivation this species presents a problem in multiple cropping systems, including nightshade fruits (Solanaceae) and Lamiaceae herbs. Though *H. maroccana* is capable of spreading phytoplasma plant viruses, this is not the primary threat to the crops that it infests (Riolo *et al.*, 2006). *Hauptidia maroccana* is typical of the Typhlocybine leafhoppers in employing a variety of feeding strategies but mostly using a pierce and flush strategy that causes characteristic stippled bleaching of leaves and fruits (Ecale & Backus, 1995; DeLay *et al.*, 2012). This feeding method damages groups of cells on the surface rather than targeting the vascular tissue as aphids do. In some cases, leafhopper feeding can cause dramatic chemical cascades within the plant tissues that lead to a non-contagious disease known as hopperburn resulting in senescence of foliage (Backus *et al.*, 2005). While hopperburn is uncommon in nightshade crops (e.g., potato, tomato, capsicum, brinjal) leafhopper damage to these crops can still be economically injurious, through loss of photosynthetic area and direct damage to fruit. Beyond the direct feeding damage resulting in stunting or quality reductions, leafhoppers also produce honeydew which allows the establishment of sooty mould (Moir *et al.*, 2018). Previous research looking for a specific biological control of this pest focused on the mymarid parasitoid *Anagrus atomus* Haliday (Hymenoptera: Mymaridae) (Cooper, 1993; Maisonneuve *et al.*, 1995; Choudhury, 2002). These efforts were hampered by idiosyncrasies in the life history of both pest and parasitoid (Maisonneuve *et al.*, 1995). In particular, commercial supply of *A. atomus* was hampered by a short adult lifespan (Meyerdirk & Moratorio, 1987) and larval development inside leaf tissue (Moratorio & Chiappini, 1995; Chiappini & Huber, 2008). These two aspects combined to make commercial distribution non-viable. Further efforts at biologically controlling leafhopper populations in glasshouse-grown crops have relied on the use of generalist predators such as *Macrolophus* spp. (Miridae; Dicyphini). Despite being capable of predating on multiple pest species, *Macrolophus* displays prey preferences, which, in some circumstances may result in ineffective control (Enkegaard *et al.*, 2001; Bonato *et al.*, 2006; Lykouressis *et al.*, 2007). In combination, these factors have led to leafhoppers being difficult to control in glasshouse environments, particularly organic production systems. In organic, cultivation sprays of natural pyrethrins provide short-term control of leafhopper population levels, (Wing *et al.*, 2000; Jacobson, 2009) however, pyrethrins may disrupt reproduction and population levels of some beneficials (Jacobson, 2009). Pyrethrins rapidly degrade on leaf surfaces (Minello *et al.*, 2005). Consequently, the efficacy of pyrethrins is reliant on monitoring pest populations for invasion and population developments so that sprays are used appropriately. For conventional growers, a common control used against leafhopper pests is the broad spectrum oxadiazine-based insecticide, indoxacarb (Jacobson, 2009). The mode of action of indoxacarb relies on ingestion, so leafhopper eggs, which are laid into leaf veins, are not controlled. Though indoxacarb is not unique in not being effective across all life stages, the sheltered nature of eggs may reduce the control afforded. However, as the development interval of leafhopper eggs is shorter than the persistance interval of indoxacarb this is unlikely to pose a substantial limitation (Liu *et al.*, 2002, 2003). With increasing numbers of cases of insecticide resistance being reported, (Sparks & Nauen, 2015) there is an incentive to not only use chemical controls at an appropriate time, but to check that any chemical controls were effective in reducing pest populations. For both goals, accurate monitoring is essential.

Sticky traps are often used in glasshouse environments as a low input method of monitoring pest presence and biological control establishment within a crop. The most commonly used colour for these traps is yellow, although other colours are used for specific pest species (Lessio & Alma, 2004; Blackmer & Byers, 2009). For example, for monitoring western flower thrips (*Frankliniella occidentalis*, Pergande), blue traps are often recommended (Kirk, 1984; Gillespie & Vernon, 1990). Previous research on insect colour preference has focused on important pollinators, or the most economically important pest species, particularly aphids (Döring, 2014). This has led to a detailed understanding of the influence of the visible spectrum on insect behaviours, but for a relatively narrow group of insects. By contrast, research done on the physiological aspects of insect vision has covered a wider range of species (Briscoe & Chittka, 2001). As a consequence of increases in global movement of goods and people, new pest pressures have arisen (Wong & Hanks, 2016; Kirichenko *et al.*, 2019; Perdereau *et al.*, 2019). Furthermore, previously overlooked pest species are proving problematic as more growers rely on the delicate ecological interactions of biological control (van Lenteren, 2012). Outbreaks of these so-called minor pests can present a problem both in the damage they cause, and also due to the fact that use of broad-spectrum insecticides to control these pests may disrupt previously established biological controls. While this disruptive potential has become less problematic as legislation around pesticide safety has improved substantially, due to the sheer number of crops and pests and potential interactions between trophic levels this risk cannot ever be fully legislated away.

The ability of colour stimuli to trigger specific behaviours has been shown to be present in a range of arthropods (Coombe, 1981; Kolb & Scherer, 1982; Judd *et al.*, 1988; Aarseth & Schram, 1999). A well-documented phenomena is the attractiveness of yellow surfaces to herbiviorous insects (Todd *et al.*, 1990; Tipping *et al.*, 2004; Döring & Chittka, 2007; Straw *et al.*, 2011; Saunders & Luck, 2013; Döring, 2014). This is thought to be a quirk of the opponent model of vision, where specific wavelengths of light stimulate tuned receptor cells in the eye to inhibit the firing of other receptor cells. In this way, yellow surfaces, which reflect proportionally less blue light than green surfaces while also reflecting a high proportion of green light, produce a supernatural stimulus to insects, appearing more attractive than green. Despite the widespread use of yellow traps for insect monitoring, there is evidence that for some Hemiptera, non-yellow colours provide a viable option (Mensah, 1996; Rodriguez-Saona *et al.*, 2012; Farnier *et al.*, 2014). Previous work has indicated a wide variety of colours that attract hemipteran pests, often related to the ecological niche these organisms inhabit (Rodriguez-Saona *et al.*, 2012). This paper reports the results of work testing the relative colour preferences of *Hauptidia maroccana* under laboratory conditions.

2.3 Materials and Methods

2.3.1 Leafhopper cultures

Cultures of *Hauptidia maroccana* were maintained in a fitotron (Weiss Technik, Ebbw Vale, UK)under controlled environmental conditions (20°C, 60%RH, L16:D8) on primrose (*Primula vulgaris*) at Harper Adams University (Shropshire, UK). Primrose plants were used as they allow *H. maroccana* populations to achieve high reproductive rates (Choudhury, 2002) while also being easy to cultivate. Plants were grown individually in 1.5L pots of John Innes No.2 potting compost (Westland Horticulture LTD., County Tyrone, Northern Ireland)

2.3.2 Sticky traps

Custom traps were compared with yellow Easistik traps (Fargro, Arundel, UK). Easistik traps were used as the manufacturer claims that they are effective at trapping leafhoppers. For each test, traps were cut to match the dimensions of the custom traps, with measurements of 100 x 150 mm.

2.3.3 Custom traps

Custom traps were made from 160 gsm A4 dyed paper card (Papeteries De Clairefontaine, Étival-Clairefontaine, France). Coloured card was used as a simple way of testing a wide range of colours in a cost effective and standardised way. To prevent changes in colour following the glue layer being added, the card was laminated with 150 µm office laminating plastic (Fellowes, Itasca, Illinois, United States). Paper card was quartered, producing rectangles of 105 x 148 mm. Seven colours of card were used; Intensive Red, Intensive Blue, Black, Intensive green (Lt Green), Forest green (Dk Green), Nasturtium (Orange) and White. After lamination, non-drying insect glue (Oecotak A5, Oecos, Hertfordshire, UK) was applied evenly to a thickness less than a millimetre with a vinyl roller.

2.3.4 Gold traps

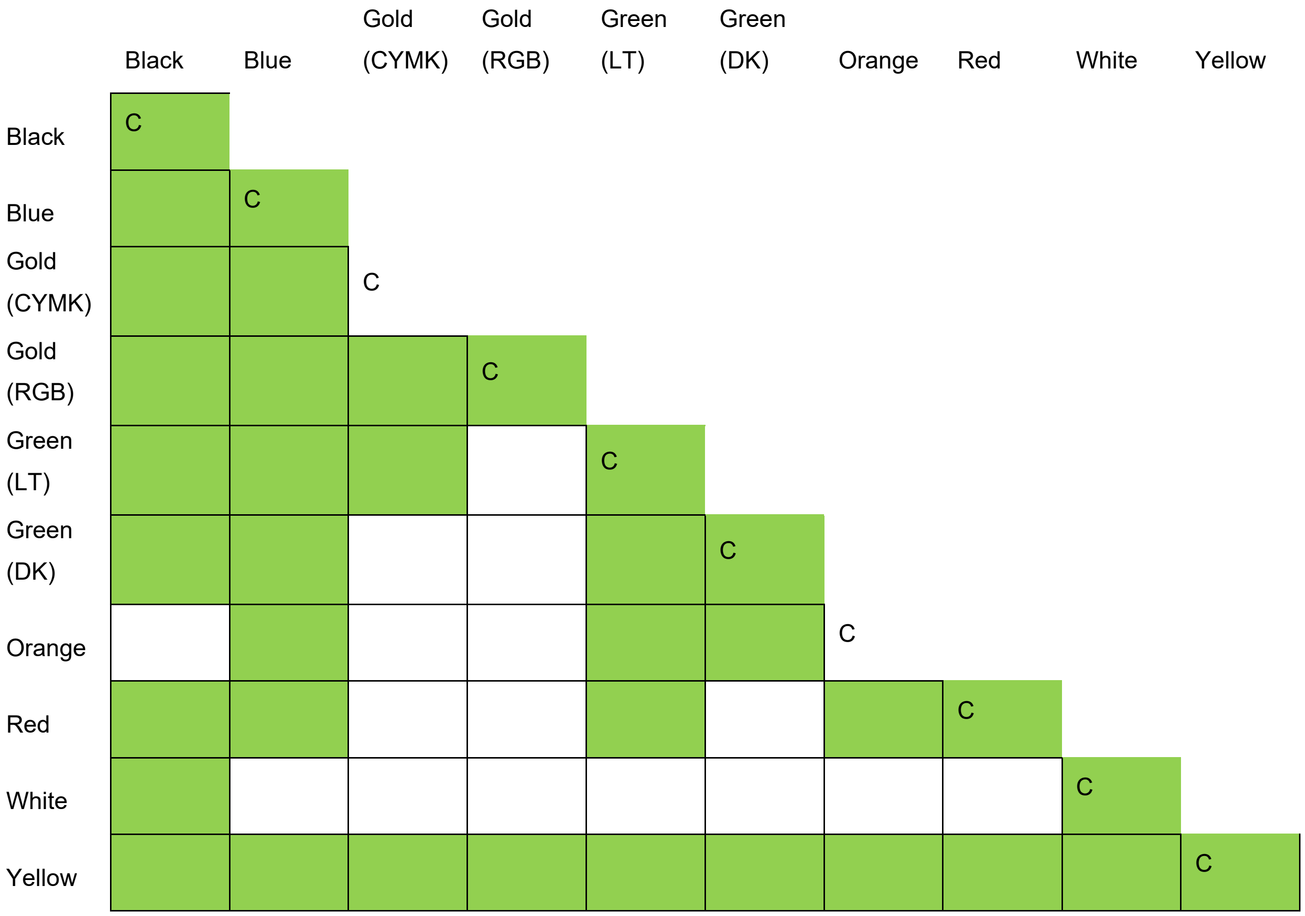
For gold coloured traps, pre-dyed paper was not available so the gold colour was produced following the methods described by Bian et al. (2014) in their study on leafhopper in tea plantations. Bian *et al.* described the colour of their trap in two colourspaces, RGB and CMYK. The term colourspace is used to describe a hypothetical 3 dimensional space that represents all the colours that can be generated using the base colours. In RGB these base colours are red, green and blue and is most commonly encountered in screen technologies such as monitors and televisions. By contrast, CMYK uses cyan, magenta, yellow and black (referred to as key) and is confined to the realm of printed or physical media. A crucial distinction between the two colourspaces is the method by which colour is produced in the eyes. CMYK is a subtractive model while RGB is an additive model. That is to say, when the human eye encounters light from an RGB screen the combination of the wavelengths emitted generates the spectrum of colours percieved. Small variations in the relative intensity of each colour (red, green or blue) changes the overall percieved colour in an additive method. I.E intense red emision with low levels of green and blue would appear red. If the intensity of blue was increased, the percieved colour would shift towards a more purple hue. In the subtractive model of CMYK, light cannot be emitted from the page and conseqently the model relies on selective wavelength absorption to generate percieved colors. Under this colourspace, wavelengths are subtracted from the reflected light in order to create the relative intensities that the eye interprets as colour. Under this model the combination of yellow and cyan would generate a percieved green hue. By using both colourspaces, Bian *et al.* (2014) were able to reproduce the colour as accurately as possible on both LCD screen (RGB) and print (CMYK). In this experiment, the described colour was reproduced digitally using both CMYK and RGB colourspaces. The colour was then reproduced in pigment (Katun Performance, Katun U.K. LTD., Berkshire, UK) on card as previously mentioned using an office printer (TASKalpha 3550ci, Kyocera Document Solutions LTD., Manchester, UK). In the case of RGB gold, the printing process requires conversion of the colourspace from RGB to CMYK within the printer.

2.4 Colour choice

Experiments were done within a 300^3 mm Perspex cube (Fig. 2.1) under controlled environmental conditions (20°C, 60%RH, 16:8 L:D). To eliminate exterior visual cues the cube was placed on a matte grey surface and surrounded on all sides and from above by matte white fabric panels (Fig. 2.1). Lighting was provided by fluorescent plant growth lights (Philips MASTER TL-D 58W/840, Philips Lighting, Guildford, UK). Sticky traps were placed in opposite corners of the box opposite the side from which leafhoppers were introduced (Fig. 2.1). Traps rested on the floor and were presented at an angle of approximately 45° relative to the plane from which the leafhoppers were introduced. Adult leafhoppers (*n*=20) were aspirated from the main culture at 1000h each day and retained in 2.5cm glass vials for 3h. As the sex ratio of the leafhoppers in culture was observed to be 1:1, no attempt was made to select by gender and a random sample of leahopper was taken from the culture at the stated time. If a sampled leafhopper was observed to be physically damaged in any way this insect was not used and a replacement was collected. At 1300h the leafhoppers were released into the Perspex cube through a port in the side of the box (Fig. 2.1). Leafhoppers were left for 21 hours inside the cube after which time the numbers on each of the sticky traps was recorded. The potentially confounding variable of side was controlled for by switching the sides on which colours were presented between replicates.

Colours were presented in pairs. Colour combinations are detailed in Table 2.1

Table 2.1 Sticky trap colour combinations tested. Each colour combination was tested in a pair, with the colours switching side between replicates. Each combination was repeated 4 times. Filled squares indicate a tested combination (row x column). Testing all combinations was not deemed necessary, due to time constraints and the capability of inductive reasoning to predict outcomes between untested combinations. Squares with a C are control tests.



	Black	Blue	Gold (CYMK)	Gold (RGB)	Green (LT)	Green (DK)	Orange	Red	White	Yellow
Black	🟩 C									
Blue	🟩	🟩 C								
Gold (CYMK)	🟩	🟩	C							
Gold (RGB)	🟩	🟩	🟩	🟩 C						
Green (LT)	🟩	🟩	🟩		🟩 C					
Green (DK)	🟩	🟩			🟩	🟩 C				
Orange		🟩			🟩	🟩	C			
Red	🟩	🟩			🟩		🟩	🟩 C		
White	🟩								🟩 C	
Yellow	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩 C

2.5 Colour evaluation

The reflectance spectrum of the traps was evaluated using a miniature spectrometer (Flame S, Ocean Optics LTD, Oxford, UK) under the same lighting conditions as the choice tests. A single trap was evaluated at a time. Traps were placed directly opposite the entry point to the Perspex box (Fig. 2.1). The spectrometer was configured with a Sony ILX-511B CCD detector with a sensitive range between 200-850 nm. Light was collected with a 5mm collimating lens attached to 400 μm fibre-optic cable. Collected light passed through a 1 nm grating before reaching the detector. The probe with collimating lens was mounted 30 cm from the trap being evaluated using a 50 ml plastic specimen tube with the bottom removed. This ensured the probe maintained the same geometry (distance and incident angle) for each sample. Fluorescent tubes flicker at twice the frequency of the input voltage (Binnie *et al.*, 1979) (50 Hz). To counter for flickering of the tubes resulting in uneven light intensity 50 readings of each trap were made. In each reading the spectral intensity was measured at a 1 nm scale for 1 μs. This process was repeated every second for 50 seconds. Signal to noise ratios were improved using a second order Savitsky-Golay smoothing algorithm (Savitzky & Golay, 1964) within the spectrometer software (OceanView, Ocean Optics LTD, Oxford, UK). The 50 readings were combined and averaged by wavelength interval, giving one number for each whole nm for each trap. This number was compared to the spectral reflectance of a diffuse white standard (Spectralon, Labsphere Inc, New Hampshire, USA)

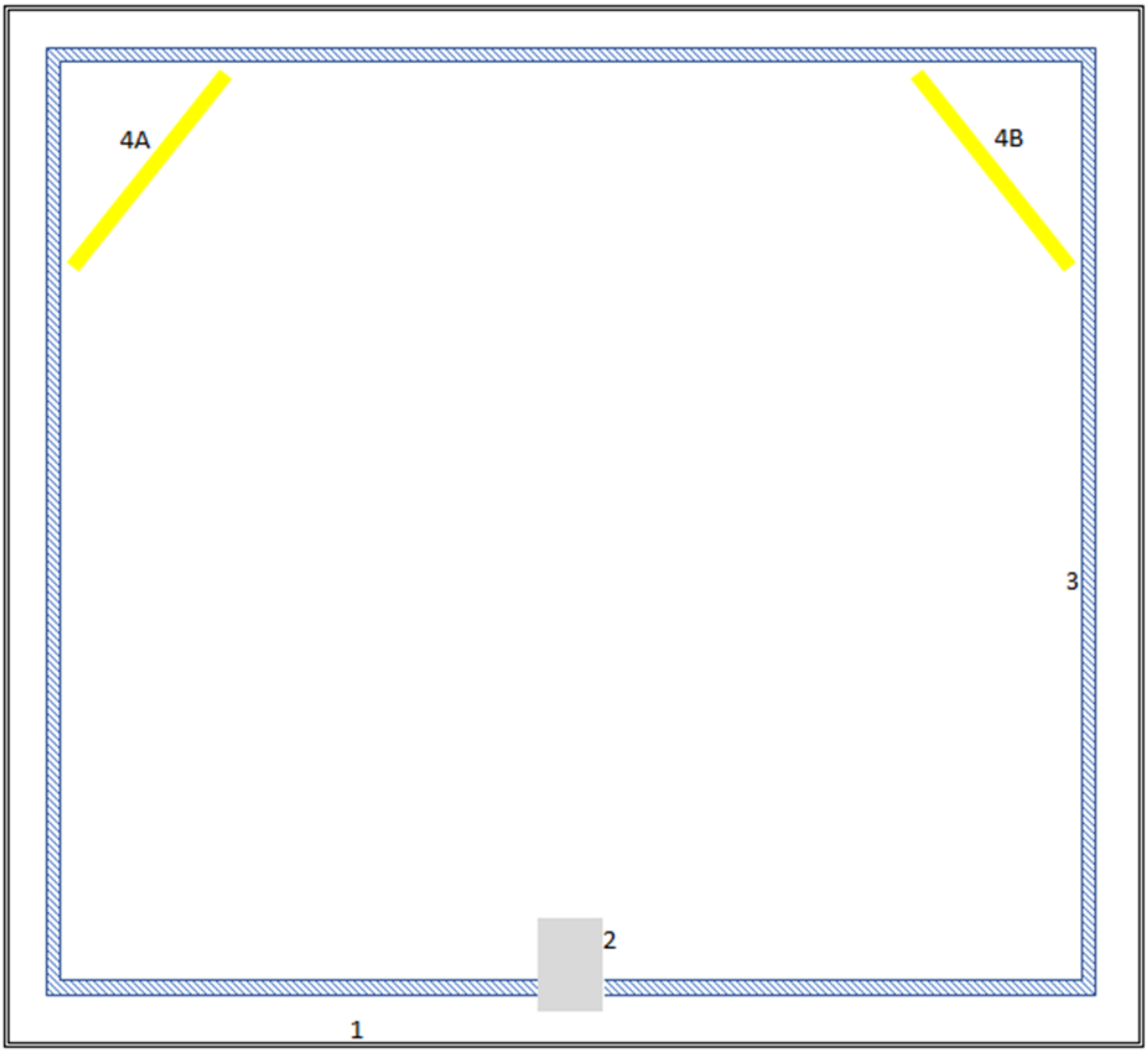


Fig. 2.1 A bird's eye view of the design of the Perspex cube and screen for colour preference bioassays. 1) cloth shielding. 2) glass tube, 3) Perspex box, 4A and 4B) sticky traps.

2.6 Statistical tests

Data were analysed using R (Version 3.5-3; R Core Team, 2019). Differences in catch numbers for individual experiments were tested with a binomial test given the low number of replicates for each combination (n=4). In binomial tests, the predicted proportion was given as 0.5. For all tests a 95% confidence was the cut off for significance. Trap catches of leafhopper were modelled using a negative binomial model. This allowed a proxy preference level to be calculated for each trap. Negative binomial models are frequently used in areas of study where the assumptions of a Poisson distribution cannot be met (Swartout *et al.*, 2015). In particular, negative binomial models allow for a greater degree of variance. *Post hoc* analysis of the negative binomial model using Tukey’s HSD.

2.7 Results

Overall, yellow traps were seen to be the most effective colour for capturing leafhoppers. This is seen in both the raw numbers of leafhoppers caught across all experiments, as well as the proportion caught (Fig. 2.2). The negative binomial model was found to fit the data better than a GLM with a Poisson distribution as seen in a reduction in the Akaike information criterion (AIC) score. As yellow is the most commonly used trap colour, and thought to be the most effective, the model was run using yellow as the baseline to which other colours were compared. From the model, yellow was seen to be the most attractive colour contributing the most to catch rates across all tests.

According to the negative binomial model, two colours performed as well as yellow. Light green showed no difference to yellow in terms of numbers of leafhopper caught (Z=-1.49, P=0.13). This is contrary to the evidence when yellow and light green were compared directly using a binomial test, which indicated the proportion of leafhoppers on light green traps was significantly lower than 0.5 (binomial estimate = 0.30, P<0.001).

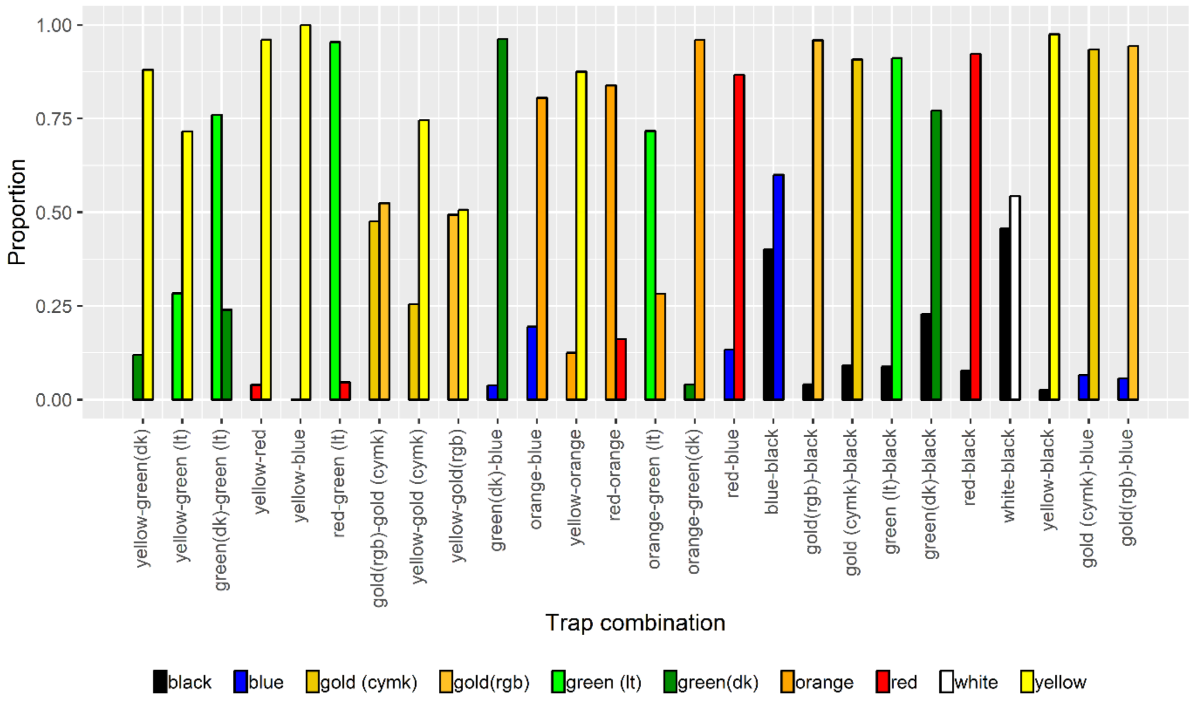


Fig. 2.2 Proportion of leafhoppers captured by each sticky trap colour in paired combinations. Each combination was presented alone and replicated 4 times. Leafhopper were screened from all other stimuli such that colour was the only cue available to insects. Error bars are not shown due to binary proportional data being presented.

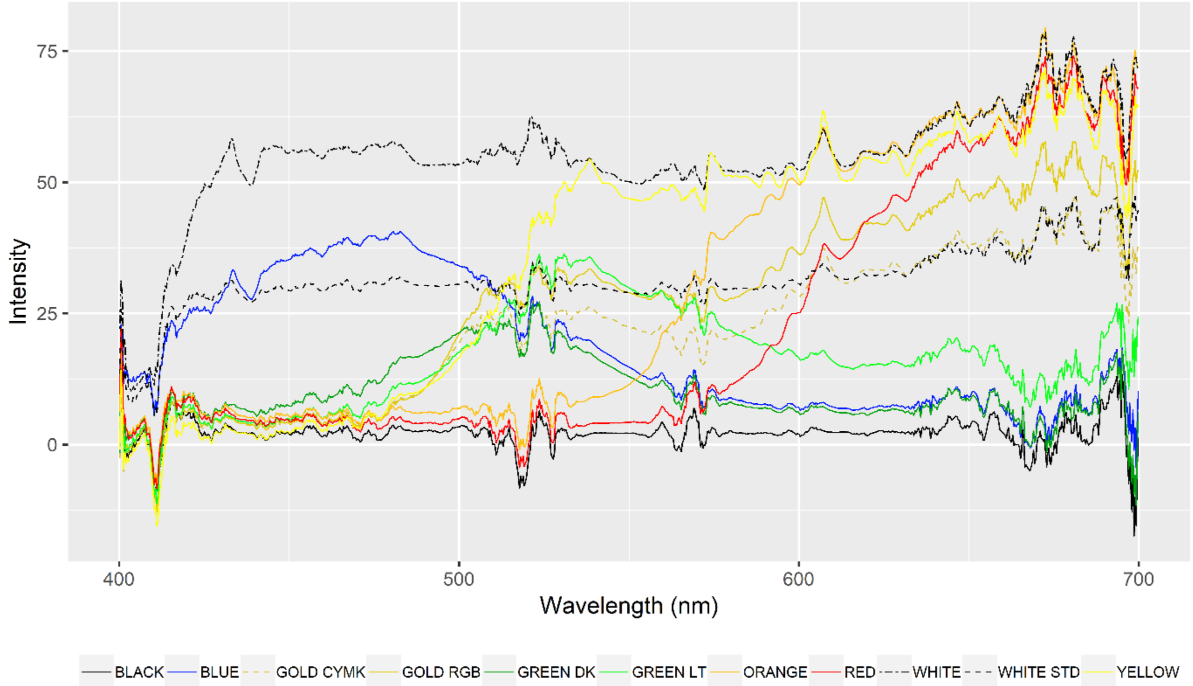


Fig. 2.3 Relative intensity of light reflected by traps under fluorescent lighting in laboratory conditions. Intensity is given in arbitrary units on a linear scale. Colours of lines are suggestive of trap colours except where this would lead to confusion.

In the negative binomial model, Gold RGB was not different to yellow (z=-1.17, P=0.08). This indicates that under experimental conditions, Gold (RGB) and yellow traps performed equally well. The results of the model carried over to the individual tests where no statistically significant difference between yellow and gold (RGB) was seen (binomial estimate =0.5, P=0.59).

Tukeys HSD test indicated that the colours formed five groups shown in Table 2.2. The colours with the highest and lowest, yellow and blue respectively, were furthest separated. Yellow was grouped with five other colours. The least effective trap colours were blue (z= -11.3, P< 0.001) and black (z= -9.873 P< 0.001). However, when compared directly, black showed no significant differences from blue (est.=0.4 P=0.85). Estimated means from Tukey post hoc analyis also indicated that light green and yellow were statistically similar, whereas direct comparison reveals a significant difference between them. Notably this pattern carries through for orange, which was seen to be similar in the post hoc analysis, but sigificantly different to both yellow and light green in direct comparison.

Table 2.2 Tukey's HSD groupings for trap counts. Est means gives the estimated marginal means. Column group shows the other colours to which the named colour was statistically similar from the Tukey's HSD test.

COLOUR	EST MEANS	SE	GROUP
Blue	0.405	0.166	a
Black	1.139	0.127	b
Red	1.580	0.138	bc
Green (dk)	2.123	0.126	cd
White	2.179	0.192	cde
Gold (cymk)	2.207	0.141	de
Orange	2.338	0.1238	de
Gold (rgb)	2.422	0.138	de
Green (lt)	2.449	0.122	de
Yellow	2.674	0.087	e

Evaluation with the spectrometer showed that the traps differed in wavelength characteristics (Fig. 2.3). The commercial yellow trap reflected far more of the light available, with higher readings for dominant wavelengths than any of the custom traps. The wavelength evaluation showed most of the traps had one main peak in reflectance that corresponded to wavelengths near the perceived colour of the trap. Commercial yellow traps had surprisingly high, even reflectance across wavelengths above 550nm, but as predicted, low reflectance for shorter, blue wavelengths (Figure 2.3).

2.8 Discussion

Yellow caught the most leafhoppers of all trap colours tested. This was unsurprising as the mechanism behind the attractiveness of yellow is well understood and thought to be common to many herbivorous insects (Kelber, 2001; Döring, 2014). The ability of gold (RGB) traps to capture leafhoppers as effectively as yellow traps under laboratory conditions was shown in this experiment. From a physiological response this is an interesting result that seems contradictory to the opponent model of insect vision. Under this model, yellow is a hypernormal stimulus that attracts insects by way of reduced blue reflectance (Prokopy & Owens, 1983). The gold (RGB) trap, presents a challenge to this theory as it contains more blue reflecting pigments (cyan) than the yellow traps. Because of the additive pigment model of the printing process, the trap will also contain magenta and black pigments (Kalloniatis & Luu, 1995) as the colour was not pure yellow. Given the non-spectral nature of magenta (Indow, 1978; Kalloniatis & Luu, 1995) it is unknown how that colour would appear to the leafhopper. Human eyes perceive magenta when a surface reflects both blue and red wavelengths of light (Pridmore, 2010). This is unlikely to translate into the same visual appearance for herbivorous insects. As such it is hard to calculate what the gold (RGB) trap would look like without relevant spectral data on the trap and wavelength sensitivities of the leafhopper.

Under experimental conditions gold (RGB) traps were shown to be as effective as yellow traps. The gold (RGB) colour used was derived from previous research on tea leafhopper *Empoasca vitis* (Göthe) (Hemiptera: Cicadellidae), in outdoor settings (Bian *et al.*, 2014). Bian et al. reported that larger numbers of leafhoppers were caught using gold (RGB) traps than when yellow traps were used in tea plantations (Bian *et al.*, 2014). Our study examined the responses of a different species of leafhopper (*Hauptidia maroccana*) in a laboratory setting rather than outside. This difference in trap catch performance between the two studies could be explained as 1) due to differing ecology or physiology of the pest species, 2) differences in the illumination changing the attractiveness of the trap or 3) an interaction between points 1 and 2. The fluorescent lights used in this laboratory study do not emit any ultraviolet light and have a different wavelength profile to that of the sun (Carter *et al.*, 2018). Organisms are thought to be able to evaluate the quality of light sources or illuminant and “discount” wavelength variation to achieve colour constancy (Foster, 2003, 2011; Chittka *et al.*, 2014). Colour constancy is where a surface or object will appear broadly the same colour under differing lighting conditions or illuminant profiles. While the precise mechanism of this is debated, there is consensus around its existence in most biological visual systems (Foster, 2003; Chittka *et al.*, 2014). It could be then that these traps presented in the absence of UV light still have the same general appearance as the same traps presented under natural lighting. It is known however, that some herbivorous insects utilise UV light as a cue for dispersal (Legarrea *et al.*, 2012) and that its inclusion in LED based trapping systems can increase catch rates (Stukenberg *et al.*, 2015) potentially due to increased activity levels. It may be, that despite the broad suggestions of colour constancy, higher catch rates can be achieved with gold (RGB) traps in the presence of UV light. Further studies with these organisms or traps should consider the impact of UV on catch rates. While glass is efficient at removing UV wavelengths, it is present in sunlight which may lead to differences in performance in glasshouses compared to in the open.

The ability of gold traps to act as effectively as yellow traps is a potentially significant discovery, as it is known that yellow traps capture beneficial insects (e.g. pollinators and natural enemies) including those deliberately released into glasshouse environments. As such, a more selective trap colour may present opportuniies to the pest management industry to improve an existing product while limiting the damage to beneficials. To establish the potential uses of this information, further research on the selectivity of the traps under field conditions, and in the presence of beneficials is recommended. Further, it has been seen that for extant colours, the use of patterning and high-contrast backgrounds has improved the catch rate. The same may be true of this new colour and again, should be investigated for potential performance enhancements.

Herbivorous insects are thought to be unable to see longer wavelengths due to a lack of red-light receptors. While the presence of red tuned opsins has been documented in some insect species, (Spaethe & Briscoe, 2004; Feuda et al., 2016) it is generally assumed that most do not possess the relevant pigments. This does not mean that red is completely invisible to insects, but that the intensity of the red light would need to be very high in order to generate any kind of nervous response in the eyes of the insects. In the experiments completed here, however, when a colour presumed to elicit a negative behavioural response (blue) was presented alongside a red trap, the red trap caught more insects. This is compatible with the current understanding of wavelength dependent behaviours with blue acting as a settling inhibitor (Kelber, 2001; Döring & Chittka, 2007; Stukenberg *et al.*, 2015). By contrast, a blue trap placed alongside a black trap captured significantly more insects than the black trap. Under those conditions, it could be expected that the black trap would perform better than the blue trap due to the absence of repellent wavelengths. It appears that for this species, black is even less effective as a trap for *H. maroccana* than blue. Why a trap that reflects almost no light would be less effective than a trap that is of a colour thought to elicit a negative behavioural response in insects is hard to explain.

When red and black were presented as a choice, however, red traps caught more leafhopper than black. It could again be assumed, that given the inability to see red light, these traps would capture equal proportions of leafhoppers, due to a similar relative intensity. As this is not what happened, the data raise the question of how the leafhoppers are able to distinguish between red and black when they are thought to lack the receptors necessary to do so. Electrophysiological characterisation of the visual system of this species would allow deductions on any potential mechanism for this preference. It should be noted that despite lacking red receptors, there is evidence that red surfaces are not invisible to herbivorous insects (Chittka & Waser, 1997).

With regards to the response to black surfaces compared with both red and blue traps, it may be useful to consider the possibility of foraging insects encountering these colours and their location in natural settings. A black surface in the natural world is rarely associated with plant tissue, (Hatier *et al.*, 2013) though there are some fruits or seeds with black surfaces (Davies, 2018) and some diseases that present as black necrotic spots. In some natural environments, dark surfaces will indicate soil, or leaflitter (Binkenstein & Schaefer, 2015), neither of which are likely to provide suitable foraging substrates to herbivores. By contrast, red and blue are common floral pigments (Weevers, 1952), and although not thought to be attractive to most folivores (though there are exceptions, see Otieno *et al.*, 2018), are more likely to be associated with food resources.

Thus, in the absence of a colour stimulus that elicits a positive behavioural response, such as yellow or green, leafhopper are more likely to be caught on traps that represent a natural colour stimulus, than an unnatural one.

It was noted that some colour preferences seemed to be consistent when presented in combination with different colours. This was seen both, when a colour that did not elicit a positive behavioural response was presented alongside yellow, or when the same colour was presented alongside a colour that also did not elicit a positive behavioural response. For example, the proportion of insects caught by red traps was higher than the proportion of insects caught by blue traps both when they were compared directly and when they were individually compared with yellow traps. This could imply an internal hierarchy of preferred colours, or wavelength specific behaviours. Such a hierarchy could help support the previous suggestion that in the absence of other stimuli, natural repellent stimuli are preferred to unnatural ones.

2.9 Conclusion

While none of these colours tested caught more leafhoppers than the standard yellow coloured traps, the potential for non-yellow colours to be as effective as yellow traps is an interesting development and could suggest ways in which alternative trap colours could be used for monitoring pest species. Yellow traps are an effective way of monitoring insect populations. They are however, a universally attractive colour, capturing pests and beneficial insects alike. With the evidence here that gold (RGB) is as effective as yellow, further tests on catch rates of beneficial insects should be completed. The potential for the development of a more selective trapping colour seems possible from the data presented here. Furthermore, the data are part of a growing body that indicate that there may be potential improvements the standard yellow trap is not the only colour that is effective for monitoring pest populations.

3 Leafhopper show volatile mediated conspecific avoidance under laboratory conditions

3.1 Abstract

The Glasshouse leafhopper, *Hauptidia maroccana*, is a sporadic, but serious pest of many glasshouse grown crops. Many species of leafhopper show aggregative and dispersive behaviours. In glasshouses, *H. maroccana* are thought to form hotspots throughout the crop. Whether this is due to aggregative behaviours or simply a lack of migration from hatch sites is currently unknown. More detailed knowledge of the dispersal behaviours of *H. maroccana* may help to accurately target controls against this pest when it is detected in a crop.

In this study the behavioural responses of starved adult leafhoppers to odours from infested and uninfested plants as well as to conspecifics was recorded in a series of Y-tube olfactometer assays completed under controlled environmental conditions. Odours were either presented in a choice or in a no choice set up.

Leafhoppers were found to have a preference for odours from uninfested plants when presented against plants infested with conspecifics. Leafhoppers were also found to move away from odours associated with conspecifics within the Y-tube. The implications of these results in explaining distribution of *H. maroccana* within glasshouse grown crops is discussed and related to possible avenues for more effective control.

3.2 Introduction

The Glasshouse leafhopper, *Hauptidia maroccana* (Melichar), is a Typhlocybinae leafhopper that is found throughout much of western Europe. This species of leafhopper typically only occasionally causes economically important levels of crop damage, but despite this when outbreaks do occur then severe damage can be caused (Seljak & Pagliarini, 2004). Attempts have been made to identify leafhopper specific natural enemies for use in biological control strategies, however the most promising candidate (*Anagrus atomus* Haliday) has not successfully been commercialised. As a result, biological control strategies have tended to focus on generalist predators e.g. *Macrolophus pygmaeus* (Rambur). *Macrolophus pygmaeus* is a generalist predator, but is selective when presented with multiple prey species (Fantinou *et al.*, 2009). In a crop with a patchy leafhopper distribution and a more preferred prey species, there may be a breakdown in the level of control provided (Barnadas *et al.*, 2011). If *Macrolophus* selectively disperse to plants that are infested with a preferred prey item and that *Hauptidia* selectively disperses away from already infested plants (particularly those infested with a conspecific) then the possibility of a spatial separation between the two increases.

With few studies focusing on *H. maroccana* little is known about the biology and ecology of this leafhopper species in glasshouse environments. Indeed, there has only been one previous study examining the life history and thermal ranges of *H. maroccana* (Choudhury, 2002). This lack of detailed knowledge about the ecology of *H. maroccana* in turn hampers attempts to control this sporadic pest. Control strategies must, therefore, necessarily be broad spectrum. Chemical controls are available, notably the oxadiazine insecticide, indoxacarb (Jacobson, 2009). Although indoxacarb appears to be largely compatible with biological control agents (Anjum & Wright, 2016; Kuk & Kim, 2017; Shankarganesh *et al.*, 2017; Ramos *et al.*, 2018), it is known to pose a risk to pollinators (Wing *et al.*, 2000) and indoxacarb resistance has been reported in dipteran and lepidopteran species (Shono *et al.*, 2004; Yu & McCord, 2007). Furthermore, the efficacy of indoxacarb against sucking insect pests is orders of magnitude less than that against chewing pests (Wing *et al.*, 2000), limiting its utility. This lack of efficacy raises the risk of resistance emerging in this pest (Morse & Brawner, 1986; Hall *et al.*, 2004). In organic production systems, control of *H. maroccana* is reliant on natural pyrethrins. Natural pyrethrins rapidly degrade on leaf surfaces and are not taken into plant tissues (Antonious, 2004), which limits the potential for uptake by leafhoppers and restricts activity to direct contact with the insect. For both organic compatible and synthetic chemical controls, targeting of insect pests will be important in resistance management and chemical stewardship (Brenner *et al.*, 1998; Bateman, 2003). Due to its readiness to take to the wing, and high dispersal ability, knowing the cues that *H. maroccana* uses to disperse or aggregate within a crop will be vital to this targeting.

Adult leafhoppers likely use a jumping escape mechanism to avoid predation, but are also capable of flying and as a result may move readily from plant to plant and disperse through the crop. If disturbed, they rapidly take flight. Once airborne they can be considered to be in a host-location behavioural state. Olfactory cues such pheromones or herbivore induced plant volatiles (HIPV) are likely to influence settling behaviour (Shockley & Backus, 2002). Long-distance conspecific perception by insects is primarily enabled by mechanoreceptors and chemoreceptors (Polajnar *et al.*, 2015). Hemipteran species are known to utilise both (Luo & Wei, 2015; Lubanga *et al.*, 2016; Inoue *et al.*, 2018; Lucchi *et al.*, 2019). Mechanical signals produced by leafhoppers are primarily vibrations generated internally or externally by drumming on a substrate (Čokl & Virant-Doberlet, 2003). Airborne and substrate borne vibrational mating signals have been documented in leafhopper pest species (Kumar & Saxena, 1978; Claridge, 1985; Čokl & Virant-Doberlet, 2003). Mating signal disruption has been trialled with evidence indicating that for species engaging in mutual display signalling behaviours, there is potential to reduce reproduction (Mazzoni *et al.*, 2009). *Hauptidia maroccana* is not known to utilise such mechanical signals and has been described as having no courtship behaviours, further limiting avenues for alternative control strategies (MacGill, 1932).

Chemosensory perception of the environment provides long range sensory information and is common among insects as a method of conspecific location (Wyatt, 2014; Fleischer & Krieger, 2018). Leafhoppers, however, generally have reduced antenna with a bristle-like arista (Pollard & Yonce, 1965), a feature retained for almost 100 million years (Poinar & Brown, 2017). Work examining the microstructure of the arista of many species have failed to locate sensilla or nerves relating to chemoreception (White & Bay, 1980; Arzuffi *et al.*, 2008; Henderson & Wellington, 2008). Furthermore, studies have shown that leafhopper species either do not or cannot utilise olfactory senses to distinguish between resistant and non-resistant crop cultivars despite being able to distinguish between them visually (Bullas-Appleton *et al.*, 2004, 2005). As such it is unlikely that olfactory information is solely relied on for the location of hosts or conspecifics.

The spatial distribution of leafhoppers, when characterised by statistical analyses, changes over time (Nestel & Klein, 1995). For example, populations of two species of leafhopper, *Edwardsiana rosae* L. and *Asymetrasca decedens* (Paoli), were sampled throughout their active season and were shown to have different patterns of aggregation and dispersal despite invading the crop simultaneously (Nestel & Klein, 1995). Similarly, the host-alternating potato leafhopper, *Empoasca fabae* (Harris), is known to aggregate in large numbers on red maple trees. Data have indicated that the insects initially aggregate in high numbers on selected plants before changing to a random distribution as populations increase (Bentz & Townsend, 2004). Data were collected from a commercial maple stand with multiple cultivars present. It was seen that *E. fabae* alters its aggregation behaviours dependent on the population levels, but that the host cultivar played a role too (Bentz & Townsend, 2004). These data indicate that leafhoppers are able to evaluate host quality and trade this off against aggregative behaviours. In other herbivorous insects, interactions between volatiles emitted by plants and volatiles given off by the herbivore have been observed. In many cases, the interaction is an additive one, with blends including plant volatiles alongside pheromone cues showing greater levels of attraction (Dickens, 1989; Loughrin *et al.*, 1995; Landolt & Phillips, 1997). There is a great deal of research documenting the changes in emitted plant volatiles that stems from plants detecting herbivore attack. These changes to the plant volatiles vary with pest species and are known to be detectible by herbivores, predators and parasitoids, as well as plants (Arimura *et al.*, 2009; Dicke & Baldwin, 2010; Peng *et al.*, 2011; Shivaramu *et al.*, 2017). Being sensitive to the HIPV of potential hosts, some herbivorous species are more attracted to infested plants than uninfested plants.

Previous ecological studies have shown that, for polyphagous insects, the host choice of the ovipositing mother can influence the host preferences of the next generation (Egas & Sabelis, 2001a, 2001b). This is significant for *H. maroccana* as it is unusual in the Typhlocybinae in being polyphagous (Le Quesne & Payne, 1981). Many of the known wild hosts of *H. maroccana* are from family Laminaceae while as a pest it primarily affects Solanaceae crops (MacGill, 1932; Fox-Wilson, 1938; Le Quesne & Payne, 1981). The development and fecundity of *H. maroccana* varies with host plant species (Choudhury, 2002). Consequently, there may be potential fitness benefits accrued by showing host switching behaviour. Choudhury (2002) describes both the development time from 1st instar to adult as well as nymphal survival on a variety of host plants. Female *H. maroccana* reared on *Primula vulgaris* had significantly slower development times compared to *Capsicum anuum,* across a range of temperatures. There was, however, a decline in the survival rate of nymphs reared on *Capsicum anuum* compared to *P. vulgaris*. Consequently, there is likely a fitness trade-off between the two plants. For pest insects, the use of preferred host-plants as a trap crop or plants which the insects avoid may be used prevent crop invasion (Cheruiyot *et al.*, 2018; Sarkar *et al.*, 2018). For polyphagous insects, knowing whether the ovipositional choice of the mother influences host choice of the offspring may be important in pest management. If insects are not inclined to switch host, or show host preference, it may be possible to use the preferred or original host as a trap crop.

The cues that lead to leafhopper aggregation initially, and the potential stimuli to shift to random distributions later in the season are not known. In many aggregating insects the cue to aggregate is a constitutively expressed pheromone (Ishii & Kuwahara, 1967; Torto *et al.*, 1994; Seybold *et al.*, 1995). Although there is little evidence to support the existence of an aggregation pheromone in leafhoppers, they are known to produce large quantities of microscopic three dimensional granules termed brochosomes (Day & Briggs, 1958). The function of brochosomes is unknown, with research suggesting potential functions in water regulation (Rakitov & Gorb, 2013) or avoidance of parasitism (Velema *et al.*, 2005). Brochosomes are produced by all stages of leafhoppers and in some cases anointed over the surface of the body (Rakitov, 1996). They are known as well to be easily dispersed from the leafhopper and have been detected in atmospheric air layers at up to 36km (Bigg, 2003; Rakitov, 2011). Though they are unlikely to be a source of olfactory cues, conspecifics are likely able to detect their presence on contact.

It is not known whether *H. maroccana* shows any aggregative behaviours. Understanding the way in which this pest distributes itself through a crop may enable more targeted deployment of insecticides or biological controls. To address this point experiments were completed to record behavioural responses to cues arising from 1) infested and uninfested host-plants, and 2) conspecifics. Experiments were conducted with leafhoppers cultured on primrose and *C. anuum* to test for evidence of host-plant conditioning, which has implications for crop invasion behaviours.

3.3 Methods and materials

3.3.1 Leafhopper cultures

Leafhoppers (*Hauptidia maroccana*) were obtained from WyeBugs (WyeBugs, Wye, UK) and were kept in 47.5 x 47.5 x 47.5 cm Bugdorm insect cages (MegaView Science, Taichung, Taiwan) on primrose (*Primula vulgaris vulgaris*) plants in controlled environment chambers (Fitotron, Weiss Technik, Ebbw Vale, UK) under standardised conditions (20°C, 60%RH, 16:8 Light:Dark). Primrose plants were used as they provide a good midpoint between allowing leafhopper to achieve high reproductive rates while also being easy to cultivate (Choudhury, 2002). Primrose plants were grown from commercially supplied seed (Emorsgate Seeds, Kings Lynn, UK) in 1.5L pots of John Innes No.2 potting compost (Westland Horticulture LTD., County Tyrone, Northern Ireland). Damaged plants were replaced every 2-3 weeks as required.

3.3.2 Experimental plants

The HIPV experiments were conducted using *Primula vulgaris* plants. *P. vulgaris* plants regularly form multiple crowns with conjoined root systems which can be separated and propagated as individual plants. In this series of experiments, the plants used for comparisons were derived in this manner, so as to avoid possible intra-species variation in the level of volatile expression (Keskitalo *et al.*, 2001). To prevent uninfested plants detecting and responding to HIPVs from the infested plants, infested and uninfested plants were kept in separate rooms. Infested plant material was sourced from the main leafhopper culture. Leafhopper infested plants were prepared by placing previously clean plants at the flowering stage from which flowers had been removed (Hess *et al.*, 1997) in the main leafhopper culture BugDorm two days prior to use in experiments. Clean plants from which flowers were also removed were retained separately in a different controlled environment chamber prior to exposure.

Pepper plants (*Capsicum annum cv*. FALKO RZ F1) were grown from seed (Rijk Zwaan UK, York, UK) in a glasshouse on site at Harper Adams University in 1.5L pots of John Innes No.2 potting compost (Westland Horticulture LTD., County Tyrone, Northern Ireland). For experiments and leafhopper culture, plants were used at growth stage 51(Feller *et al.*, 1995).

3.3.3 Olfactometer choice tests

The olfactometer had an internal diameter of 14mm and a stem length of 12 cm. The arms of the olfactometer joined the stem at an angle of 72°. The branched arms were 10 cm long with the same internal diameter as the stem. Arms were connected to modified thistle funnels with 6mm outlets that allowed connection to Swagelok brass 6mm-3mm reducing unions sealed with polytetrafluoroethylene (PTFE) ferrules leading to PTFE tubing with an outer diameter of 3mm (Swagelok, Manchester, UK).

Visual stimuli were minimised by surrounding the olfactometer with a frame of white cotton cloth panels. Light was provided by a fluorescent tube bulb (5500K,85W 5000lm; PhotoSEL LTD, London, UK) mounted 47.5 cm above the olfactometer. A diffuser screen was placed between bulb and olfactometer. Forty adult leafhoppers were aspirated from the main culture and placed into a 25ml polypropylene reagent tubes (Sarstedt, Nümbrecht, Germany) lined with damp cotton wool. Leafhoppers were starved for 18 hours under the same environmental conditions in which they were reared. Olfactometer assays commenced at 1000 h the following day in a separate controlled environment chamber. Individual leafhoppers were aspirated out of the polypropylene tube into a custom aspirator that allowed opening at both ends.

The open-ended design of the aspirator allowed the base of the olfactometer to be inserted directly into the aspirator, minimising the risk of the leafhopper escaping during this transfer. Leafhoppers were allowed to acclimate for 60 seconds before being moved into the base of the olfactometer using a fine paintbrush. This value was arrived at through trial and error as the minimum time needed for acclimation.

Leafhoppers were allowed 5 minutes to make a choice. A choice was recorded as being made when the insect crossed a mark at 7.5 cm past the branch point of either arm of the olfactometer. If the insect did not cross the mark within the 5 minutes the replicate was marked as a no choice. Insects were used only once. In both experiments all conditions of volatile streams were kept the same. Airflow was provided by a micro diaphragm gas sampling pump (KNF Neuberger, Inc., NJ, USA) at a rate of 0.4 L/min controlled by a flowmeter (GPE Scientific LTD, Bedfordshire, UK). The low rate of airflow was found to provide a better level of response from leafhoppers in method development trials than values recommended in the literature e.g Bullas-Appleton *et al.* (2004). Airborne contaminants were eliminated by activated charcoal and the humidity was raised by bubbling the airflow through distilled water before entering the volatile source. Between changes in volatile source glassware was cleaned using HPLC grade acetone (Sigma-Aldrich Co. Ltd., Dorset, UK) and dried in a glassware oven at 150°C for 5 minutes. At the end of each day glassware were washed again in acetone and heated to 250°C for 3 hours. All glassware, membrane pump, and olfactometer were connected using PTFE tubing with an outside diameter of 3mm (Airline Fittings, Matlock, United Kingdom), 6mm brass tube fittings, and 6mm to 3mm brass tube reducing unions (Swagelok, Manchester, United Kingdom).

3.3.3.1 HIPV attractance

At the start of the experiment 6 randomly selected fully expanded leaves were cut from infested and uninfested plants respectively and placed in 15ml glass vials with water.

Infested plants had insects removed before use. These were retained inside 2L Dreschel bottles (Sci-Glass Consultancy, Bere Alston, UK). Plant material was retained in the Dreschel bottle for 15 minutes with zero airflow. Prior to introducing insects into the olfactometer the pumps were switched on to a higher level (1.0 L/min) to flush the headspace through the any airborne contaminants from the system. Leafhopper choices were tested for the following combinations; 1) uninfested primrose and blank air; 2) infested primrose and blank air; and 3) uninfested primrose and infested primrose. Each combination was tested daily with ten insects per day for ten days, giving a total of 100 leafhoppers per combination. To account for any left-right bias, the position of each stimulus was swapped between sides of the olfactometer after five replicates. During switching, non-filtered air could enter the Dreschel bottles and the system was flushed for 5 minutes after each swithc to remove airborne contaminants. Combinations were tested in a randomised order each day to minimise the potential effect of circadian rhythm on olfaction (Krishnan *et al.*, 1999; Page & Koelling, 2003; Cortés *et al.*, 2010).

3.3.3.2 *Host conditioning attraction*

Prior to experiments, 50 leafhoppers from the main culture were removed and released into a new insect cage containing only *C. anuum* plants at growth stage GS51. These insects were allowed to remain and feed on plants until 1st instar nymphs were observed approximately 2 weeks later. At this point all adults were removed. Nymphs were allowed to complete their development and reproduce on the *C. anuum* plants, which took a further 3 weeks. A second generation was allowed to reach adulthood, to ensure host conditioning and to allow leafhopper numbers to increase. Plants were regularly replaced. Choice tests were conducted in a similar manner to those on HIPV; Adult leafhoppers were aspirated into glass vials from both the main culture (*n*=10) and the secondary culture (*n*=10) on *C. anuum* plants. Plant volatiles were provided by 6 excised leaves from each culture in glass vials inside 2L Dreschel bottles. Experimental method was as previously described. Leafhopper were given a choice of volatiles originating from either the host plant they were raised on, or a novel host. For example, leafhopper raised on primrose were given a choice between a familiar host (primrose) or the novel host *Capsicum anuum* . Choices were tested in an alternating host order. Left-right bias, was mitigated by swapping the position of each stimulus after ten replicates. Airflow and glassware were as previously described.

3.3.3.3 *Conspecific volatile attractance*

To provide a source of leafhopper volatiles adult leafhoppers (n=50) were aspirated from the main culture using a modified barrel aspirator at 0900 and retained in a 25ml polypropylene tube (Sarstedt, Nümbrecht, Germany) for an hour prior to experimentation. After acclimation for an hour the 50 leafhoppers were inserted into a 10 cm glass cylinder of internal diameter 3.5mm open at both ends and sealed with silanised glass wool. The leafhoppers were retained in the glass tube for 15 minutes to acclimate before the start of the experiment. This was done to allow the leafhopper to acclimate and cease emission of any potential alarm pheromone. Starved leafhoppers were presented with a choice of leafhopper volatiles or blank air. In the blank air condition, an empty glass tube sealed with silanised wool was used as a control. The way that leafhoppers were introduced into the olfactometer, replication and responses recorded were the same as that described for the plant volatile choice tests.

3.3.4 Entrainment of herbivore induced plant volatiles

Ten primrose leaves were cut at the base of the petiole. The petioles were then wrapped in cotton wool moistened with distilled water and wrapped in a layer of aluminium foil in order to retain moisture and minimise plant stress. Each set of ten leaves were then placed individually into a 1 L nylon roasting bag (Bacofoil, UK) with care taken to avoid causing further damage to the plant tissue other than the initial stem cutting.

Two plant treatments were used during this study: uninfested and infested primrose. Infested plant leaves were cut from plants in the main leafhopper culture. Uninfested plant volatiles was obtained from plants from the previously described clean plants.

Air was introduced into the system through a Dreschel bottle with activated charcoal filtered at a higher rate (500 ml min^{-1}) than the sample rate of 200ml min^{-1} using a set of two diaphragm pumps (KNF Neuberger, Inc., NJ, USA). Air was removed from the bag for 180 minutes passing through a stainless-steel sorbent tube containing 200 mg of Tenax-TA sorbent (Markes International, Llantrisant, United Kingdom) in order to collect HIPVs on the sorbent tube.

As with previous experiment roasting bags, glassware, membrane pumps, and sorbent tubes were connected using PTFE tubing with an outside diameter of 3mm (Airline Fittings, Matlock, United Kingdom), 6mm brass tube fittings, and 6mm to 3mm brass tube reducing unions (Swagelok, Manchester, United Kingdom). Prior to undertaking entrainments, the 1 L roasting bags were heated in a dedicated glassware oven at 250°C for 30 minutes and then purging with activated charcoal filtered air for 15 minutes.

3.3.4.1 Identification of herbivore induced plant volatiles

Spectrometry and identification of compounds was conducted at Harper Adams University. Tenax-TA tubes were desorbed using a UNITY series 2 thermal desorption unit (Markes International, Llantrisant, United Kingdom). Tubes were heated to 250°C for 10 minutes under a Helium flow at 20ml/min. Desorbed volatiles were collected in a general-purpose C4–C32 carbon cold trap (Markes International, Llantrisant, United Kingdom) at −10°C. Volatiles were then ballistic heated to 300°C for sharp injection into the capillary column of the gas chromatograph-mass spectrometer (GC-MS). The temperature program of the GC-MS was from 40°C (5 minute hold) to 280°C (2 minute hold) at 10°C/min (total run time: 32 minutes) [GC (Agilent 7890B with an HP-5MS column: 30 m x 0.32 mm x 0.25 μm, injection temperature: 250°C, splitless injection); MS (Agilent 5977A mass selective detector, 70 EV, scan range: 50 - 500 M/Z, source temperature: 230°C, quadropole temperature: 150°C, solvent delay: 0 minutes)]. Spectra were compared with data mass spectra database (NIST MS search 2.2; National Institute of Standards and Technology, USA) and published linear retention indices.

3.3.5 Statistical analyses

For olfactometer tests, insects not making a choice were omitted from statistical analyses. Statistical significance was determined using binomial tests of significance in R 3.6.1 (R Core Team, 2019). Choice differences from host priming were tested with a chi square test.

3.4 Results

3.4.1 Y-Tube olfactometer tests

3.4.1.1 Plant Choice preferences

The overall number of leafhoppers responding, regardless of choice was not seen to differ significantly between combinations ($p>0.05$) (Fig. 3.1). In combinations 1 (uninfested-blank) and 2 (infested-blank) no significant differences were seen in the numbers of leafhoppers responding to each treatment (infested or uninfested) and blank humidified air.

A significant difference was seen in combination 3 (Fig. 3.1, infested-uninfested) where more leafhoppers entered the arm containing the odour of uninfested primrose than the arm containing the odour of the infested primrose ($f = 0.32$, $p=0.02$). The mean number of choices made by insects per day was seen to vary, however day was not seen to have a significant influence on choice number.

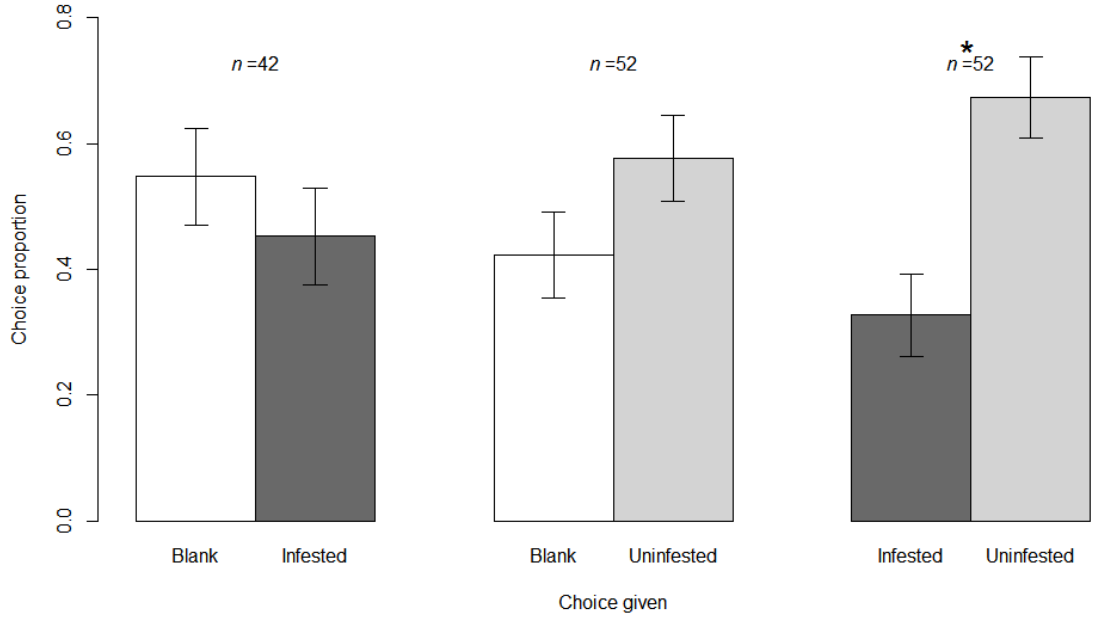


Fig. 3.1 Proportion of choices made by H. maroccana when presented with different combinations of plants. Bars show proportion of responding leafhoppers for each choice ±SE. Asterisk denotes significant differences. A slight, non-significant increase in the number of individuals making a choice was seen when leafhoppers were exposed to uninfested plant volatiles. Blank indicates a treatment with no plant matter present

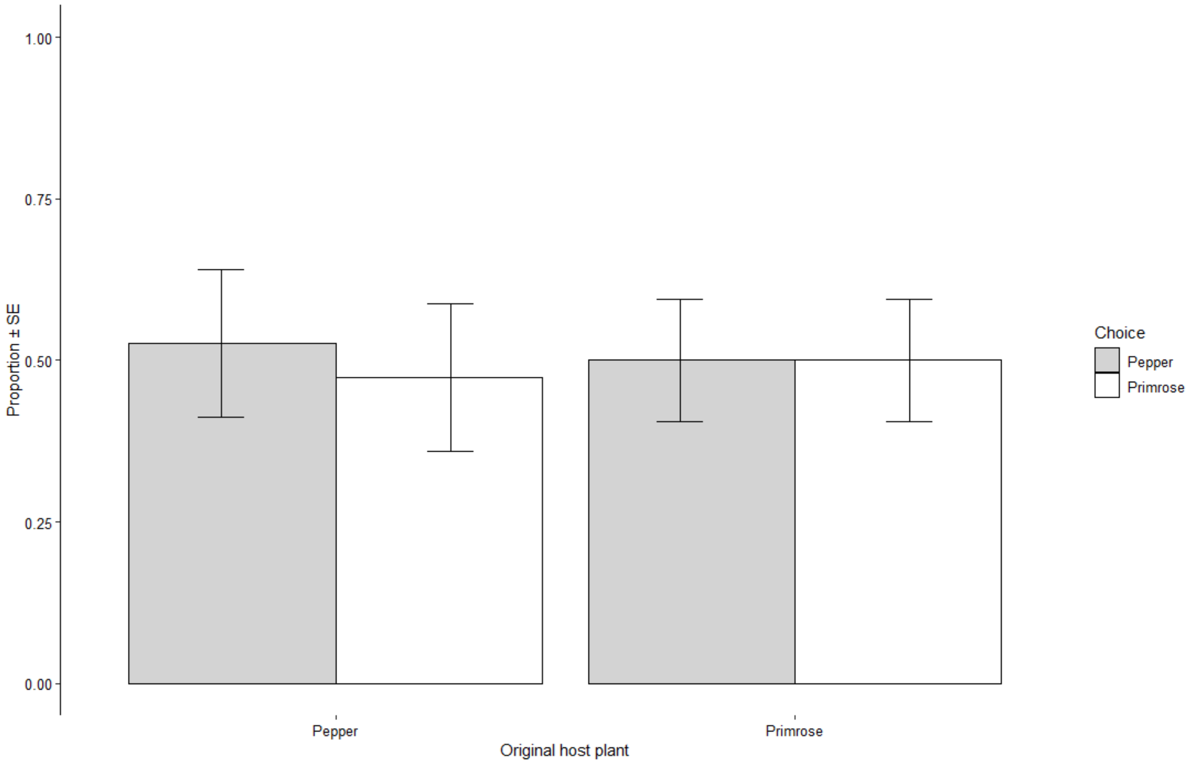


Fig. 3.2 Leafhopper odour plume choice following cultivation on different original host plants for at least 1 generation. The original host was seen to make no significant difference to the choice of plant volatiles. Error bars show SE.

3.4.1.2 Host conditioning choice test

Leafhopper were not seen to display any significant preferences in volatile choice regardless of host conditioning (χ=0, *df*=1, *p*=1). Overall, no significant differences were seen regardless of the independent variable (Fig. 3.2).

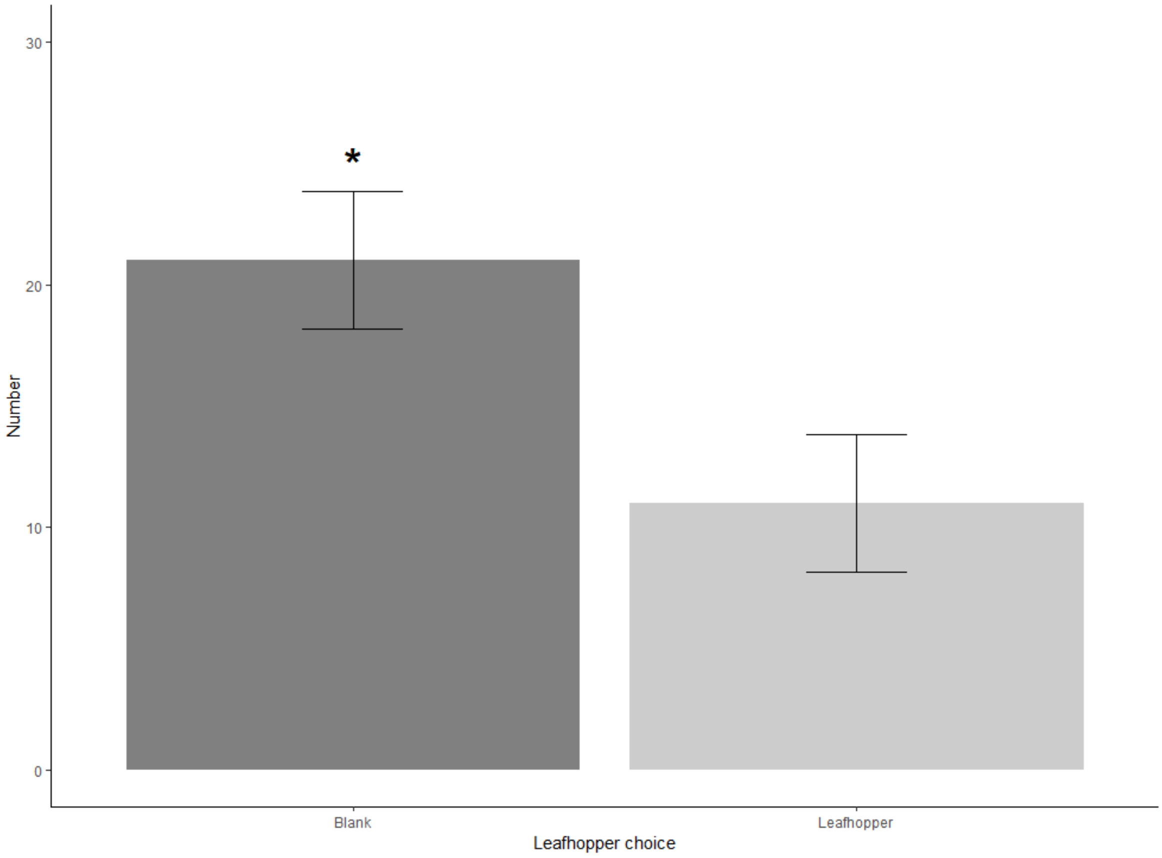


Fig. 3.3 leafhopper choices when presented with blank air or air containing odours from conspecific adults. Leafhoppers did not show an attraction to potential volatiles produced by conspecifics. n=50. Error bars give SE.

3.4.2 Conspecific volatile choices

Leafhoppers presented with a choice between blank air or air carrying the scent of conspecifics preferentially moved towards the blank air (Fig. 3.3). A binomial test confirmed that these differences were significant (*f*=0.34, *p*=0.97) Plant volatile entrainments

Quantitative and qualitative differences in the volatile bouquet were seen between uninfested and infested plants (Fig. 3.4). Volatiles present in both infested and uninfested primrose increased in quantity detected from infested plants. Infested plants also showed a more complex volatile blend, with an increase in the number of distinct chemicals detected. It was also observed that heptanal, butyrolactone and undecone were produced when the plant was undamaged, but were no longer detected after being damaged by leafhopper. Other chemicals had substantial increases or were only detected after leafhopper damage was present. Of particular note were (*E*)-& (*Z*)- β-Ocimene, *γ*-terpinene, indole, *α*-cubebene, linalool, caryopyllene, germacrene D, humulene, *γ*-muurolene, *γ*-cadinene, (*E*,*E*)-TMTT and hexadecane.

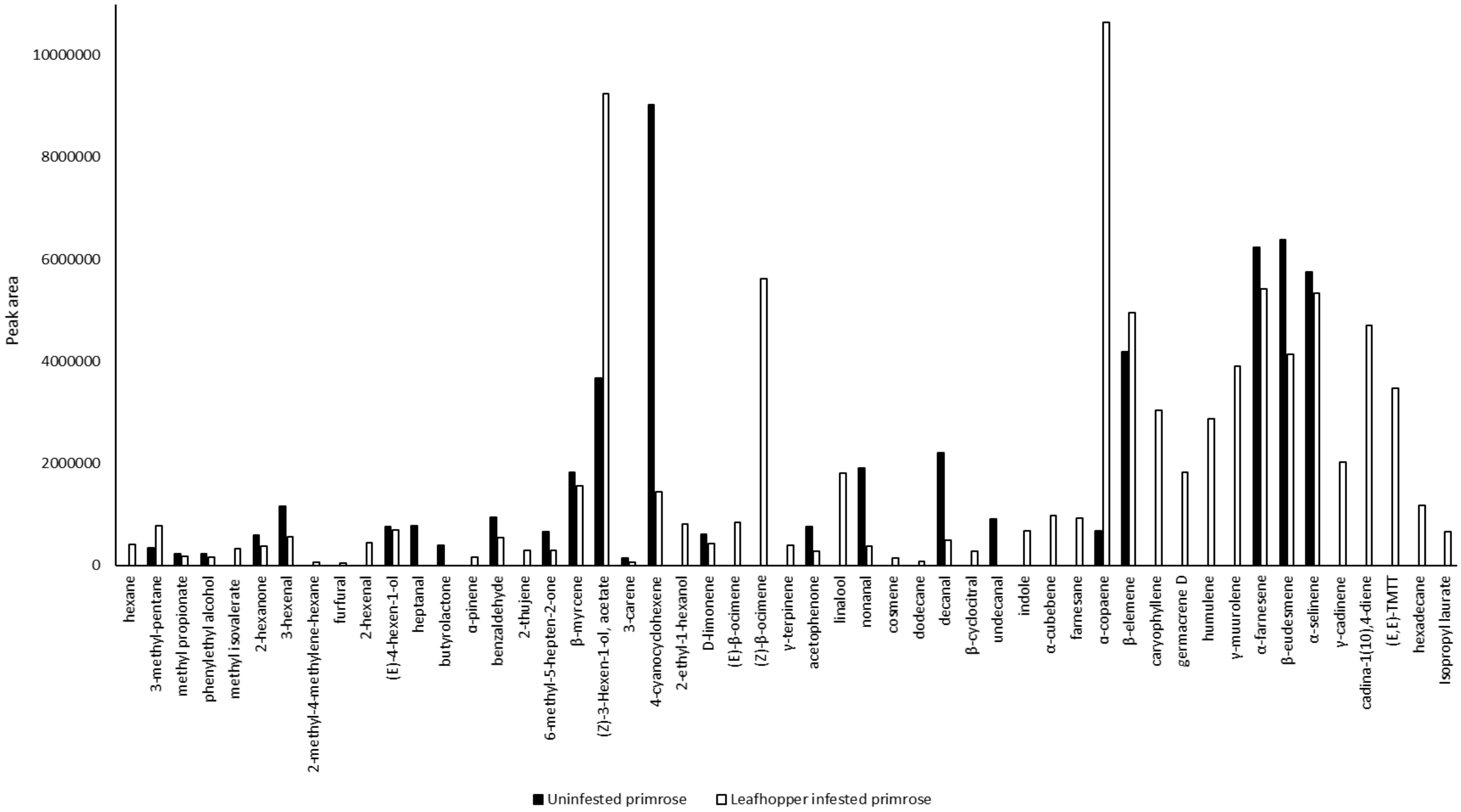


Fig. 3.4 Relative abundance of volatile chemicals in the odour plumes of primrose plants.The height of each bar represents the relative amount of each substance detected, but cannot represent absolute quantities. Both increases and decreases in the relative abundance were observed as well as an overall increase in the number of volatiles detected after infestation with leafhopper.

3.5 Discussion

This study set out to test for evidence of behavioural responses of adult *H. maroccana* to a variety of ecologically relevant odours. This included plants either uninfested or infested with conspecifics, the odour of conspecifics, and a conditioned host alongside a novel host. The data presented shows that under laboratory conditions leafhoppers move towards uninfested leaves rather than infested leaves or blank air (Fig. 3.1). They were also more likely to move towards blank air when given a choice between volatiles from infested plants and blank air (Fig. 3.1). From these results, it seems possible that *H. maroccana* will display dispersive behaviours. These results may reflect three behavioural drivers: optimal foraging, predation avoidance, mating/reproductive behaviours.

Within optimal foraging theory the primary driver is assumed to be energy (Ydenberg *et al.*, 1994). This may help to explain the avoidance of conspecifics, which would reduce the availability of a finite resource (plant tissue fluids). This is a common limitation for foraging animals, but is of particular importance to Typhlocybinae leafhoppers that permanently damage the cells of the leaves on which they feed. Thus, for new resources to be generated by the plants, new leaves must grow. With this limitation, the drive for foraging leafhoppers to avoid competition may be particularly high (Denno *et al.*, 1995). Furthermore, *H. maroccana* is a generalist feeder. Plants can produce secondary metabolites as defence against the activity of herbivores. For specialist herbivores these defences are often mitigated by detoxification or sequestration of metabolites (Arany *et al.*, 2008). In plants under attack by herbivores, the expression of these metabolites is upregulated. This may present a greater risk of toxicity for generalist feeders as they lack the specific detoxification pathways (Arany *et al.*, 2008). This would provide a second motivating factor to avoid already infested plants.

Avoiding plants that are emitting HIPVs may also represent a potential predator avoidance strategy for herbivores. A great deal of work has established the ability of predators and parasitoids to detect and respond to HIPVs, however, this response is most effective when specialist parasitoids or predators are involved (Ali & Agrawal, 2012). Previous research has demonstrated that leafhopper specialist parasitoids are strongly attracted to plants damaged by their host leafhopper species (Lou *et al.*, 2005b). *Macrolophus sp.* is currently deployed in some situations for control of *H. maroccana* (N. Ward, *pers comm.*) and is known to feed on a wide range of invertebrate pest species as well as plant tissues (Perdikis & Lykouressis, 2004; Vandekerkhove & De Clercq, 2010; Backer *et al.*, 2014). When considering the impact of HIPVs on this predator, it has been seen that under conditions experienced in an olfactometer, *Macrolophus* will preferentially move towards infested plants over uninfested (Lins *et al.*, 2014). It was also seen that this behavioural response was stronger if multiple herbivore species were infesting a plant (Moayeri *et al.*, 2006; Lins *et al.*, 2014).

As an obligate sexual species, *H. maroccana* must mate in order to reproduce (MacGill, 1932). *Hauptidia maroccana* mates only once, and following that single mating instance adults do not attempt to mate again (Choudhury, 2002). As a mixed population, it is likely that the leafhoppers selected for use in the olfactometer assays had previously mated and were, therefore, unlikely to respond to the scent of conspecifics. This would support the evidence that the leafhoppers moved towards the blank air stream more often than the leafhopper entrained air. Further considering the effect of mating status on the leafhoppers used, there is evidence showing that the level of expression of HIPV genes is related to the level of infestation on the plant (Ghirardo *et al.*, 2012). Under the culture conditions in this experiment, high populations of leafhopper were possible on the plants. It may be that foraging leafhoppers are more likely to settle on a plant with a lower level of HIPV expression when faced with a choice between plants of lower or higher HIPV production. The data presented here, imply that this would be a difficult test to conduct under similar conditions given the already low level of response to stimuli seen.

It is unlikely that volatile cues are the only stimulus that foraging leafhoppers are sensitive to when choosing a host plant. For example, previous studies have suggested that leafhoppers are able to integrate olfactory and visual cues for host location (Bullas-Appleton *et al.*, 2005) and that this is true across species (Gerk *et al.*, 1995). Leafhopper damage causes large patches of discolouration to the upper surfaces of leaves, which may provide visual cues to dispersing insects about the quality of potential hosts for example (Bullas-Appleton *et al.*, 2004; Backus *et al.*, 2005).

The air entrainment data showed a number of responses to infestation by leafhopper. As expected, plants damaged by leafhopper released a higher number of volatiles (Kessler & Baldwin, 2002; Dicke *et al.*, 2009). Of note were a number of volatiles shown to be relevant to other leafhopper species for host location and evaluation. Benzaldehyde has been seen to be a key attractant to host plants for *Empoasca onukii* (Matsuda), and was present in both uninfested and infested primrose plants (Cai *et al.*, 2017). There was a qualitative reduction in the amount of benzaldehyde detected from infested plants in this experiment. Given the role of benzaldehyde as an attractant at low levels in air (20ng L^{-1}, Cai *et al.*, 2017) the decrease seen between the two treatments here may help explain the decrease in attraction for infested plants. It should be noted, however, that for *E. onukii,* responses to benzaldehyde in air was reported at levels as low as 3.4ng L^{-1}. Among the detected volatiles was (*Z*)-4-Hexen-1-ol, while (*Z*)-3-Hexen-1-ol was absent. (*Z*)-3-Hexen-1-ol is a well-documented green leaf volatile, and is known to be behaviourally relevant to a number of herbivorous species (St Onge *et al.*, 2018; Vuts *et al.*, 2018; Francese *et al.*, 2019)

Leafhoppers were not seen to show a preference for either host when presented with a choice between a novel or familiar host (Fig. 3.2). This is despite *Primula vulgaris* and

Capsicum anuum presenting differing qualities of host (Choudhury, 2002). Host switching behaviour, like many behaviours, is plastic and is influenced by biotic and abiotic factors. This experiment showed that leafhoppers were either unable to distinguish between host plants, or that the stimuli provided were equally attractive. Given that care was taken to minimise the possibility of abiotic influences (temperature, humidity, lighting) the lack of host switching or host fidelity may indicate that for *H. maroccana*, host choices are influenced by a cue, such as colour or non-volatile surface chemicals or structures (e.g trichomes), that was absent in this study. There are few studies that explicitly consider the impact of prior experience or external factors on host choice in invertebrates. The presence or absence of predatory species has been shown to have an impact on host selection by *Tetranychus kanzawai* Kishida (Prostigmata; Tetranychidae) (Murase & Fujita, 2018). This contrasts with evidence from a lepidopteran pest which did not alter oviposition behaviour when exposed to predator cues, but did preferentially select larger plants with higher nitrogen content (Lund *et al.*, 2019). As such, the lack of any predation, or predatory cues during these experiments may have removed a cue that is used during host choice.

The use of excised leaves as a source of volatiles for olfactometer studies is well established in the literature, with many authors using it. This is despite the fact that it is well documented that plants respond to purely mechanical damage as well as feeding damage by herbivores (Walling, 2000; Schmelz *et al.*, 2001). Despite this, there are few studies comparing the release of herbivore-related cues on excised leaves compared to whole plant emissions. Of particular note is research conducted that indicates that excised leaves vary substantially in their volatile emissions compared to those from whole plants (Schmelz *et al.*, 2001). Despite this, the persistence of this method in the literature does imply a level of reliability in the method. Further, in this case, as both treatments are excised, any change in the volatile expression would be present in both, and variation in the leafhopper responses (see Fig 3.1) can be assumed to be due to the changes caused by the infestation condition of the plant. However, this may help to explain the low level of responses seen by the leafhopper in this experiment.

Many insects show changes in the level of activity during a day, with periods of greater activity and relatively quiescent periods (Fleissner, 1982; Tomioka & Matsumoto, 2010). Indeed, some plants are able to synchronise their defence hormone expression with insect circadian rhythms (Goodspeed *et al.*, 2012). The specific activity peaks of *H. maroccana* are not known, nor are its locomotion preferences. When presented with the volatiles in the olfactometer assay, the leafhoppers first orientated to face towards the flow of air before walking along the stem into the current. During the observation period of the experiment, the majority of insects were seen to attempt to transition to jumping along the tube. Due to the narrow diameter of the olfactometer, this method of locomotion was not successful and frequently resulted in the insects facing a different way, or being inverted. The jumping behaviour in response to volatile cues hints at potential long-range dispersal by these insects towards plant odours. As the leafhopper in this trial were not able to fully exhibit this behaviour, there is a possibility this may have contributed to the low response rate seen in the data. The use of narrow-gauge olfactometers has in the past been seen to influence the behaviour of tested species, limiting the full range of behavioural expression (Guerrieri, 1997). However, experiments under these conditions have had similar results to those under conditions where behaviours were not limited (Gerk *et al.*, 1995).

It should be noted that this study presented starved insects with volatile cues *in vitro*. Insects that are already on a food plant may be less responsive to cues from other plants and therefore respond less to cues of uninfested plants.

The overall picture of the data presented here is mixed, with no clear evidence for *H. maroccana* showing any aggregative behaviours. As such, the hotspots observed in crops may well arise due to a lack of migration away from a hatch site by emerging nymphs. Further studies to elucidate this should examine the influence of feeding status (starved, satiated), predator detection and avoidance, oviposition host choice, and examine both nymphs and adults for aggregative behaviours.

4 Green and UV light enhanced yellow traps are more effective at capturing Leafhoppers under laboratory conditions

4.1 Abstract

Light Emitting Diodes (LEDs) are becoming more common in glasshouse environments due to decreases in costs, power requirements and size. Coupled with increasing specificity of available wavelengths, the potential for altering the lighting environment in glasshouses has never been higher. Many insects rely on visual cues for host location and settling responses. This experiment examines the use of narrow wavelength LED lighting for improving catch rates of yellow sticky traps. Traps were illuminated with green or ultraviolet light (UV) under laboratory conditions. Traps illuminated by green light alone showed significant reductions in catch rate. UV light made no difference to catch rates alone. When combined on a single trap, UV and Green light significantly increased the number of leafhoppers caught by sticky traps.

4.2 Introduction

Hauptidia maroccana (Melichar) is a poorly studied, sporadic pest of horticultural and vegetable crops in the Europe. Unusually for the Typhlocybinae, *H. maroccana* feeds on a wide range of wild and cultivated plants (Le Quesne & Payne, 1981). Though capable of vectoring tomato pathogens, *H. maroccana* is not considered to an important vector of these diseases (Maisonneuve et al., 1995; Hogenhout et al., 2008) and there is no published literature on the status of this leafhopper as a vector of diseases of solanaceous crops.

Control of *Hauptidia maroccana* is primarily broad spectrum (Jacobson, 2009). Within the EU, there are few options for chemical control and the list of available active ingredients keeps getting shorter. For example, a highly effective chemical heptenophos (Helyer & Ledieu, 1986), had its EU pesticide approval removed in 2001. Development of a new chemical control strategy that is compatible with available biological control agents has been investigated, with suggestions that indoxacarb (Wing *et al.*, 2000) is compatible with some species of biocontrol (Dinter & Wiles, 2000). A recent development of a fatty-acid based control solution may provide growers with a more flexible option, however it is too early to comment on the uptake of this product and it should be noted that it’s use as a control of leafhoppers is via an extension of minor use, rather than a labelled pest. Wild populations of related leafhopper species are subject to predation and parasitism by a range of other insects and there have been efforts to find parasitoids, most notably from the family Mymaridae, suitable for commercialisation. *Anagrus atomus*, an egg parasitoid of *H. maroccana* has been the focus of most research in this area but this parasitoid has several obstacles to commercialisation. Perhaps the most important of these obstacles are issues surrounding the distribution of wasps to growers . This is because *H. maroccana* lays eggs into leaf tissue, which are then parasitised by *A. atomus* (Agboka *et al.*, 2004). As the parasitised leafhopper eggs cannot be removed from within the leaf tissue and unparasitised eggs are highly cryptic, the risk of including unparasitised leafhopper eggs in a shipment to growers is high (Moratorio & Chiappini, 1995). As a relatively low priority pest, it is unlikely that further research into developing specific biocontrols for *H. maroccana* will be completed. Developing a simple, low cost control method for *H. maroccana*, that can be deployed with minimal disruption to control of other pests would benefit growers in the years when this leafhopper emerges as an economically important problem.

Trapping of pest insects in glasshouse environments has been primarily used as a monitoring strategy (Lu *et al.*, 2012), but improvements in the efficacy of these traps, could represent a potential control method. Evidence from some trials indicates that some highly phototactic species may be susceptible to control by mass trapping using sticky traps alone (Sampson & Kirk, 2013). The catch rate of these traps may be improved using pheromone lures or enrichment with coloured lights (Broughton *et al.*, 2015). Herbivorous insects locate host plants through a combination of olfactory and visual cues with the relative importance of each depending on many aspects of the ecology and biology of host and herbivore (Mayhew, 1997; Döring & Chittka, 2007; Shivaramu *et al.*, 2017). The visual system of most herbivorous insects is thought to be a trichromatic system with peak sensitivities in blue, green and ultraviolet spectra (Kelber, 2001; Döring & Chittka, 2007). Previous work on visual behaviour has shown discrete behaviours in connection to colour; with green and blue acting oppositionally as attractive and repellent stimuli respectively (Stukenberg *et al.*, 2015). The action of ultraviolet light on insect behaviour is more complex but often results in increased movement of the insect (Döring, 2014).

Development of Light Emitting Diode (LED) technology has allowed the production of sophisticated lighting arrays with narrow peak wavelength (Yam & Hassan, 2005). This has allowed the testing of specific light wavelengths in isolation and in combination to determine their impact on insect behaviour (Stukenberg *et al.*, 2015; Stukenberg & Poehling, 2019). The increasing use of LED lighting in glasshouses raises the possibility of developing lighting arrays that provide benefits to plants photosynthetically, whilst at the same time increasing the efficacy of chromatic traps.

In previous studies, insects have been shown to respond positively to direct coloured light sources (Stukenberg *et al.*, 2015). Under natural conditions, herbivores will primarily encounter reflected light. Reflected light (e.g. an LED, the sun) is more highly scattered and more diffuse compared to light from a point source (Stover, 2016). Reflection will reduce the radiant flux (Φ_e) through absorption by the reflecting surface, and potentially alter the spectral intensity ($I_{e,\Omega,v}$) of the light stimuli by absorbing some wavelengths more readily than others (Stover, 2016). Reflection of light may also lead to an increase in the radiosity (J_e) of the stimuli through an increase in the area of emittance (Stover, 2016). Through the generation of scattered, diffuse light, the angle of incidence upon the lenses of observing insects will be more stochastic, which is known to alter electrochemical responses (Zettler & Järvilehto, 1972). Given the ability of a reflecting surface to alter the spectral qualia of light, and the use of narrow band LEDs to increase the attractiveness of trap surfaces, there is a need to understand the effect of reflected light on visually attractive traps.

UV electric insect killers are commonly used as attractants for pest insects in a variety of settings, but these often require high voltages to drive the bulb and must be out of reach of humans due to risk of injury (Sliney *et al.*, 2016). Furthermore, the role of UV light in insect behaviour is not yet completely understood (Antignus, 2000; Döring, 2014). In this study, the potential for LED enhancement of sticky traps for control of *H. maroccana* is investigated in a laboratory setting.

4.3 Materials and methods

4.3.1 Leafhopper cultures

Continuous cultures of *Hauptidia maroccana* were maintained in controlled environment chambers (Weiss Technik, Ebbw Vale, UK) under standardised environment conditions (20°C, 60%RH, 16:8 Light:Dark) on Primrose (*Primula vulgaris vulgaris*) plants. Lighting in the controlled environment chamber was provided by high brightness fluorescent tube lamps (TL-D 58W/840 1SL/25, Philips Lighting UK, Surrey, UK). This lamp is rated at a nominal luminous flux of 5150 lm, and a correlated colour temperature of 4000K. Primrose were selected for use as a host-plant as they allow *H. maroccana* to achieve high reproductive rates while also being easy to cultivate (Choudhury, 2002). Primrose were grown from root stock from an existing culture at Harper Adams University in John Innes No. 2 potting compost (Westland Horticulture LTD., County Tyrone, Northern Ireland).

4.3.2 LED enriched traps

Previous research has indicated that a light wavelength of 525nm (green) was a principle predictor of catch rates on coloured traps. Light emitting diodes (LEDs) of three peak wavelengths were used singly and in combination to illuminate traps. Wavelengths used were Green 525nm (ASMT-AG00-NUV01, Broadcom Inc., San Hose, USA), Green 535nm (XPEBGR-L1-0000-00G01, Cree, Inc. Durham, USA) and UV 365nm (SN-HPUV365nm-3W, Epileds Technology, Inc., Tainan, Taiwan). Seven combinations were tested: 1) Green 535 vs unlit yellow trap; 2) Green 525 vs unlit yellow trap; 3) Green 535 vs Green 525; 4) UV 365 vs unlit yellow trap; 5) Green 535 vs UV 365; 6) Green 535 vs Green 535 + UV 365; and, 7) Green 535 + UV 365 vs unlit yellow trap. During tests, LEDs were positioned at the top of the trap at an acute angle so that light falling on the trap would form a large diffuse radiant area on the surface of the trap. Though under specific circumstances the photons of narrow wavelength light can interfere, this is unlikely to happen in this setup due to the use of incoherent light sources (Deng & Chu, 2017). In addition, by positioning the LEDs in this way light was reflected from the trap towards the insects approaching the trap and direct light from the LED source was not visible to insects. Lights were powered using 2 rechargeable lithium ion batteries (NCR18650B, Panasonic, Kadoma, Japan), with voltage and current regulation provided by an LED driver PCB (LMS2596, Texas Instruments, Texas, USA). Circuits were configured to provide the minimum operating voltage (forward voltage) of the LED (3.2V-4V) at 350mA. For traps with no illumination, an unpowered LED of the same type was positioned in the same way as the illuminated trap.

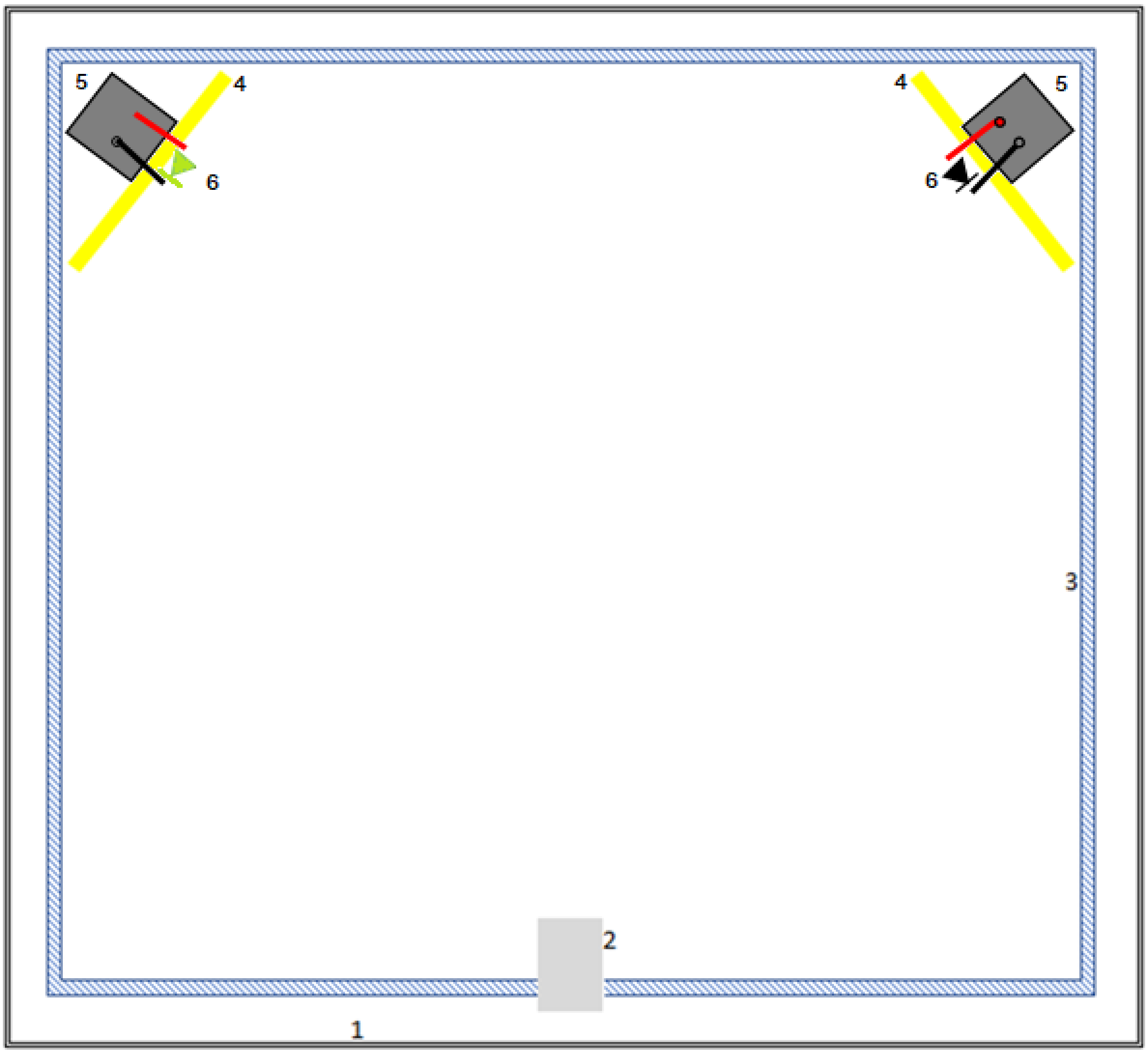


Fig. 4.1 design of cube and shield for colour preference bioassays. LED circuits were placed behind the sticky trap such that only the wiring and LED (represented by the symbol for diode) itself were visible. Unilluminated traps had the same type of LED and battery pack in an off state. 1) Cloth shielding, 2) glass tube, 3) Perspex cube, 4) sticky traps, 5) Battery holder and PCB, and 6) LED placement.

4.3.3 Colour choice

Experiments were conducted within a 30x30x30cm Perspex box under controlled environment conditions (20°C, 60%RH, 16:8 L:D). To eliminate exterior visual cues the Perspex cube was placed on a matte grey surface under fluorescent growing lights (Philips TL-D 58W 840, Philips UK LTD, Surrey, UK) within a 45 cm^3 matte white fabric frame that blocked any visual cues around the vertical faces of the cube. Sticky traps (Easistick, Fargro, West Sussex, UK) were placed in opposite corners of the Perspex box opposite the side from which leafhoppers were introduced. Full size sticky traps were cut in half to 10x12cm for use in this experiment. Traps rested on the floor and were presented at an angle of approximately 45° relative to the plane the leafhoppers were introduced from (Fig. 4.1). Adult leafhoppers (n=20) were removed from the main culture at 1000h each day and retained in 2.5cm glass vials under growing lights for 3h before the start of the experiment. At 1300h the leafhoppers were released into the Perspex cube through a port in the side of the box, that minimised disturbance of the leafhopper. Leafhoppers were left in the Perspex cube for 20 hours before numbers caught on each trap were recorded. Between experiments the cube was washed with hot water to remove cues arising from the insects, in particular honeydew residue. The trap treatments were alternated left-right to prevent possible directional bias.

4.3.4 Wavelength Measurement

LED spectral radiosity of the reflected light from the trap was measured using a miniature spectrophotometer (Flame NS, Ocean Optics, Oxford, UK). Radiosity was compared to a baseline reading taken using a white reflectance standard (Spectralon, Labsphere, Inc., New Hampshire, USA) under the growing lights of the growth chamber. The spectrometer was configured with a Sony ILX-511B CCD detector with a sensitive range between 200-850 nm. Prior to sampling, the spectrometer was calibrated using a Mercury-Argon reference light (HG-2, Ocean Optics LTD, Oxford, UK). Light was collected with a 5mm collimating lens attached to 2m of ø400 µm fibre-optic cable. Collected light was focussed with a 1 nm grating before reaching the detector. Readings were made under the same experimental conditions as choice tests. Readings were taken from the entrance port to the Perspex cube in a plastic frame to ensure the same angle and distance. The probe was inserted at the opening of the Perspex box, pointing at a trap that was set up in one of the treatments previously described. To counter for random fluctuations in light intensity from the source 50 readings under each situation were made. In each reading the spectral intensity was measured at a 1nm scale for 1µs. Intensity was measured from 189nm to 885nm. Boxcar smoothing (was applied to the reading, giving three measurements for each integer wavelength interval. The mean was calculated for the three, giving a single, unitless intensity value for each interval. This process was repeated every second for 50 seconds. Data signal to noise ratio was improved using a polynomial Savitsky-Golay smoothing algorithm (Savitzky & Golay, 1964). All 50 readings were collated and the mean was calculated for each interval, giving a single unitless intensity reading for each whole wavelength interval of each individual trap.

4.3.5 Statistical tests

Data were analysed using R (R Core Team, 2019). Differences in catch rates between traps were analysed using a binomial test. Peaks in wavelength data were extracted using the find_peaks command within the R package ggpmisc (Aphalo, 2019). This method looks for local maxima within a spectrum and marks them.

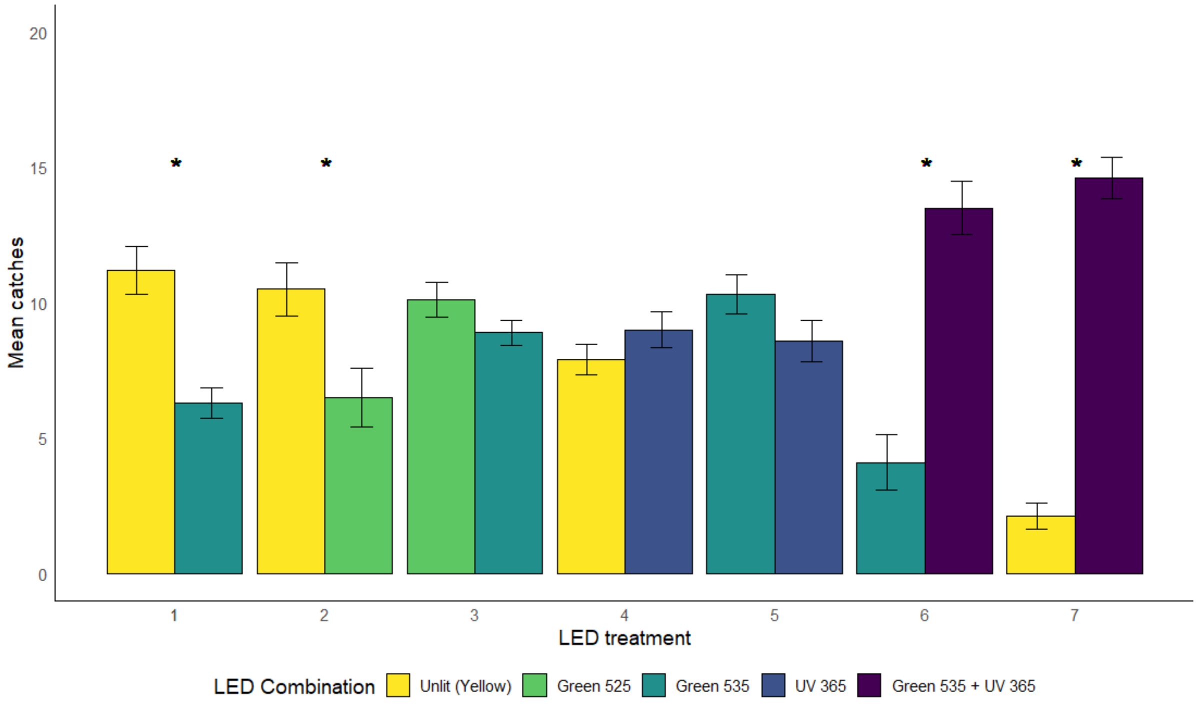


Fig. 4.2 Mean catches on traps under different lighting conditions. Asterisks denote significant differences at the 0.05 level. Error bars show SEM. Bar colours are suggestive of, but not accurate to, the colours used.

4.4 Results

The use of LEDs affected the numbers of leafhoppers caught on yellow sticky traps. There was no consistent effect of the LEDs on catches of leafhopper. The use of green LEDs was seen to significantly lower the number of leafhoppers caught on illuminated traps. This was true of both 535nm (Combination 1, *f*=0.64, *p*<0.001) and 525nm (Combination 2, *f*=0.61, *p*=0.003). When the green LEDs were compared directly there was no difference in the numbers of leafhoppers caught (*f*=0.53, *p*=0.43). The use of UV light did not affect the numbers of leafhoppers caught on the sticky yellow traps, with no significant difference seen between illuminated and un-illuminated traps (*f*=0.46, *p*=0.44). When LEDs were used in combination, however, there was a strong positive effect on the numbers of leafhoppers caught. UV lights used together with Green 535 light showed the greatest difference when compared with unlit traps, with a binomial estimate (*f*) of 0.13

(*p*<0.0001). UV lights used together with green lights also significant increased trap catches compared with green lights used on their own (*f*=0.23, *p*<0.0001).

Peaks were extracted from the mean values of the measurements. Reflected wavelengths from the traps varied in the UV range. Traps without UV enhancement did not have any readings in the UV range, while those that were enhanced did. There was an anomalous group of peaks between 449nm and 489nm for all traps except Green 535. These peaks were similar in intensity and wavelength, but are of unknown origin. The detected peaks are in the region of light that appears blue to human eyes, ranging from “royal blue” (RGB: 0,65,255, Hex: #0041ff) to “turquoise” (RGB: 0,251,255 Hex: #00fbff). Traps all reflected at key wavelengths in the 600nm range (611nm, 625nm, 630nm) at similar intensities. These are the dominant wavelengths reflected by the traps under the lights within the controlled environment chamber. A substantial difference in wavelength intensity was seen in the region of 520nm where the measured brightness varied by two orders of magnitude. None of the traps perfectly reflected the light shone on them. The UV light was most accurately reflected, with a reflected peak at 367nm compared to the observed dominant direct wavelength at 365nm. By contrast the green LED light was largely absorbed by traps. Peaks were seen in the relevant regions, but none were within 10nm of the direct peaks.

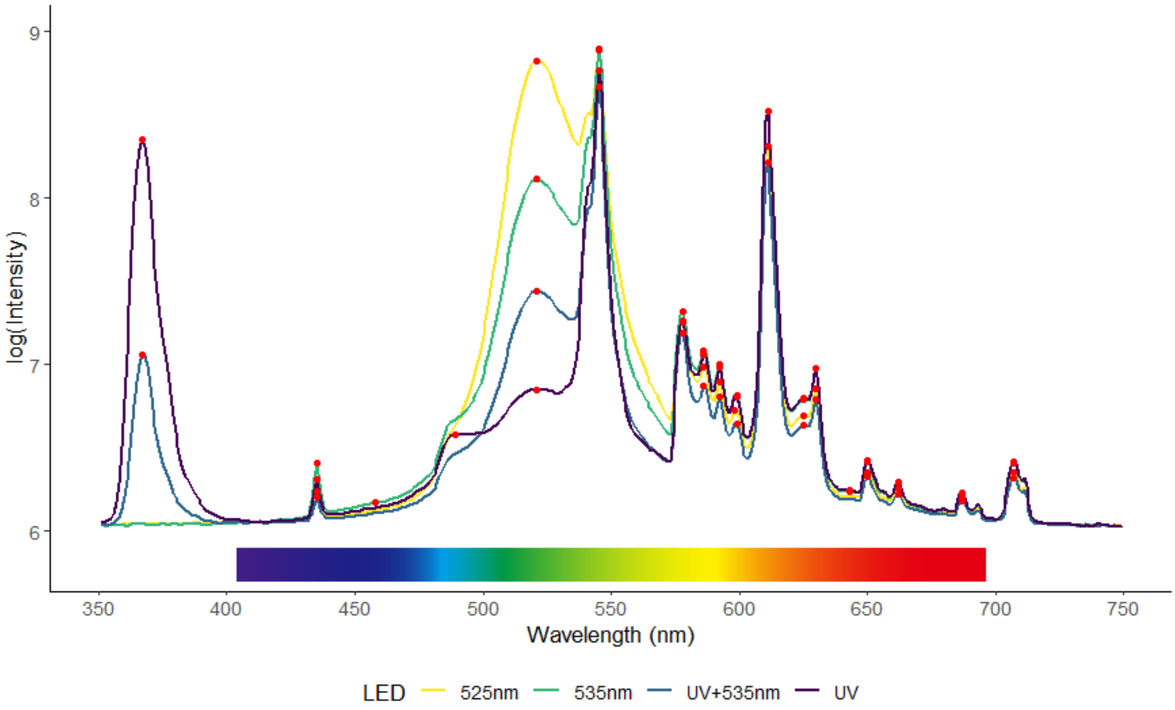


Fig. 4.3 Spectral intensity graph for sampled traps. Intensity is relative to the reflectance of a yellow trap under growing lights (i.e. unilluminated) under which all experiments were conducted

4.5 Discussion

The results indicate that it is possible to influence insect behaviours with narrow band LED light sources. The reduction in numbers of leafhoppers caught when traps were illuminated with green LEDs alone was unexpected. The prediction that illuminating traps with wavelengths of green light would increase catch rates was based on the well-established efficacy of yellow traps which are thought to provide a supernormal stimuli due to the ratio of green: blue light reflected (Döring & Chittka, 2007). Thus, increasing the amount of green available to be reflected could be predicted to increase the overall catch rates of the traps. This is the opposite of what the data indicate. This result may be in part due to the feeding location of the leafhopper, which predominantly feed on the abaxial surface of leaves (MacGill, 1932). The trade-offs or interactions between phototaxis and geotropism as a method for determining up/down and mobility vary between species, but in many, lighting is a key cue for choosing feeding areas (Li & Margolies, 1991; Fiene *et al.*, 2013; Sudo & Osakabe, 2013). A low-processing method of distinguishing upper and lower surfaces that uses relative brightness (lower surfaces will be darker) may help explain the results presented here as insects would be preferentially drawn to the unilluminated trap and geotaxis would play little to no role. Contradicting this theory is the evidence of increased catch rates on the combination illuminated traps. As *H. maroccana* are thought to be able to perceive UV light, traps illuminated with both LEDs may be perceived as being brighter by the leafhoppers than the singly illuminated trap. Furthermore, UV light is strongly absorbed by shielding pigments in leaf tissues, as it poses a mutagenic risk to eukaryotes (Day *et al.*, 1993; Ohtsuka & Osakabe, 2009). Thus, a surface with a high level of UV reflection is more likely to be the upper surface of a leaf. As such, attraction to the darker trap for reason of it appearing as the lower surface is unlikely to explain the results presented here.

The negative response of leafhoppers to the green LEDs may be a factor of their brightness. The LEDs selected were close to the suspected peak sensitivity of herbivorous insects (Prokopy & Owens, 1983). The luminous flux (lumens) of the 525nm Green and 535nm Green LEDs was 105lm and 130lm, respectively. It was not possible, however, in the present study to calculate the absolute luminosity of the traps under illumination. This data would be valuable to understanding the leafhopper behaviours seen. Further study may also be improved with electroretinography data on the leafhopper eyes. It is possible to say however, the light reflecting off the surface of the traps would be more intense in the specific wavelength of the LED, though the overall intensity is likely to be lower than a yellow trap under full direct sunlight (Gashniani *et al.*, 2018).

The effects of UV light on insect behaviour has been harder to describe than that of visible light with the consensus tending towards UV light having a non-directional stimulating effect on motion (Ben-Yakir & Fereres, 2016), unlike green or blue light which are observed to induce directional responses (attractive or repellent respectively). It is thought that *H. maroccana* has ultraviolet receptors in the compound eyes that allow it to perceive and respond to UV stimuli (Weintraub *et al.*, 2008). This may be supported by the data from this experiment, where a strong, positive response was seen to UV light when combined with 535nm Green light. By contrast, the lack of statistical difference between numbers of leafhoppers caught when UV light was used on its own could indicate that UV light is only relevant when perceived alongside other stimuli. This is more likely to be the situation in nature, as the sun radiates across almost all of the electromagnetic spectrum and UV light is readily absorbed by the environment and plant tissue (Appleton, 1945; Iqbal, 1983; Osmelak, 1987; Day *et al.*, 1993; Hernández-Andrés *et al.*, 2001; Ohtsuka & Osakabe, 2009). The chance, therefore, of a surface predominantly reflecting UV light in nature is small and an artificial one would present neither a positive nor negative stimuli. Evidence from other pest insect species have described an avoidance of UV light particularly UV-B (280-315nm). In this experiment, UV-A (315-400nm) LEDs were selected as UV-A is dominant in the natural environment, is more closely aligned to insect sensitivity peaks, and poses less of a risk to human health than shorter wavelengths (El Ghissassi *et al.*, 2009). Biological relevance, other than toxicity, of UV-A contrasted to UV-B light for herbivorous arthropods is poorly studied though most arthropods are assumed to be sensitive to UVA (Ben-Yakir & Fereres, 2016). There is evidence that the two interact to limit the phototoxic effect of UV-B via the photoreactivation pathway (Murata & Osakabe, 2014). Some studies have indicated that UV-A does not pose a risk in the same way as UV-B (Onzo *et al.*, 2010; Fukaya *et al.*, 2013), while others have shown UV-A to be a powerful killing agent (Meng *et al.*, 2010; Zhang *et al.*, 2011). As previously stated, a surface reflecting predominantly UV-A light (Combination 4) is likely to be a stimulus far removed from nature, while a surface with a mixture of visible light and UV-A would more closely mimic a leaf surface under natural light.

The use of LED technology in crops is an area of increasing interest due to a potential role in improving the quality of food as well as influencing pest behaviour. Manipulation of lighting within a glasshouse using LED technology can have multiple benefits dependent on the wavelength (s) of light used (Samuolienė *et al.*, 2016). It is standard practice to use sticky traps for monitoring of pests within glasshouses and data presented here show that LEDs can influence, both positively and negatively, catches of leafhoppers under laboratory conditions. Further research on the use of LED lights used in conjunction with sticky traps is required to optimise catches of pests whilst at the same time minimising catches of natural enemies and pollinators.

5 Potential use of generalist predator, *Macrolophus pygmaeus (*Rambur), Hemiptera: Miridae, for controlling glasshouse leafhoppers (*Hauptidia maroccana,* Melichar)

5.1 Abstract

Leafhopper can be a significant challenge to pest managers in crops. The lack of specific biocontrol combined with high dispersal ability by the adults means that controlling this pest in glasshouses is difficult. Control can be achieved with chemicals and generalist predators, but these risk disrupting biocontrol strategies for other pests.

Another strategy is the use of the polyphagous predator *Macrolophus spp.*, which has been suggested to provide some control in glasshouses. This experiment tested the ability of *Macrolophus spp.*to predate leafhopper adults and nymphs. Further testing provide data on the host searching abilities of *Macrolophus spp.* and its potential to move towards odour plumes from plants infested with leafhoppers in comparison to plants infested with aphids, and plants infested with both.

Results indicate that *Macrolophus spp*. is unable to predate adult leafhoppers, with very low levels of consumption seen in practice. Leafhopper nymphs are more suitable prey, with consumption rates comparable to those seen for other prey at similar densities. *Macrolophus spp.* responded to plants infested with both aphids and leafhoppers when these plants were presented alongside uninfested plants.

5.2 Introduction

Biological control with generalist predators can be an effective strategy for managing pest populations within a crop (Symondson *et al.*, 2002). Unlike specialist predators or parasitoids, which require careful identification of pests, generalists can be speculatively deployed within a crop to manage marginal pests. Generalists may also provide a level of protection against pests for which no such specialist is available (Symondson *et al.*, 2002; Hoefler *et al.*, 2006; Zappala *et al.*, 2013).

Hauptidia maroccana is a sporadic, but serious pest of glasshouses in the UK. Able to feed on a wide range of crops and spread plant diseases, *H. maroccana* invasion into crops poses a risk to growers due to the lack of effective biological and chemical control options currently available (Choudhury, 2002). Current control methods rely on use of chemicals, primarily indoxacarb (Jacobson, 2009). Although indoxacarb has been seen to be largely compatible with biological control agents there are still negative outcomes for pollinators in fruiting crops such as tomato or sweet pepper (Wing *et al.*, 2000; Kuk & Kim, 2017). There remains, therefore, an incentive to test novel control methods or novel applications of pre-existing controls.

*Macrolophus spp.*is primarily used for control of thrips and whitefly, but it is promoted as a generalist predator able to feed on multiple species across pest guilds (Lucas & Alomar, 2002; Lykouressis *et al.*, 2007; De Backer *et al.*, 2015; Pappas *et al.*, 2015). There is evidence however, that it shows significant prey preferences when presented with a choice of prey, and that this can, under experimental conditions, alter predation rates (Foglar *et al.*, 1990; Enkegaard *et al.*, 2001; Cuthbert *et al.*, 2020). Many experiments examining the ability of *Macrolophus spp.*to control pests present these pests in isolation (Perdikis & Lykouressis, 2004; Lykouressis *et al.*, 2007; De Backer *et al.*, 2015; Maselou *et al.*, 2015). Under no-choice scenarios *Macrolophus spp* .shows significant polyphagy. This facultative polyphagy is common among the generalist predators and may contribute to lower than expected control of pest species. This effect has been documented in the opposite direction as well. When feeding on low quality hosts, the western flower thrips, *Franklinella occidentalis* (Pergande) will increase the rate at which it consumes the eggs of the pest mite *Tetranychus urticae* Koch (Janssen *et al.*, 2003). Further, there is increasing evidence that many species are facultatively omnivorous, and will consume plant matter in the absence of sufficient prey, or low quality prey items (Agrawal & Klein, 2000; Coll & Guershon, 2002; Janssen *et al.*, 2003). It has been suspected that this might drive plants to become low quality hosts, leading to omnivores switching to feeding more on prey, however this was not seen to be the case in field studies (Eubanks & Denno, 2000).

Another risk associated with generalist predators is intraguild predation (IGP) where predators prey on other predators or parasitoids within the crop. The impact of IGP on biocontrol systems is complex and still being established. In some cases, IGP may result in a reduction in the level of control (Chong & Oetting, 2007), while in other cases, interactions do not result in a change (Chow *et al.*, 2008). In some cases, compatibility between predators and parasitoids has been documented resulting in increased control (Zang & Liu, 2007). As a biological interaction, the extent and intensity of IGP depends on the conditions under which the species interact. In one case, predation of parasitoid mummies by a generalist predator resulted in significantly greater populations of aphids later in the year when infested plants were short, but this was avoided if plants were tall (Snyder & Ives, 2001). In other cases, risks posed by predators to parasitoids could be avoided by allowing an interval between the introduction of the parasitoid and the predator sufficiently long that the parasitised prey hardened into a “mummy” (Chong & Oetting, 2007). In some cases, the fitness implication of IGP has been sufficient that IGP prey species have developed avoidance behaviours to limit their exposure to IGP predators (Nakashima & Senoo, 2003; Nakashima *et al.*, 2004, 2006). Due to the complexity inherent in IGP interactions, potential effects are hard to predict and testing is necessary.

Plants are able to detect herbivore damage and respond by releasing a blend of volatile chemicals termed herbivore induced plant volatiles (HIPV). These chemicals serve a number of purposes; from direct repellence of herbivores through noxious effects (Veyrat *et al.*, 2016), signalling competition to other foraging herbivores, and attracting higher trophic level organisms that may reduce the pest pressure (Dicke & Baldwin, 2010). Plants are able to discriminate between different herbivores and produce chemical blends that are indicative of that species (De Moraes *et al.*, 1998; Sobhy *et al.*, 2017). In some cases, the sensitivity is such that discrimination between pest life stages is possible (Takabayashi *et al.*, 1995). The chemicals are often exploited by foraging carnivores to locate hosts or prey, and for species with narrow host ranges or prey specialisms, these cues can be vital. Generalist predators and parasitoids could be assumed to have less of an evolutionary pressure to be so attuned to the volatiles released by plants in response to specific pest damage and this has been documented in specific instances (Ngumbi *et al.*, 2009). Evidence from a literature review implies that this effect is mediated by the specific life stage targeted by the predator, with specialists parasitising adult individuals showing greater sensitivity and selectivity of HIPV than those parasitising larval stages (van Oudenhove *et al.*, 2017). For a generalist predator deployed in a crop, the ability of foraging individuals to locate prey will be influenced by the production of volatiles which will in turn be influenced by the pest species present. This information will likely be influenced by many other external factors including prey preferences. This experiment tests the ability of *Macrolophus pygmaeus* to act as a predator *of Hauptidia maroccana*, as well as the host location and preference of this generalist predator under laboratory conditions.

5.3 Methods and materials

5.3.1 Leafhopper culture

Hauptidia maroccana cultures were maintained in 47.5x47.5x47.5cm^3 Bug dorms (BD4S4545, MegaView Science Ltd., Taichung, Taiwan) under standardised conditions (20°C, 60%RH, 16:8 Light:Dark) in controlled environment chambers (Weiss Technik, Ebbw Vale, UK) on Primrose (*Primula vulgaris vulgaris*) plants. Primrose were grown from root stock in John Innes No. 2 potting compost (Westland Horticulture LTD., County Tyrone, Northern Ireland). Plants were periodically replaced to ensure adequate food supply.

5.3.2 *Macrolophus* culture

Approximately 500 adult and late instar *Macrolophus pygmaeus* were acquired from a commercial supplier (BioLine AgroSciences Ltd., Essex, United Kingdom) in the form of the product MacroLine. *M. pygmaeus* were retained in 47.5x47.5x47.5cm Bugdorms (BD4S4545, MegaView Science Ltd., Taichung, Taiwan) under the same environmental conditions as leafhopper (20°C, 60%RH, 16:8 L:D). *M. pygmaeus* can reach adulthood on some crop plants, but this is undocumented on primrose. To increase longevity and resilience for experiments, plant diet was supplemented with *Ephestia* eggs as Bugfood E (BioLine AgroSciences Ltd., Essex, United Kingdom).

5.3.3 Aphid culture

Aphids for the culture were accessed from a long-term culture present at Harper Adams University. Uninfested primrose (*Primula vulgaris vulgaris*) were placed in 47.5x47.5x47.5cm Bugdorms in controlled environment chambers (20°C, 60%RH, 16:8 L:D). Ten adult aphids (*Aulacorthum solani*) per plant were introduced. Aphid introductions continued until first instar nymphs were observed on primrose to ensure successful establishment.

5.3.4 Doubly infested culture

As with previous cultures, clean primrose plants were placed in 47.5x47.5x47.5cm Bugdorms in controlled environment chambers (20°C, 60%RH, 16:8 L:D). Twenty adult leafhopper and 10 adult aphids (*Aulacorthum solani*) per plant were introduced as previously described.

5.3.5 Leafhopper predation bioassay

Adult *M. pygmaeus (n*=20) were removed from the culture at approximately 1700h each day. *M. pygmaeus* were retained individually in 7.5cm Petri dishes with dampened filter paper in growth chambers under the same conditions as cultures. Experiments began each day at 1000h when 16 surviving *M. pygmaeus* had 10 leafhoppers introduced. Starving individuals for longer than 17h, raised the level of mortality unacceptably high. Individuals were sexed prior to introduction to the Petri dish. As with many Miridae, sexing adult *Macrolophus* can be done by examining the ventral surface for the presence of an ovipositor. *M. pygmaeus* were presented with either 10 adult leafhoppers or 10 mid instar nymphs. *M. pygmaeus* and leafhopper numbers and status were recorded after 6h and 24h. Leafhopper that were seen to be dead were examined under a dissecting microscope for signs of being fed on. Consumed leafhopper adults could be distinguished by the shape of the abdomen, which was notably flattened in consumed leafhoppers. The same was true for nymphs.

5.3.6 HIPV olfactometer assay

M. pygmaeus adults (n=40) were removed from culture at 1630h each day. Though only 36 were required for each day, a greater number were aspirated to account for possible mortality. *M. pygmaeus* were starved in 50ml Polypropylene sample tubes (Sarstedt AG & Co., Nümbrecht, Germany) with dampened cotton wool overnight. Screwcaps were perforated to reduce condensation or asphyxiation.

Leaf material for volatiles were excised just prior to use in experiments. Five fully expanded leaves from each culture (leafhopper, aphid, clean, doubly infested) were cut at the base of the petiole. Excised leaves were wrapped in tinfoil with dampened cotton wool to maintain leaf hydration. Volatiles from the leaves were collected using a 2L glass Dreschel bottle (Sci-Glass Consultancy, Bere Alston, UK) with a 6mm outlet. The opening of the Dreschel bottle was sealed externally with Parafilm (Parafilm M, Bemis Company, Inc., WI, USA) and bulldog clips. Airflow was provided by a micro diaphragm gas sampling pump (KNF Neuberger, Inc., NJ, USA) at a rate of 1 L/min controlled by a flowmeter (GPE Scientific LTD, Bedfordshire, UK). Air was drawn into entrainment through a 1L Dreschel bottle containing activated charcoal to remove potential contaminants. The volatile sources were connected to the olfactometer via ⌀3mm PTFE tubing (Airline Fittings, Matlock, United Kingdom) and 6mm to 3mm brass tube reducing unions (Swagelok, Manchester, United Kingdom). All brass fittings were made airtight with PTFE ferrules (Swagelok, Manchester, United Kingdom). A single glass Y-tube olfactometer was used to expose the *M. pygmaeus* to entrained air. The olfactometer was connected to the tubing using thistle funnels with a 6mm outlet. Visual stimuli were blocked using white fabric panels mounted on a 47.5x47.5x47.5cm Bugdorm frame (BD4S4545, MegaView Science Ltd., Taichung, Taiwan). Light for the experiment was provided by a single photography fluorescent bulb mounted on top of the frame (PhotoSEL LTD, London, UK). A diffuser filter prevented polarised light acting as a cue.

The olfactometer Y-tube was 22cm long, with a stem of 12cm and arms of 10cm. The angle of the branch was approximately 72° and the internal diameter was a constant 14mm.

Experiments began the day after aspirating at approximately 1030h, 2.5 hours after simulated dawn in the growth chamber. After excised leaves were placed into Dreschel bottles, the system was purged with airflow at 2L/min for 5 minutes. Each infestation state was counted as a treatment. Treatments were compared in pairs giving 6 combinations: 1) Aphid-Leafhopper, 2) Aphid-Clean, 3) Aphid-Aphid+Leafhopper, 4) Clean-Leafhopper, 5) Clean-Aphid+Leafhopper and, 6) Leafhopper-Aphid+Leafhopper. Each combination was tested 6 times. After three tests in one orientation, the sides that each treatment was on was swapped. Between combinations, all glassware was washed with HPLC grade acetone (Sigma-Aldrich Co. Ltd., Dorset, UK) and dried at 75°C in a glassware oven for 5 minutes. It was then allowed to cool for at least 5 minutes before the next combination was tested. Combination order was randomised each day for 6 days. *M. pygmaeus* were given 5 minutes to make a choice. A choice was counted when an individual passed a mark 7cm after the branch point of the Y-tube.

5.3.7 Statistical tests

Data were analysed using the R programming language. In the bioassay tests, differences in consumption between samples and genders were tested with a Mann Whitney U test. Possible interactions between leafhopper stage, predator gender and time were modelled. Two models were used and compared. Initial analysis was conducted using a Poisson distribution generalised linear model. A zero-inflated regression using the tool ZEROINF from R package PSCL (Jackman *et al.*, 2017) was also evaluated. This was compared using a Vuong test of closeness (Vuong, 1989).

Y-tube olfactometer tests were analysed with repeated binomial tests of difference.

5.4 Results

Macrolophus. pygmaeus consumption of adult leafhoppers was extremely low. Mean consumption after 6 hours was seen to be less than 0.1 for both genders, rising after 24h to 0.12 for males and 0.18 for females (Fig. 5.1). This increase was statistically significant, however small (W=2878, *p*=0.03).

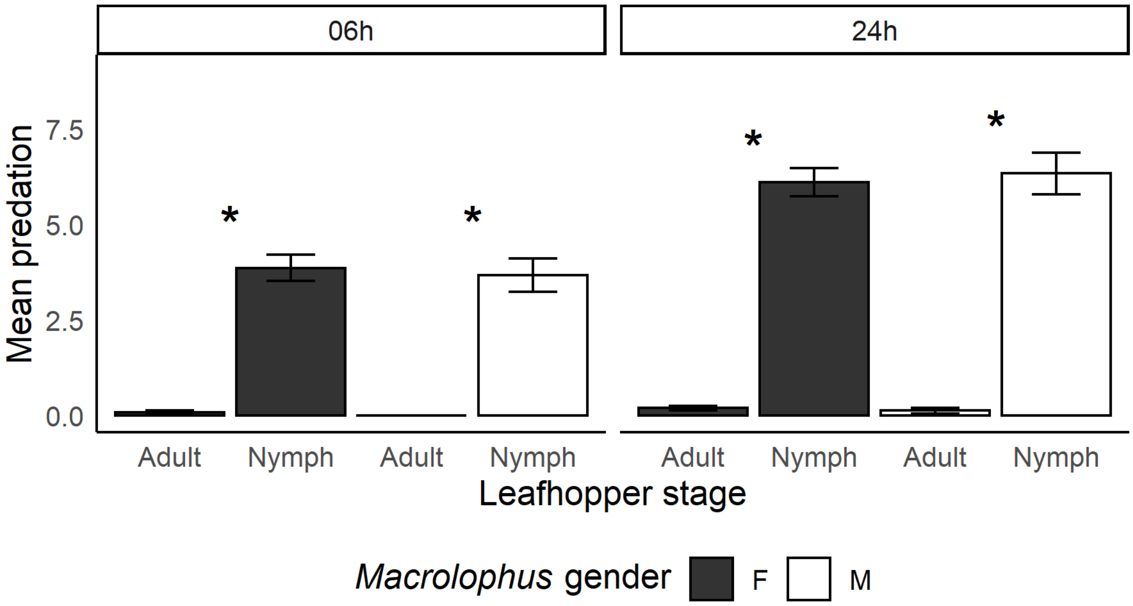


Fig. 5.1 Mean predation of H. maroccana individuals being grouped by sex and prey life stage. Error bars give SEM.

The gender of the *Macrolophus* attacking adult leafhopper was also observed to have a weak increase, with female *M. pygmaeus* consuming significantly more leafhopper than male (W=3337, *p*=0.04). It must be stressed however, that although significant differences were seen, the number of adult leafhoppers consumed by starved *M. pygmaeus* was below 1 on average.

M. pygmaeus presented with leafhopper nymphs consumed many more than those presented with adults. Combined sexes consumed a mean of 6.2±2.7 nymphs after 24h. A

Wilcoxon rank Sum test showed no difference between *M. pygmaeus* genders at either 6h (W=725, *p*=0.6) or 24h (W=2766, *p*=0.8).

A zero-inflated regression with interaction terms indicated that the developmental stage of the leafhopper (i.e. adult vs. nymph) and sample period were the only variables influencing consumption rate. The same results were seen with a Poisson distribution GLM using the same terms. In both no significance of the interaction terms was seen. However, a Vuong test of closeness indicated that under all assumptions the zero-inflated regression provided a better fit to the data (BIC Correction, Z=-2.24, *p*=0.01). Consequently, it was seen that the developmental stage of leafhopper prey was the most significant predictor of feeding level (Z=5.78, *p*<0.0001).

M. pygmaeus olfactometer tests showed inconclusive preferences. Overall, plants absent of any herbivore damage (Clean) were seen to be the least attractive, showing significantly lower choices when presented against Leafhopper (C-L, *H*=0.24, *p*=0.015) and multiple infestation (AL-C, *H*=0.77, *p*=0.009). Aphid infested plants were chosen significantly more than clean plants when presented together (A-C, *H*=0.68, *p*=0.043). Further significant differences were seen when *M. pygmaeus* were presented with volatiles from plants infested with aphids alongside multiple infested plants, with a significant preference for the multiple infested plants (A-AL, *H*=0.22, *p*=0.0059). No significant difference in choices were seen when leafhopper infested plants were presented alongside aphid infested plants (A-L, *H*=0.62, *p*=0.307), nor when leafhopper volatiles were compared to multiple infested plants (AL-L, *H*=0.6, *p*=0.36).

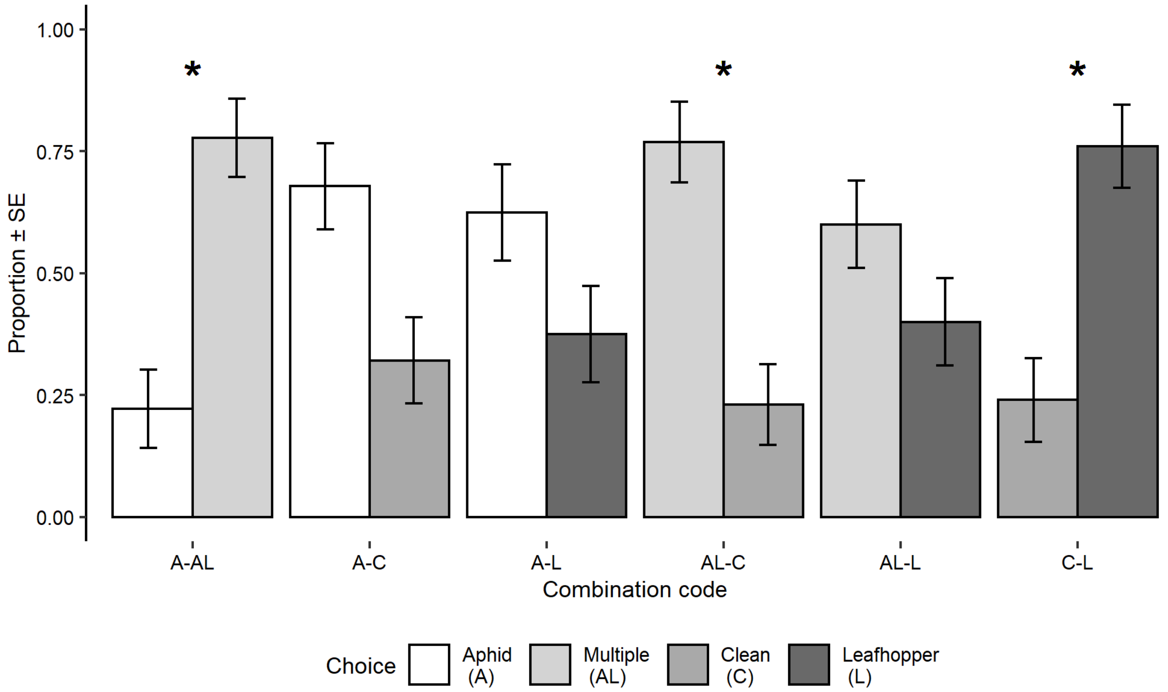


Fig. 5.2 Proportion of Macrolophus moving towards the odour plumes from plants. Proportion reflects the proportion of Macrolophus making a choice rather than the proportion of the total number tested. Error bars give SE. Stars indicated siginficant differences. Codes for treatments are given in brackets in legend.

5.5 Discussion

The low level of consumption of leafhopper adults by *M. pygmaeus* was striking. As a generalist predator, the use of *M. pygmaeus* alone as a control method for leafhopper is unlikely to provide adequate control. The reasons for this lack of predation are unknown, and would require further behavioural assays to describe. It may be that the leafhoppers present an unappealing prey item, that despite a 17-hour starvation period *M. pygmaeus* are unwilling to attack. Conversely, and more probably, the starved *M. pygmaeus* are unable to successfully attack the leafhopper adults due to anti-predator behaviours. Selective predation on less-developed and potentially more vulnerable larval stages, such as eggs or nymphs, over adults has been observed across many predatory insects and mites experimentally (Bazgir *et al.*, 2020; Devasia & Ramani, 2020; Kumar *et al.*, 2020; Pirzadfard *et al.*, 2020). As samples were only taken at the two stated times it is unknown whether the predated leafhoppers seen were attacked while alive or opportunistically after dying for other reasons. *M. pygmaeus* is a facultative omnivore and will consume dead prey items under starvation conditions. Future research on this topic should take this into account in experimental design through inclusion of control dishes for monitoring mortality without predators.

The ability of adult leafhoppers to avoid predation through behaviour may rely on their strong jumping response. This is a well-documented behaviour (Sutton, 2014; Clemente *et al.*, 2017). In some aphid species, a defensive kicking response to parasitoids has been documented (Gerling *et al.*, 1990; Wyckhuys *et al.*, 2008). While this has not been demonstrated in leafhopper, planthoppers under attack from parasitoids will kick to defend themselves (Mckamey & Deitz, 1996; Uy & Espinoza, 2018) which raises the possibility of active defence beyond escape mechanisms. Furthermore, it was shown that later instar nymphs were more successful at defending themselves from attack by parasitoid (Uy & Espinoza, 2018). This may contribute to explaining the results seen here as adult leafhopper would be able to defend themselves more actively than nymphs. This pattern is further documented in the jumping escape response where the jumping ability of leafhopper nymphs is less than that of adults (Burrows & Wang, 2007). These combined changes between adult and nymph may be sufficient to explain the lack of predation if the *M. pygmaeus* are willing to attack adult leafhopper.

If the predation levels seen here are carried over to a glasshouse, the potential for *M. pygmaeus* to act as a successful biocontrol may be similar to its performance controlling other pest species. In other studies with different prey species, the prey items per predator consumption rate for the same prey density was 7.1±0.452 (*Trialeurodes vaporariorum*, Hamdan, 2006), 10±0.01 (*Tuta absoluta*, Urbaneja *et al.*, 2009), and between 6.9±0.43 (n=8) & 10.7±0.37 (n=12) (*Myzus persicae*, Maselou *et al.*, 2015). The net mean consumption of nymphs seen in this experiment was 6.18±0.30. While this is lower than all other reported consumption rates, the nymphs presented are larger than the previously studied prey, which may explain the lower value seen here. Studies examining the total biomass consumed by feeding *M. pygmaeus* may indicate whether this is a relevant point. Other reasons for difference in the feeding level may relate to the suitability of the nutritional content of the prey items.

The results of the olfactometer tests indicate that *M. pygmaeus* can distinguish between HIPV plumes from infestation. This is not uncommon in predatory insects, and various preferences have been demonstrated for *Macrolophus*. The attraction of *M. pygmaeus* to aphid specific HIPVs have not been tested and there are few studies documenting the influence of jointly infested plants on *M. pygmaeus* attractance. One of the few that does indicates that for *Macrolophus basicorni*s, tomato plants infested with two potential prey species (*Tuta absoluta* larvae, and *Bemisia tabaci*) are not more attractive than plants singly infested with *Tuta absoluta*, but were more attractive than plants infested by *B. tabaci* alone (Silva *et al.*, 2018). This is similar to the results seen here which indicated that a doubly infested plant (AL) was more attractive than a plant infested with one species (*A. solani*, AL-A), but not the other (*H. maroccana*, AL-L). Interestingly there could be a trend, in that a phloem feeder alone (*A. solani*, *B. tabaci*) gives rise to volatiles that are less attractive than those induced by a more destructive, folivorous feeder (*T. absoluta*, *H. maroccana*) that directly damages leaf cells. Unfortunately, a direct comparison between the two was not conducted in the previous study. In the study reported here a direct comparison between the two feeding strategies alone does not result in significant differences. Plants are able to detect herbivore damage and upregulate genes associated with defence (Chaudhary *et al.*, 2018). This detection is sensitive to the form of damage sustained and can discriminate between the physical method of damage as well as sensitivity to specific proteins in the insect saliva (Delphia *et al.*, 2007; Kim *et al.*, 2011). This allows plants to produce different volatile blends for different pest pressures which will be more, or less attractive to higher trophic levels. It is also known that when tobacco plants are attacked by a caterpillar and a thrips species the volatile blend resembles that of attack by the caterpillar solely, but with much more chemical released (Delphia *et al.*, 2007). It may be that the reason *Macrolophus* showed no difference in attraction between multiple infested plants and leafhopper infested plants is that the same pattern of volatile production is observed here. Characterisation of the volatiles produced by multiple infested plants would allow this theory to be tested.

Starved *M. pygmaeus* did not show a choice preference between leafhopper or aphid infested plants. It is unknown why this is. It is unlikely that the two odour streams are similar, given the differences in the feeding mechanisms (Dinant *et al.*, 2010) and probable distinct saliva contents (Harmel *et al.*, 2008; DeLay *et al.*, 2012). As plants can detect and respond to both different herbivory mechanics and insect saliva proteins (Hilker & Meiners, 2010; Barah & Bones, 2015), there is likely a qualitative and quantitate difference in the volatile blends produced. For the tested individuals to show no preference suggests that *M. pygmaeus* is either insensitive to, or unable to evaluate the differences in the volatiles produced by infested plants. Given that *M. pygmaeus* show prey preferences that impact the fitness of the individual, it seems reasonable to suggest that there would be an evolutionary pressure to be able to locate more beneficial prey items. It raises the question therefore of what cues within the multiple infested plant volatiles the tested *M. pygmaeus* are responding to. It is known that multiple infestation results in an increase in the volume of volatiles produced (Dicke *et al.*, 2009). That is, volatiles that are present when each pest is feeding singly are produced in larger quantities when both pests are feeding simultaneously. Further, increased damage results in increased emission of HIPV (Dicke *et al.*, 2009). Under the doubly infested condition, the plant can be safely assumed to be experiencing a greater level of damage than under either of the two single-infestation conditions. It could be suggested that *M. pygmaeus* shows a response to an increase in the quantity of volatiles rather than a specific blend or component, as a stronger signal promotes a stronger response (Cai *et al.*, 2017). There is, however, evidence against this theory within the data presented here. If the quantity was the only cue *M. pygmaeus* were attentive to, there would be (presumably) a difference between AL-L, with AL preferred. This was not supported in the data with a non-significant difference seen between these two treatments at the 0.05 confidence level.

Control of leafhoppers in glasshouses is primarily through chemical means. There is a desire to shift toward biological control methods that will likely be more compatible with existing control strategies (Radcliffe *et al.*, 2009). The evidence presented here is that *M. pygmaeus* as a biological control agent for leafhopper is unlikely to provide the levels of control desired if it only encounters adults. Predation levels on nymphs was higher and *M. pygmaeus* may result in sufficient levels of control in glasshouses this way. *Macrolophus* is a noted egg predator, however many of the eggs it feeds on are laid externally on leaves, whereas most Cicadellidae lay their eggs within leaf tissues for protection. The ability of *Macrolophus* to locate leafhopper eggs under the leaf epidermis and to penetrate and feed on them is unknown. Further research on this topic should be undertaken to get a fuller picture of the potential of *Macrolophus* to control leafhopper in glasshouses.

6 General discussion

This thesis was researched and written with the title *improving biological control in protected crops*. To this end, the research undertaken was done so with the intention of filling in some gaps on control of a sporadic pest that nonetheless is able to cause substantial damage when control fails, or when invasion is not noticed (Seljak & Pagliarini, 2004).

The use of insect traps for monitoring pest populations is a crucial tenet of IPM. Without knowledge of the timing of invasion of pests into cropped environments it is impossible to attempt to control them in a targeted manner. Even for prophylactically deployed species, the potential for negative interactions between controls necessitates careful deployment that considers the presence of suitable hosts. When releasing controls for which the level of interaction is likely to be low (e.g. two specialist parasitoids targeting different species) the need for monitoring for invasion will be reduced. Nevertheless, even under these circumstances, keeping track of the populations of the pest and parasitoids within the glasshouse is important to ensure the system is working satisfactorily. The use of accurate monitoring must be coupled with detailed record-keeping so that trends in pest threat levels can be interpreted. The value of this data will only increase in the face of climate change which is likely to alter the distribution and development times of many significant pests (Bale *et al.*, 2002; Trumble & Butler, 2009). The results of the experiments here indicate that for *H. maroccana*, and presumably other insects, there are still avenues that can be explored to improve the trapping, and therefore monitoring sensitivity, of this pest (Non-yellow traps for glasshouse leafhopper monitoring; evidence for effective alternative colours, p31). With a number of other pests showing similar trends, there is enough evidence to suggest that re-thinking the dominance and ubiquity of yellow traps may well be worth doing for pest species that show less than satisfactory catch rates with yellow traps (Rodriguez-Saona *et al.*, 2012; Bian *et al.*, 2014; Mcneill *et al.*, 2016; Kirkpatrick *et al.*, 2018). The evidence here for examining the responses of insect pests to visual cues is backed up witht the results seen using LED lighting to increase and alter the visual signal. The LED peak wavelengths (525, 535nm) were selected using statistical analysis of data from a pevious experiment. These wavelegths were close to the reported peak sensitivity of the green receptor of other herbivorous insects (556nm, Giurfa *et al.*, 1997; 540nm; Antignus, 2000; 540nm; Chittka *et al.*, 2014; 504nm; Chen *et al.*, 2016c). Given the widely reported attractive nature of green wavlenghts the opposite result seen here illustrates again that there may be a greater degree of complexity to colour perception and decision making. This is true too of the environment that has been created within the glasshouse as it was seen that UV and green light alone were not attractive, but when combined acted to significantly increase the catch rate of the traps. Given that glass of any thickness reduces the level of UV light present, there is a possible impact on the behaviour of the insects. The role of UV on insect behaviour is a complicated picture with evidence that UV reflective traps with a hihg level of UV reflection caught fewer leaf feeding thrips, while attracting significantly more flower feeding thrips (Matteson & Terry, 1992). By contrast, it has been documented that aphids reared under UV blocking film had slower population increase (Legarrea *et al.*, 2012). It can be assumed therefore that the UV light confers some benefit on the pest, or enhances the quality of the food source. It is unlikely to be directly conferring benefit on the pest by exposure as this contrasts with the many reports of insect pests avoiding UV light (Mazza *et al.*, 1999; Ohtsuka & Osakabe, 2009; Murata & Osakabe, 2014; Ben-Yakir & Fereres, 2016; Kim *et al.*, 2019). UV light not only alters the insect's behaviour, but the biochemistry of the plants on which they feed. It has been shown that UV increases the production of secondary metabolites in plants, many of which are the flavourful compounds that the crop is grown for (Dou *et al.*, 2019). Through this mechanism the behaviour of insect pests can be altered. The settling behaviour of Bemisa tabaci on eggplant is significantly reduced when plants are exposed to UV light for short periods of time (30-90 minutes Prieto-Ruiz *et al.*, 2019). Foraging thrips avoid not just UV light, but leaves that have been exposed to increased levels of UV (Mazza *et al.*, 1999). This behaviour creates a cascade of changes in the ecosystem as a secondary pest then avoids feeding on thrips-damaged leaves (Mazza *et al.*, 1999). The implications of introducing UV light into a glasshouse cropped environment is therefore likely to need careful and cautious testing before any system is fully deployed.

Taken in total, the results here largely match those seen in other experiments and largely meets objective 1 of testing the studied species against other coloured traps. The key interpretation of the data here is that more can be done with simple tools to improve monitoring sensitivity and potentially control efficacy. The use of additional lighting in glasshouses has historically relied on the use of broadband emitting light sources, often at low power efficiencies (e.g. High Pressure Sodium lamps; Bredmose, 1993). These lighting systems have high power demands, which increases the running costs, and generate a substantial amount of heat. As such, use of these lights may incur potential risk to growing plants. When comparing LED technology to conventional lighting arrays, the key features are wavelength specificity and power consumption. Current high power diodes are able to produce in the region of 125 lumens per watt consumed (Morgan Pattison *et al.*, 2018). By contrast, conventional compact fluorescent tubing has an efficiency of approx. 70 lumens per watt (Morgan Pattison *et al.*, 2018). LED technology also generates far less heat, making it safer for workers, plants and beneficials alike. With all of these potential benefits in mind, the flexibility of LED illumination in glasshouses is far greater than historic light sources. For example, in this study, high power LEDs were powered by a self-contained, waterproof, rechargeable driver circuit. The design allowed the LED to be powered on at maximum intensity for many hours. Further optimisations in the design with a better understanding of circuit architecture may result in improvements in the longevity of the illumination allowing for multi-day battery powered illuminated traps. The potential of these traps to increase trapping rates was demonstrated in this project. The method in which the traps were illuminated would need to be tested for scalability, and under large-scale commercial production, it may be easier to have a single, mains-voltage circuit with LED drivers wired in parallel to each trap. This may pose an increased risk, due to the generation of potentially lethal current from mains circuitry, however this can be overcome using appropriate testing and protective housings for live components. A significant limitation for this technique is that no electrophysiological information is available for *Hauptidia maroccana*. Without an understanding of how *H. maroccana* perceives light, both in terms of wavelength sensitivity and intensity, the questions about why green LED enhanced traps will remain challenging to answer and robust justification of this as a potential trapping method will continue to be hard. Importantly, the impact on pollinators, and introduced biocontrol agents was not tested here and would need rigorous evaluation before wide-scale adoption.

Another key aspect of IPM is the management of pest populations once they go above the economic injury level (EIL). This prevents prophylactic control tactics which may help reduce the potential for resistance developing in populations (Onstad, 2008). Crucially for this project there is no known EIL for *H. maroccana*. Without this basic understanding of the risk posed by the pest to crops, the management will continue to be potentially less effective than necessary, regardless of the specificty of any and all control methods. The lack of an EIL for this species was not seen as being a limitation to this project, as any progress in control would constitute an improvement for this understudied species. Calculation of an EIL for pest species is important for IPM strategies, however, there are costs associated. EIL for other leafhopper damaged crops have been seen to vary with growth stage (Lefko *et al.*, 2000), with tolerance to leafhopper damage increasing tenfold between seedling and year old alfalfa plants (Lefko *et al.*, 2000). While this does raise the possibility that leafhopper EIL would need to be calculated for multiple plant growth stages, in glasshouse *Capsicum anuum* production, plants are replaced on a yearly basis. Further alterations to the EIL are seen when resistant plants are grown (Hunt *et al.*, 2000). While the resistance to pests is likely to be a selling point for crops, if every cultivar potentially has a different EIL, the amount of work necessary to accurately advise growers will be significantly increased. The relevance of this factor is likely to grow as breeding for resistance to pests is a common IPM technique (Onstad, 2008; Radcliffe *et al.*, 2009). Given the sporadic nature of *H. maroccana* and the high cost of developing an IPM protocol, there is a question as to whether or not the benefits to growers outweigh the costs of development. This is particularly relevant given that there is a legal and effective chemical control that can be integrated with biocontrols relatively simply, and in the belief that the generalist predator *Macrolophus caliginosus* will provide adequate control. The evidence here indicates that *Macrolophus caliginosus* will not provide adequate control. The current study did not make an attempt to characterise the potential of *Macrolophus* to predate leafhopper eggs, and an evaluation of this may provide a reversal of the previous claim. *Macrolophus* are sometimes deployed in glasshouses as a control for leafminers (Maselou *et al.*, 2015) and that this predation takes place after the larvae have migrated to within the leaf tissue (A. Urbaneja, 2016, pers comm.). There will be a trade-off between the costs of developing the necessary IPM protocol and the benefits provided. Given the lack of specific control agent, and the cost and effort needed to develop one, the equation seems to be shifted in favour of the status quo.

One thing that may necessitate a more thorough analysis of this pest would be a change in it's status as a disease vector. Currently, *H. maroccana* is not a known plant disease vector in the literature, though whether this is due to lack of study or an actual chemical incompatibility is unknown. Both instances have been seen in other invertebrate pests. There are documented cases of a known pest being discovered to transmit pathogenic organisms long after the pest and the disease were recognised to be sympatric, (*Frankliniella cephalica*, Ohnishi *et al.*, 2006). This contrasts with pest species that are seen to have chemical compatibility with plant pathogens, and are able to acquire and spread them under experimental conditions, but show no in-field vectoring ability (Hogenhout *et al.*, 2008). In the case of *Hauptidia maroccana*, the low frequency of outbreaks have resulted in little work examining the vector capability of this organism. Further adding to the difficulty in establishing the vector potential of a pest is evidence that the source of infection may alter the transmissibility of the pathogen (Yule *et al.*, 2019). In this case, the same virus (Tomato yellow leaf curl Thailand virus), spread by the same vector (*Bemisia tabaci* Genandius) could be vectored between two crop species (Tomato and Sweet pepper), but only in one direction. Cases such as these emphasise the need to closely examine the relationships between plant diseases and vectors, even in situations where there is potentially little evidence. Given the documented vectoring capability of other species in the same family (Cicadellidae), the potential for *H. maroccana* to act as an as-yet undiscovered vector may be higher than for other species. Further, the global trade in plants increases the risk that new pathogens will enter areas they were not previously documented in. Though quarantine mechanisms and plant health regulations exist in many countries and trading blocs, the scale of global trade and lack of regulations on individuals means that the risk of introduction of alien pathogens and pests remains (Schrader & Unger, 2003). The introduction of these raises the possibility of a pathogen encountering a novel, compatible vector species. It is by this mechanism that *H. maroccana* may become a more significant pest species.

Objective 2, to test the capability of the generalist predator *Macrolophus caliginosus* was answered in the negative by the data here, within the limits of the tests conducted. With low predation levels on adults and indications that it prefers volatiles emitted by aphid-infested plants within a crop, the use of this biocontrol agent alone to manage populations of *H. maroccana* should not be recommended. However, the predation on nymphs and the ability of *Macrolophus* to detect and move towards infested plants indicates that as a generalist, the presence of *Macrolophus* may have some potential to reduce leafhopper populations through opportunistic predation on nymphs. In order to fully understand this potential, further experiments in glasshouses over a longer period would need to be conducted. In particular, for the use of *Macrolophus*, careful evaluation of the population levels relative to pest pressure must be conducted, due to its potential to transition from beneficial to pestiferous at high populations and low pest levels (Castañé *et al.*, 2011). As previously stated for a sporadic pest that is currently controlled chemically, the level of research into new biocontrol agents is low. The ineffective control provided by *Anagrus atomus*, in part due to its life cycle and nature of the host, may also have put growers off, as negative experiences can reduce the uptake of biocontrol (Barratt *et al.*, 2018). Therefore, there may be an uphill battle to persuade growers of the efficacy of new biocontrol for leafhopper, and the continued use of *Macrolophus* presents a risk that this mistrust will be exacerbated.

Plant volatiles mediate a great many ecological interactions. Both predators and herbivores are sensitive to plant volatiles for resource location and predator avoidance (Bruce & Pickett, 2011; Benelli *et al.*, 2016; Shivaramu *et al.*, 2017). The data here indicate both are at play. The seemingly dispersive behaviours of the leafhopper when presented with either direct conspecific cues or conspecific induced volatiles suggest that in a crop, foraging leafhopper would be more likely to move away from plants already infested with leafhopper. Changes in herbivore behaviour due to the feeding action of other herbivore species is primarily documented with avoidance of plants being seen (Mazza *et al.*, 1999; Delphia *et al.*, 2007). This may be to avoid competition for space or nutrition, or exposure to induced plant defences by the original pest. The avoidance of multiple infested hosts may reduce the chances of predation by a generalist predator as data shown here indicate that multiple infested plants are more attractive to generalist predators. In order to simplify the data, experiments here were conducted in vitro under controlled environmental conditions with starved leafhoppers. Under real-world conditions, with increased variability, the leafhoppers may be exposed to other cues that alter the foraging behaviour. Furthermore, the tested leafhopper were off-plant. The on-plant behaviour of leafhopper was not evaluated in this project. From a host acceptance perspective, there is an un-answered question as to whether insects already feeding on a plant leaf will disengage and switch host. In this potential “steady state” the optimal foraging strategy is likely to be to remain on the current host, rather than leaving a known host and following cues to a new one. The jumping/flight escape response of *H. maroccana* may represent a moment in which this switch takes place as the insect is off-plant. The interaction of this pest and introduced predators in cropped environments was not examined, but it is suggested that this might be a common response to threats. It may be that for feeding leafhoppers on a sub-optimal host with no other external stimuli, moving from plant to plant in search of superior host material represents a far greater fitness cost due to increased risk of predation or other factors. In this specific state, and under the suggested fitness pressures, the results seen here are not likely. By contrast, if a foraging leafhopper is triggered to jump from the leaf by the presence of a predator, then it will be off-plant and the host-selection behaviours seen in this project may kick in. This kind of behavioural trigger is already taken advantage of by growers who have reported greater catch rates on sticky traps mounted to the front of greenhouse harvest trolleys which move through the crop causing many leafhoppers to jump from leaves (S. Budge, *pers comm.*)

Growers may benefit from further work that examines the degree to which insects already on plants make host-switching choices and what impact population density has on those choices, as these may lead to the formation of hotspots. The predator *Macrolophus* was presented with plant volatiles in a y-tube arrangement and showed mixed responses to these volatiles that imply prey preferences. How this translates into satisfactory levels of control of leafhopper in glasshouses remains to be seen.

This project has provided some potential avenues for the improvement of control of leafhopper in glasshouses, but the majority of work was conducted under laboratory conditions. There is the possibility that under glasshouse conditions the performance of methods described here may not translate to real-world benefits to growers. This possibility was seen at one point in the study, where the gold (RGB) sticky traps that proved comparable to yellow traps were tested in a commercial glasshouse. 50 yellow sticky traps and 50 gold (RGB) traps were deployed evenly into a commercial pepper crop with a leafhopper outbreak in Essex. The catch rates of leafhopper on each colour of trap was recorded and differences were examined. This data was not reported here due to limitations in the execution of the study; 1) the site was discovered very late in the year when leafhopper populations were low and declining, 2) the deployment of the traps was hampered by difficult working conditions and lack of support, and 3) due to a miscommunication with the crop manager and farm staff, many of the traps were damaged or destroyed by machinery. Nevertheless, on examination of the data collected, it was seen that there was a statistically significant difference in the catch rates favouring the yellow traps over the gold. The reasons for this difference in catch rate are unknown, but it is suggested that the presence of UV light or reduced background contrast are possible avenues for investigation.

Despite progress in the topics discussed in this project the control of leafhopper in glasshouses remains a challenge. Further work examining the ecology of this sporadic pest must be undertaken so that control can be integrated into current systems and disruption of other control systems be avoided. In particular, a long term field study at an appropriate glasshouse examining the effect of Macrolophus on leafhopper distribution and population levels is suggested.

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8 Appendices

8.1 Appendix 1: List of documented hosts of genus Anagrus with citing source

Host species	Reference
Arboridia adanae	Öncüer, C. 1991, A catalogue of the parasites and predators of insect pests of Turkey pp.239
Arboridia adanae	Yigit, A.; Erkiliç, L. 1987, Studies on egg parasitoids of grape leafhopper, Arboridia adanae Dlab. (Hom., Cicadellidae) and their effects in the region of South Anotolia. Türkiye I. Entomoloji Kongresi Bildirileri, 13-16 Ekim 1987, Ege Universitesi, Bornova, Izmir pp.35-42 Ege Universitesi Atatürk Kültür Merkezi, Bornova/Izmir, Turkey
Arboridia kermanshah	Triapitsyn, S.V. 1998, Anagrus (Hymenoptera: Mymaridae) egg parasitoids of Erythroneura spp. and other leafhoppers (Homoptera: Cicadellidae) in North American vineyards and orchards: a taxonomic review. Transactions of the American Entomological Society 124:82
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Megamelus notula	Herting, B. 1972, Homoptera. A catalogue of parasites and predators of terrestrial arthropods. Section A. Host or Prey/Enemy. 2:4 Commonwealth Agricultural Bureaux, Slough, England
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Megamelus notula	Trjapitzin, V.A. 1978, Hymenoptera II. Chalcidoidea 18. Mymaridae. *Opredeliteli Nasekomykh Evropeyskoy Chasti SSR* 3:521
Quadraspidiotus perniciosus	Herting, B. 1972, Homoptera. *A catalogue of parasites and predators of terrestrial arthropods. Section A. Host or*

	Prey/Enemy. 2:173-175 Commonwealth Agricultural Bureaux, Slough, England (Host identification probably incorrect)
Quadraspidiotus perniciosus	Neuffer, G. 1966, On the parasite fauna of *Quadraspidiotus perniciosus* with particular reference fo the imported *Prospaltella perniciosi* Tower (Hym. Aphelinidae). *Entomophaga* 11 (4):383-393
Panstenon oxylus	Raatikainen, M. 1967, Bionomics, enemies and population dynamics of *Javasella pellucida* Fbr. (Homopt., Delphacidae). *Annales Agriculturae Fenniae* 6 (2):1-149
Malacosoma neustria	Thompson, W.R. 1958, *A catalogue of the parasites and predators of insect pests. Section 2. Host parasite catalogue, Part 5.* pp.571 Commonwealth Agricultural Bureaux, Commonwealth Institute of Biological Control, Ottawa, Ontario, Canada
Yponomeuta malinellus	Thompson, W.R. 1958, A catalogue of the parasites and predators of insect pests. Section 2. Host parasite catalogue, Part 5. pp.566 Commonwealth Agricultural Bureaux, Commonwealth Institute of Biological Control, Ottawa, Ontario, Canada (Record probably incorrect)

8.2 Leafhopper colour choices – control data

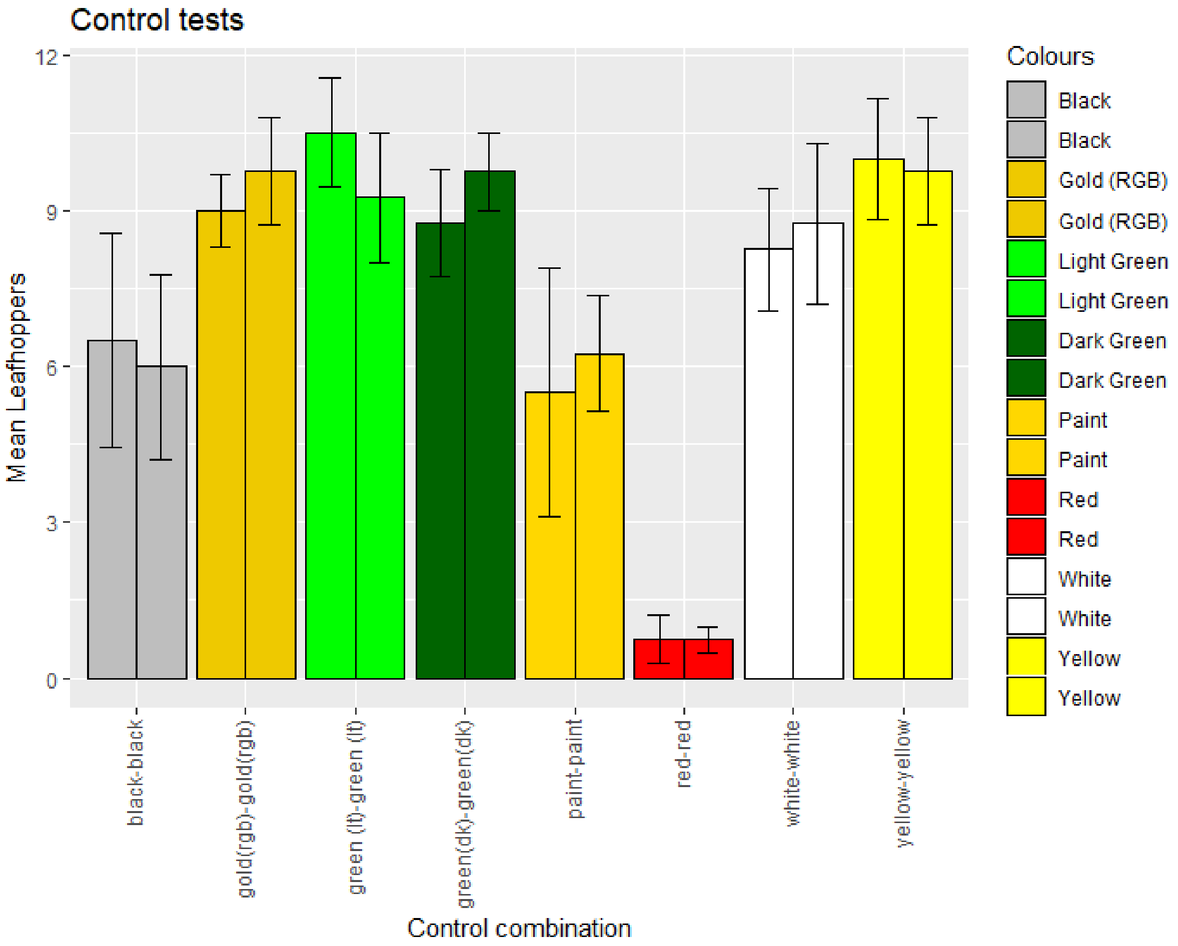

Fig. 8.1 Leafhopper colour combinations. Control data. Each combination was the same colour presented as laid out in the methods in chapter 2.4 (p. 35)